

UNIVERSITY OF SOUTHAMPTON

Faculty of Science

Department of Biology

MOVEMENT AND DISPERSION

OF THE SMOOTH SNAKE CORONELLA AUSTRIACA LAURENTI

IN RELATION TO HABITAT.

Submitted by

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ABSTRACT

FACULTY OF SCIENCE
BIOLOGY
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MOVEMENT AND DISPERSION OF THE SMOOTH SNAKE
CORONELLA AUSTRIACA LAURENTI IN RELATION TO HABITAT

by Antony Hugh Gent

A study of the ecology of the smooth snake Coronella austriaca (f. Colubridae, Ophidia) was conducted on snakes from several locations within the New Forest, Hampshire, England. Field studies, which used a combination of radio-telemetry (with externally attached transmitters) and visual location, were supplemented by laboratory studies on the physiology, thermal biology and behaviour of the species.

Short term movements in the field were generally small, with the median hourly rate equalling 0.54 m/ hr (n= 1074) and the equivalent daily rate being 13.30 m/ day (n= 138). Maximum movement rates were 44.26 m/ hr and 166.81 m/ day. Movement was greatest at intermediate field temperatures (typically 19.0° to 21.9°C). No difference was observed in movement between the sexes. Activity recording indicated that the species is almost exclusively diurnal.

Home range areas were calculated using convex polygon analysis and varied between 34 m² and 17215 m², with a median of 688 m² (n= 55). These estimates were affected by sample size and observation period and were regarded as being underestimates of lifetime ranges. Although many habitat types were occupied, dry and humid heath, bracken and gorse/ bramble bushes were selected by C. austriaca. The importance of less frequently used habitat types and the provision of 'corridors' between adjacent snake populations to the conservation of the species is discussed.

The mean body temperature recorded in the field was 23.48°C ± 3.95 (n= 327), which was lower than the selected temperature measured in the laboratory (29.6°C ± 3.15 (n= 324)). This appeared to reflect an inability to sustain 'preferred' body temperatures in the field due to climatic factors and the need for other behavioural considerations (e.g. foraging and cryptic anti-predator behaviour). A low food intake was suggested from field and laboratory observations. Low body temperatures, movement rates and food intake suggested that C. austriaca may be adapted to having a low energy throughput.

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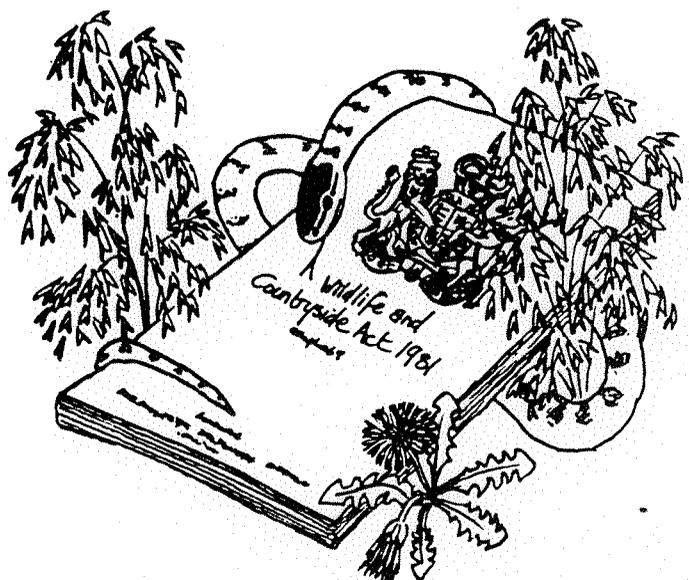
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I. Introduction



CHAPTER ONE

INTRODUCTION

1.1. Taxonomy and distribution

The smooth snake, Coronella austriaca austriaca Laurenti, is a slim, live bearing species of snake in the family Colubridae (Plate 1). The Colubridae is the largest of the 11 families in the suborder Ophidia (the snakes) (containing some 250 genera and 2500 species (Webb et al. 1978)) and is widely distributed throughout the world, being absent only from southern Australia, some islands (e.g. Ireland and New Zealand) and the cold Arctic and Antarctic regions (Arnold and Burton 1978).

The genus Coronella contains two species, the smooth snake C. austriaca and the southern smooth snake C. girondica. These species are very similar in appearance although the former species tends to be broader with a more pointed snout and lacks the patterned belly of the latter.

The smooth snake is found throughout Europe, from southern England, France, the Netherlands, Belgium, Luxembourg, Germany, Switzerland and Austria with the range extending northwards to southern Scandinavia (up to 60°N), south-west into northern Spain and northern Portugal and south-east into Italy and Greece and eastwards into Poland and the USSR (see Fig. 1.1). C. austriaca is also found northern Asia Minor to northern Iran. Throughout its range, the smooth snake is found in a variety of different habitat types. In continental Europe and Scandinavia it occurs in woodland, hedgerows, vineyards, bushy slopes and embankments. Further to the south the species tends to occupy more open ground, often with only sparse vegetation, such as screes, stone piles and even cliffs and becomes increasingly montane and may be found up to heights of 1800 to 2000 m above sea level. Smooth snakes are additionally found in wetter ground such as marshes (Glant 1972, Andren and Nilson 1976, Arnold and Burton 1978, Goddard 1981,



Plate 1 : The smooth snake Coronella austriaca in typical habitat.

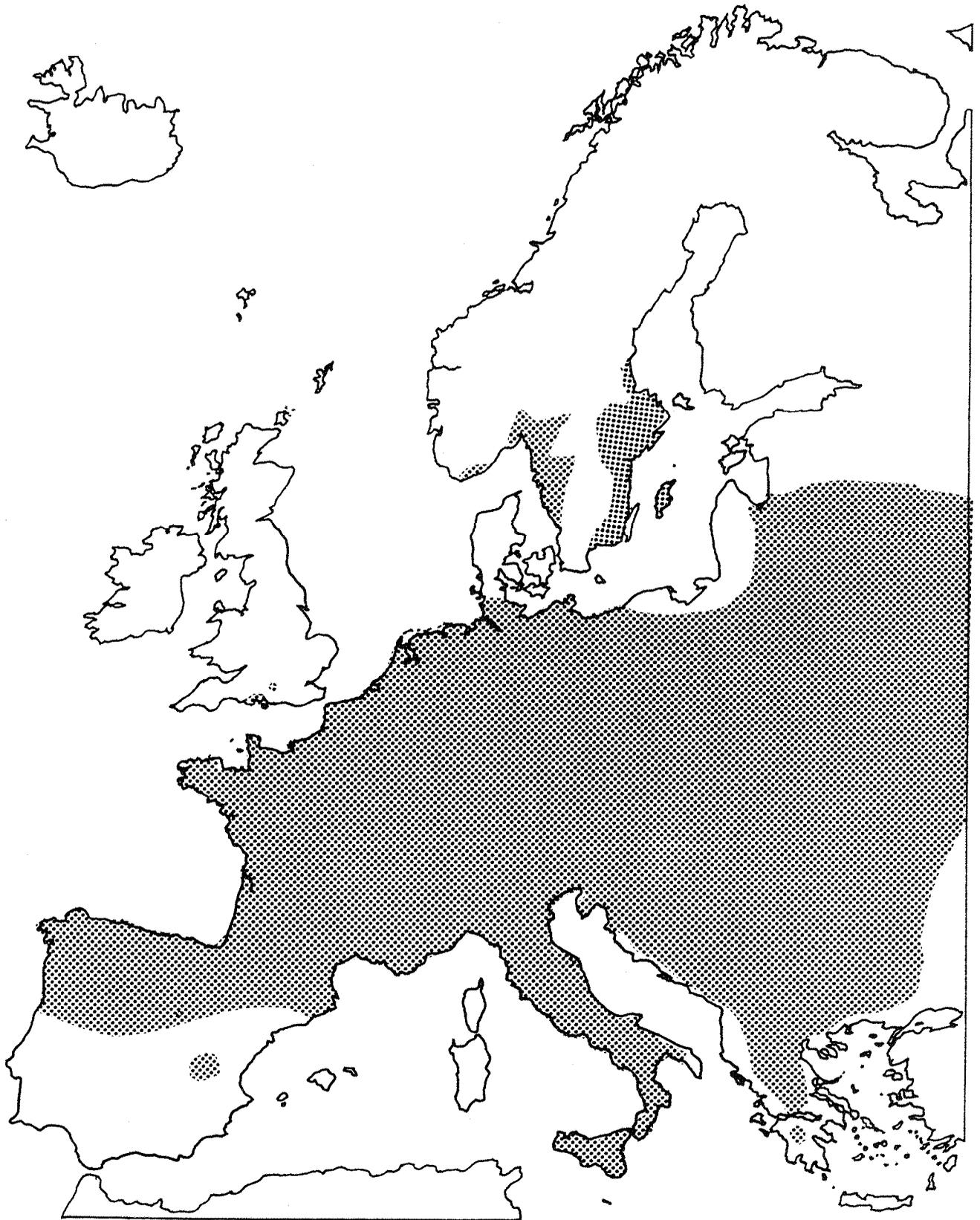


Fig. 1.1 : The distribution of the smooth snake in Europe (redrawn from NCC 1983, original information from Dr. E.N. Arnold, British Museum (Natural History), London).

Groombridge 1986, G.J.M. Hirons, pers. comm.). In Britain, however, smooth snakes are generally associated with lowland heaths dominated by Calluna and Erica species (Spellerberg and Phelps 1977, Arnold and Burton 1978, Goddard 1981, NCC 1983, Groombridge 1986).

The range of the two Coronella species overlaps throughout Italy, Sicily, southern France and northern Spain, with C. girondica also being found to the south west (Spain and north west Africa). Where the ranges overlap, C. girondica tends to inhabit lower ground than C. austriaca (Arnold and Burton 1978).

In Britain the smooth snake is one of six indigenous species of reptile, three of which are snakes and three lizards. The other two snake species are the grass snake Natrix natrix helevelica (Lacépède) (family Colubridae) and the adder or viper Vipera berus berus (L.) (family Viperidae). The lizard species are the common lizard Lacerta vivipara Jacquin, the sand lizard Lacerta agilis (L.) and the slow worm Anguis fragilis (L.). Of the lizards the first two species above are members of the family Lacertidae and the latter is a member of the family Anguidae. The distribution of the six British species are described in a variety of sources (e.g. Smith 1973, Arnold and Burton 1978, NCC 1983, Cooke and Scorgie 1983, Frazer 1983) and the pattern of distribution of reptiles with latitude in British Isle is summarised by Spellerberg (1982). All six species occur in the south of England with decreasing species richness being observed with increasing latitude such that only three (Vipera berus, Lacerta vivipara and Anguis fragilis) are observed in Scotland. A single species of reptile, Lacerta vivipara, is found in Ireland.

The smooth snake is at the north western edge of its range in Britain where it has only a limited distribution (see Fig. 1.2). The species now appears to only be found in the southern counties of Dorset, Hampshire and Surrey where it mainly associated with the Tertiary sands and lower

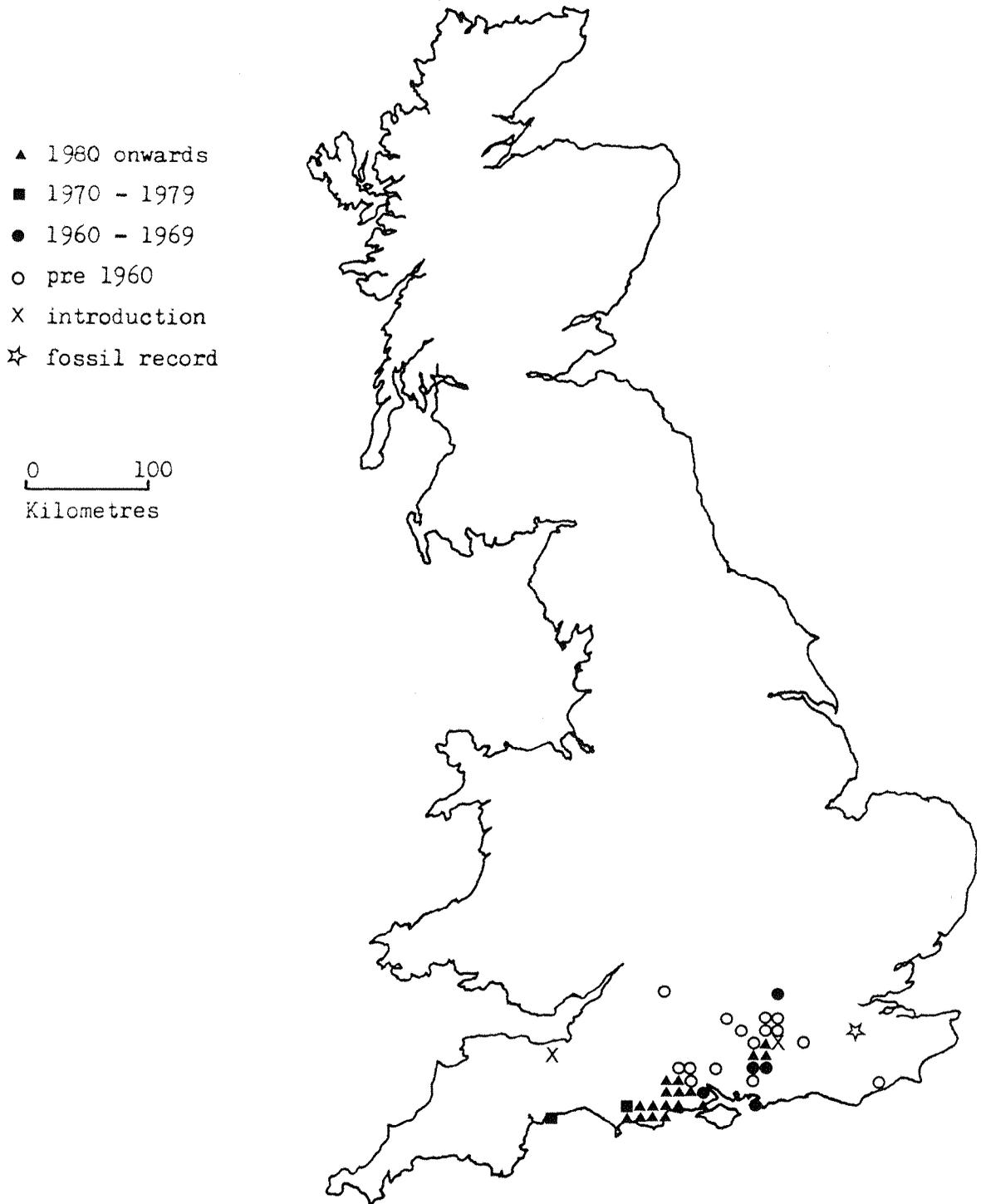


Fig. 1.2 : The distribution of the smooth snake in Britain based on 10 x 10 km grid squares (redrawn from Biological records centre information in NCC 1983 with additional information from Frazer 1983 and Holman 1985).

Greensands (Corbett 1978), although records prior to 1980 indicate that the range of C. austriaca included areas within Berkshire, Buckinghamshire, Wiltshire and Sussex (Smith 1973, NCC 1983). Earlier records, between 1900 and 1908, (see McLellan 1975) also report sightings in the Isle of Wight and Devon. Fossils collected from the late Pleistocene fissure at Ightham, near Sevenoaks, Kent, included bones of at least two C. austriaca indicating that the species was present in that county during Flandrian times (probably), about 9500 years before present (Holman 1985). Introductions of C. austriaca into Somerset and Surrey are marked in Fig. 1.2, although the authenticity of these records is questioned (Phelps in McLellan 1975).

The status of the smooth snake within the countries of the European Economic Community (EEC) has been reported as being 'Vulnerable' (Groombridge 1986), that is a species that is "believed likely to move into the endangered category in the near future if the causal factors continue operating (included are taxa of which most or all of the populations are decreasing because of over exploitation, extensive destruction of habitat or other environmental disturbance; taxa with populations that have been seriously depleted and whose ultimate security is not yet assured; and taxa with populations that are still abundant but are under threat from serious adverse factors throughout their range)" (Honegger 1975 (IUCN red-data book definition)). The smooth snake has become extinct in Denmark within the last 50 years (Honegger 1978). Throughout its range C. austriaca populations are declining and the species is described as being rare and seriously threatened with extinction in parts of West Germany and the Netherlands. In the United Kingdom the smooth snake is rare and is seriously further declining (Prestit et al. 1974, Goddard 1981, Groombridge 1986). The status of the species in Italy, Sicily and Greece is either unknown or appears not to be threatened (Groombridge 1986). Much of the decline of this species in Northern Europe can be attributed to habitat destruction and cultivation (especially afforestation and development) and interference by man

(e.g. collecting) however the diminution of C. austriaca in France seems largely unrelated to human activities (Groombridge 1986).

The rarity and threatened status of C. austriaca has led to the species being nominally protected in six EEC countries (namely Federal Republic of Germany, France, Greece, the United Kingdom (see Section 1.3. below), Luxembourg and the Netherlands) and in nine non-EEC countries (Bulgaria, German Democratic Republic, Hungary, Liechtenstein, Poland, Slovenia, Sweden, Switzerland and the U.S.S.R).

Details of the morphology, populations and general biology of the smooth snake are given in Chapter 3.

1.2. Previous research

The smooth snake was first recorded in Britain in 1859 (Gray 1859) when a specimen was captured near Bournemouth, Dorset and sent to the British Museum. A specimen had, however, been captured some five or six years earlier (the date of this find was subsequently quoted inconsistently) near Ringwood, although this was only reported in response to Gray's publication (Bond 1859, Cambridge 1872, 1886). Subsequently many records for C. austriaca were published and, apart from some rather anecdotal observations of behaviour, feeding preference and habitat use (e.g. Baldry 1880) these were almost exclusively concerned with the distribution of the species in Britain. Reviews of this literature can be found in Smith (1973) and McClellan (1975).

As part of a larger scale exercise concerning all the British reptila and amphibia, the distribution of the smooth snake in the United Kingdom was described by Taylor (1948, 1963) in conjunction with the British Herpetological Society (hereafter referred to as BHS). This work was further revised between 1965 and 1970 (Prestit et al. 1974). Distribution maps have subsequently been published for the smooth snake in Britain using 10 x 10 km grid squares

(Arnold 1973, NCC 1978 and NCC 1983). These surveys determined that smooth snakes have always been restricted to southern Britain and are primarily associated with areas of mature dry heath. The contraction and fragmentation of the distribution of the smooth snake since 1900 seems inextricably linked to the pattern of heathland destruction through afforestation, urbanisation, military activity, mineral extraction, public pressure and agricultural reclamation (Prestt et al. 1974, Spellerberg 1975, Goddard 1981). Beebee (1978) speculated upon the apparent limitation to the distribution of smooth snakes shown in the above distribution studies. He concluded that prey distribution, itself restricted by thermal limitations, may be an important factor.

Much of the available literature concerning C. austriaca is anecdotal (see McLellan 1975 for review). Little quantitative work on the biology and ecology of the species, with the exception of work by Duguy (1961) based on dissection and observations made by Rollinat of specimens from the Indre region of France around the turn of the century, was published until the 1970s. Breeds (1973), with his study of snakes observed in four sites in east Dorset, and Spellerberg and Phelps (1977), working at sites in Dorset and Hampshire, conducted the first intensive studies on the ecology and general biology of C. austriaca in Britain. Phelps (1978) subsequently published data on the seasonal movements of British snakes observed in Dorset. This work was greatly extended by Goddard (1981, 1984) in a three year study on the general biology and ecology of C. austriaca. Research on smooth snakes abroad includes that by Andren and Nilson (1976, 1979) on the general biology of populations in Sweden and Norway and a recent study of thermal ecology (Bont et al. 1986) in the Netherlands.

1.3. Background to the present study

The smooth snake was given legal protection in Britain on the 1st August 1975 under the Conservation of Wild Creatures and Wild Plants Act (HMSO 1975) and subsequently

included in Schedule 5 of the Wildlife and Countryside Act 1981 (HMSO 1981). However, despite this legal protection, the smooth snake is still believed to be seriously declining in the United Kingdom (Groombridge 1986). Spellerberg (1975) stressed the need for ecological research on Britain's rare reptiles to ensure the conservation of these species. Although much valuable background work has been done in the last decade or so (Breeds 1973, Spellerberg and Phelps 1977, Phelps 1978, Goddard 1981) several areas requiring further research have been identified as being important for helping with the conservation of C. austriaca (Goddard 1981, NCC 1983).

Much of this work has not been previously accomplished because of the difficult nature of the species as a study animal, it not being readily encountered in the environment and appears not to be very numerous. Further, being an endangered species, physiological and biochemical analysis using post mortem examination is undesirable.

Goddard (1981) identified four areas requiring further research, namely reproduction, movement (and home range), feeding and population ecology - these points all being included in recommendations for further research by the Nature Conservancy Council (NCC 1983). Additionally the NCC stressed the need to identify the habitat requirements of the species and factors that limit the distribution of C. austriaca. The current distribution of the smooth snake in Britain needs to be ascertained, this aspect of research is at present being contracted to the BHS.

1.4. Aims of the present study

With the view to addressing some of the areas requiring further research as outlined by Goddard (1981) and NCC (1983) (see section 1.3. above), this project was designed to investigate aspects of the movement biology and habitat requirements of the smooth snake.

The development of small radio-transmitters meant that

radio-tracking, which had not previously been employed on snakes in Britain, could be used with C. austriaca. Radio-tracking is a method that permits the frequent location of even the most cryptic animals whilst avoiding observer bias in searching. It provides a useful technique for studying movement behaviour and activity patterns of, and habitat selection by, animals in the wild and therefore offered an opportunity to gain further information on the behaviour of C. austriaca than had been possible in the earlier studies by Spellerberg and Phelps (1977) and Goddard (1980, 1981).

The project encompassed two broad, but closely related, aspects of the movement biology of C. austriaca namely 'movement behaviour' and 'habitat use'. 'Movement behaviour' entailed the observation of the movement rates and activity patterns of the species and the effect of intrinsic (e.g. breeding and feeding conditions) and extrinsic (e.g. environmental temperature, time of day) factors on these. This aspect was also studied so that the dispersal potential of the species, which is generally regarded as being poor (e.g. Spellerberg and Phelps 1977), could be quantified.

The habitat of an animal has been defined as 'the range of environments in which a species occurs' (Krebs 1978) which relates to many biotic and abiotic elements (Putman and Wratten 1984). The primary objective in determining the biotic habitat was the determination of vegetation communities associated with C. austriaca and hence provide information useful to conservation management. Vegetation communities were assessed by looking at species composition and the structure of the vegetation. The biotic habitat also includes other faunal components and the relationship between the distribution of the reptilian species and of small mammal species with C. austriaca was investigated.

The abiotic elements of the habitat studied were primarily aspects relating to temperature - these being regarded as particularly important to an ectothermic animal at the north western edge of its range and possibly limited in its

distribution by temperature (Beebee 1978). Other abiotic factors in the environment, e.g. soil type and structure, are only superficially mentioned, these being deemed unlikely to vary too much within the relatively small areas studied.

Laboratory studies, particularly on temperature related parameters, were investigated to provide an understanding of the basic thermo-physiological factors that would underlie the animal's ecology and behaviour in the field.

1.5. The New Forest and the lowland heathlands

a. The New Forest

The New Forest is an area of 37907 ha of mixed woodland, heath, grassland and marsh in Hampshire, southern England (Fig. 1.3). The area is unique in that it has avoided urbanisation yet has been shaped by many hundreds of years of interaction between man and nature. The history, natural history and ecology of the New Forest have recently been reviewed by Tubbs (1986) from which most of the below account is taken.

The New Forest was established as a 'Royal Forest' by William the Conqueror over 900 year ago. Strict Forest Laws were made over the successive centuries to protect the Royal interests, which were initially deer conservation and latterly timber production. With these laws came certain rights and privileges for the Commoners, such as the rights of pasture (grazing), mast (turning pigs out in the pannage season), marl (clay digging), turbary (turf cutting) and estovers (collecting fuel wood). The exercise of these common rights have impacted greatly on the environment and have helped form the vegetation and topography seen in the New Forest today.

The administration and management of the New Forest became the responsibility of the Forestry Commission under the Forestry (Transfer of Woods) Act 1923 (HMSO 1923). The

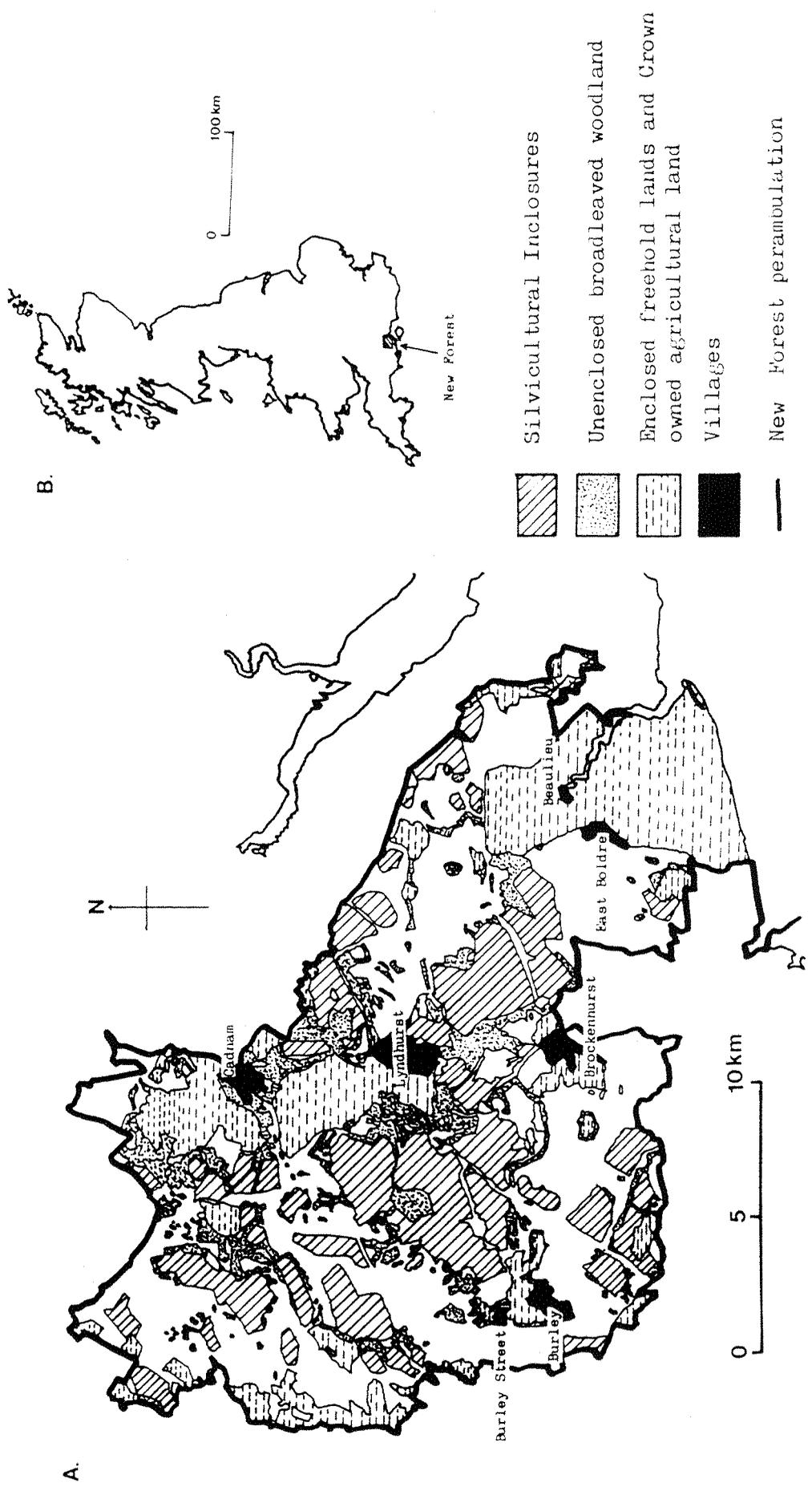


Fig. 1.3 : The New Forest, Hampshire; A. showing land use (redrawn from Tubbs 1986) and B. the location of the New Forest in Britain.

Forestry Commission is equally responsible for the maintenance of plantations and of the unenclosed open forest. This latter responsibility primarily involves the removal of self sown pine trees and ensuring suitable areas for grazing; much of this management is by controlled burning (Tubbs 1974).

The location of the New Forest, being situated within short travelling distance of all of the heavily populated south of England, has meant that the area is visited by large numbers of holiday makers and day trippers. This additional component adds to the already great pressure from the traditional uses of the land, particularly the exercise of grazing rights, forestry and hunting. Within such an area the use of the land for diverse commercial and recreational reasons will often result in conflicts of priorities. The Forestry Commission has the responsibility to try to ensure satisfaction of human requirements whilst balancing these with the ecological needs of the area.

The vegetation in the New Forest can be arbitrarily divided into plantations (totalling 8379 ha) and unenclosed lands (totalling 19771 ha) and a further 9757 ha of land which is classified as village or agricultural land. The plantations are primarily conifers (4744 ha) with hardwoods (2744 ha) and mixed plantations (891 ha) accounting for the remainder. A further 3671 ha of broadleaved woodland and 211 ha of natural pinewood grow outside the enclosed plantations. Of the remaining unenclosed land the majority is dry and humid heathland (8121 ha), with mires and wet heath occurring over 2894 ha. Three types of grassland are found: Acid grassland 3993 ha, of which 266 ha has been limed and/or fertilised), re-seeded grassland (528 ha) and neutral grassland (353 ha).

The flora and fauna of the New Forest is both diverse and abundant, benefitting from the warm climate of southern England, the variety of habitats and the long history without urbanisation, and includes species, such as the wild gladiolus Gladiolus illyricus and New Forest cicada

Cicadetta montana, that are found nowhere else in Britain. All six species of British reptile are found in the New Forest (Tubbs 1986), however, the present status of Lacerta agilis is the subject of some debate. Corbett (1980) states that the New Forest sand lizard population has become extinct, this largely being related to the increase in heather burning since the last war, whereas Tubbs (1986) estimated that a population of less than 100 individuals, some being derived from introductions, remained. Tubbs also indicated that the population size of C. austriaca in the New Forest was probably between 100 and 500 individuals.

In 1971 the whole area was notified as a Site of Special Scientific Interest (SSSI) and renotified in 1986 under the Wildlife and Countryside Acts 1981, 1985 (HMSO 1981, 1985).

b. Lowland heathlands

The term 'heathland' is generally applied to a lowland plant community, dominated by Calluna vulgaris and other Ericaceous shrubs, growing on inorganic, nutrient deficient soils (cf. 'moorland', which generally refers to similar plant communities in upland areas, growing on organic (peat) soils). The heathlands of southern Britain were undoubtedly created by the forest clearing activities of man during the Bronze Age (about 3600 before present) and maintained as a plagio-climax by grazing (Webb and Haskins 1980). Large tracts of heathland once existed, with a continuous band spreading from Surrey through Hampshire and into Dorset and other heaths being found in Cornwall, Devon, Breckland and Suffolk. With the formation of the heathland an associated fauna developed. This heathland has, however, undergone a marked decline in area and, as the remaining areas are becoming increasingly fragmented, it, along with its fauna and flora, is becoming increasingly threatened. This decline of heathland is largely associated with urbanisation, afforestation, agricultural reclamation, public pressure, military activity and mineral extraction.

The two largest tracts of lowland heath in Britain are

those associated with the Tertiary sands of the London and Hampshire basins in southern England (Moore 1962). These areas are in close proximity to very large and expanding centres of population, namely London and the Bournemouth-Poole conurbation. The decline in the heathland area of the Poole basin (the western end of the Hampshire basin) has been well documented: between 1811 and 1960 the area of heathland in the Poole basin decreased by 66% (from 30000 to 10000 ha), this being associated with large scale urban development and afforestation (Moore 1962) and between 1960 and 1978 a further 4168 ha had been lost (Webb and Haskins 1980). Webb and Haskins (1980) concluded that the total area of heathland remaining in the Poole basin in 1978 was 5832 ha, a mere 14.6% of the 39960 ha that existed in 1760.

Similar losses of heathland have been reported elsewhere in Britain, notably in the Breckland of East Anglia and the greensand heaths of Surrey and Hampshire. Between 1966 and 1980 a reduction of 19.4% of the area of heath in Northern Hampshire was recorded (Goode 1981). Throughout Hampshire the area of heathland decreased from 37,000 to 18000 ha between 1810 and 1982 and most of the remaining area is concentrated in the west of the county (Hazel 1983).

Lowland heathlands are characteristically occupied by a low diversity of plant and animal species (Webb and Hopkins 1984). Many of these species are specific to, and dependent upon, heathland. These include plants (such as marsh gentian Gentiana pneumonanthe, wild gladiolus Gladiolus illyricus, heath spotted orchid Dactylorhiza maculata, bilberry Vaccinium myrtillus and bell heather Erica cinerea), invertebrates (including the ladybird spider Eresus niger, heath grasshopper Chorthippus vagans, green tiger beetle Cicindela campestris, silver-studded blue butterfly Plebejus argus and small red damselfly Ceriagrion tenellum) and vertebrates (for example the dartford warbler Sylvia undata, stonechat Saxicola torquata, sand lizard Lacerta agilis, natterjack toad Bufo calamita and the smooth snake Coronella austriaca). These heathland species are threatened by the reduction in the total area of

heathland and additionally by the fragmentation of the remaining patches. Smaller areas of heathland become increasingly affected by invasion of plant and animal species from adjacent habitat types resulting in an increased species diversity (Webb and Hopkins 1984).

1.6. Study sites

Ten study sites located in the New Forest, Hampshire were defined and used during the course of the study. The New Forest was selected as the study area as it offered a diversity of habitats, known (and previously studied) populations of smooth snakes and due to its proximity to Southampton University. Only Sites One and Two were studied during all three years, Sites Three and Four being visited during years two and three and Sites Five to Ten being used only in the final year of the study. All sites were administered by the Forestry Commission.

Site One (see Plate 2) was an inclosure but incorporates the immediate surrounding heath and adjacent 'grazing strip'. Formerly heathland, this site was first afforested in 1959 with scots and corsican pine (Pinus silvestris L. and P. nigra Arnold), sitka spruce (Picea sitchensis (Bong) Carr.) and larch (Larix kaempferi (Lamb) Carr.). Birch (Betula pendula Roth.), beech (Fagus sylvatica L.) and sweet chestnut (Castanea sativa Miller) were also planted in small numbers. Where afforestation had occurred much of the original heathland had been destroyed. Considerable areas of the heathland were left unplanted, however, these consisting of ling (Calluna vulgaris (L) Hull), bell heather (Erica cinerea L.), cross-leaved heath (Erica tetralix L.), purple moor grass (Molinia caerulea (L.) Moench) and bristle leaved bent grass (Agrostis setacea Curtis). Two species of gorse, Ulex europaeus L. and U. minor Roth., were also abundant. Bracken (Pteridium aquilinum (L.) Kuhn) was invading many areas of the heathland and also the plantations where there is sufficient light. Site One therefore provided a mosaic of different habitat types with deciduous and coniferous trees



Plate 2 : Site One showing an area of mature heathland between conifer plantations.



Plate 3 : Site Two.

and areas of dry and humid heath and grassland, which was dissected by numerous rides.

Site Two (see Plate 3) was approximately 2 km south west of Site One and was dominated by two parallel embankments providing steep north and south facing slopes. The southern embankment and the north facing hill behind it were burnt in March 1979. Only sparse vegetation occurred along this embankment and Molinia caerulea and Agrostis setacea grew below a thick covering of bracken on much of the hill. Further to the west some Erica tetralix amongst Molinia led up to a small patch of mature Calluna that had not been affected by the burn. The northern (south facing) embankment and the heathland beyond had not been recently burnt. Thick gorse dominated parts of the embankment, with the three heath species, bare ground and grasses (particularly Agrostis setacea) covering the majority of the remainder. To the north lay a Calluna dominated heath that merged into a bog (that was initially predominantly E. tetralix, but Molinia and Sphagnum sp. became increasingly abundant as the bog neared a small stream). At the east end of the site the dry heath led into wet heath and bog, dominated by bog myrtle (Myrica gale L.), Molinia grass and rushes (Juncus spp.).

Site Three was a small area of undulating dry heathland separated from Site One by a major road. The site was dominated by a long, east facing embankment sparsely covered by Calluna, Ulex europaeus, Erica cinerea and self seeded pine and birch trees. Behind was a mature Calluna dominated heath in which Ulex europaeus was abundant. Site Three was subsequently incorporated into Site One (with no distinctions being made between them for the purpose of all analyses) following the movement of one snake between the two areas. No radio-tracking, however, was undertaken on this area due to its exposure to large numbers of people.

Site Four was located in the centre of the New Forest and was 11 km north east of Site One. This site was essentially a flat and open area although the ground sloped gently away

to the north. This site offered large areas of Calluna dominated dry heathland of different ages, resulting from controlled burning during the recent past, with humid and wet heath on the slopes and in the lower ground to the north of the site. During the final year of the study, Site Four was used as one of the three sites chosen for the Habitat Selection experiment (see Chapter 2, Section 2.2.5.), taking advantage of the different ages of dry and wet heathland found there.

Site Five was located in the east of the New Forest, some 16 km north east of Site One. The area studied was centred around a valley lying to the west of a mature inclosure of Corsican and Scots Pine. The ground in the valley was wet with bog vegetation, but Calluna, E. tetralix and Molinia grew on the higher ground by the perimeter of the Inclosure. To the west the ground became drier and was dominated by thick, mature dry heath (primarily Calluna).

Site Six was in the northern half of the New Forest (about 9 km north of Site One) and was dominated by mature, unenclosed pine woodland adjacent to a wet valley bog. Ground vegetation was sparse with few tussocks of E. tetralix and Calluna growing amongst the close cropped grass amongst the pine trees. The bog vegetation was primarily moss (Sphagnum sp.).

Sites Seven and Eight lay to the south and north of an Inclosure, 2 km north of Site Four, respectively. Site Seven lay on a gentle south facing slope, dominated by mature Calluna. The ground became increasingly damp to the south where E. tetralix and Molinia became more abundant. Site Eight had formerly been dry heath, but was dominated by short grass following a recent burn.

Sites Nine and Ten were selected for use in the Habitat Selection experiment (see Chapter 2, Section 2.2.5.) and were located in the northern half of the New Forest, some 7 and 6 km north of Site One respectively. Site Nine offered a variety of dry and wet heathland vegetation in an open

area to the east of an Inclosure. Lower ground to the north and the south of the study area provided areas of wet ground, dominated by Myrica gale and Molinia, with the higher ground in the centre and to the east of the site being covered mostly by Calluna or E. tetralix dominated heathland. An area of mature pine in the Inclosure to the west of the site was also surveyed for the presence of reptiles.

Site Ten was separated from Site Nine by a major road and was characterised by a gentle slope to a river in the east of the site. The higher ground was dominated by thick Calluna heath, although much of the site was becoming invaded by bracken. The centre of the site had been dry heathland but this had been cut in one area and burned in another and throughout the course of the season these areas became covered with bracken. The lower ground to the east of the site was a mixture of short grass and bracken which merged into mixed deciduous woodland that ran along the edge of the river. The lower ground to the south of the site was wet heathland, dominated by Molinia, E. tetralix and Myrica gale.

Sites One (and Three) and Two were favoured for logistic reasons, being conveniently close to each other and to the campsite that was used as a field base, and also for 'historic' reasons. Both sites were previously studied by Goddard between 1976 and 1978, while part of Site One was used by Spellerberg and Phelps (1977). The majority of the search effort was directed towards Sites One and Two and these were the only sites at which radio-tracking was undertaken. Concentrating effort on a few sites seemed preferable as this allowed more thorough sampling of these areas. Smooth snakes had previously been found at Sites Five and Six by Goddard during his study between 1976 and 1978 (Goddard, pers. comm.). Recent sightings of C. austriaca had also been reported at Sites Nine and Ten by Forestry Commission employees (M. Clarke and D. Thompson, pers. comm.).

1.7. Layout of thesis

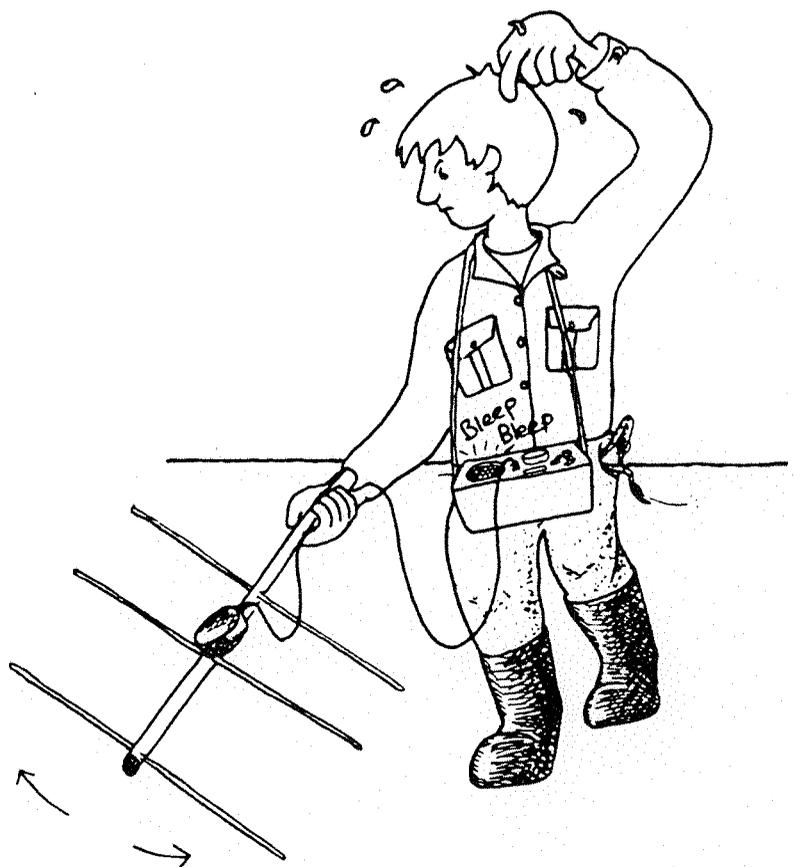
This report is concerned with aspects of the biology of C. austriaca and particularly the movement and ranging behaviours and the thermal attributes associated with site selection. General aspects of the biology, morphology and populations of smooth snakes are discussed but the bulk of this research divides into two sections, namely i. Movement biology and ii. Thermal biology. Each of these sections are subdivided into two data chapters. Each data chapter is presented as a separate topic, and is divided into the following sections: Introduction, Methods and Materials, Results, Discussion and a brief Summary.

The methodology used for all aspects of this research is presented in Chapter 2. Aspects of the general biology, morphology and populations of the study species from field observations and from published sources are presented in Chapter 3.

Movement biology incorporates the animal's vagility (Chapter 4) and ranging behaviour and habitat use (Chapter 5), these providing the headings for the two chapters. The thermal biology study divides into two chapters; namely the observed thermal habitat use in the field (Chapter 6) and laboratory investigations into the underlying physiology of C. austriaca (Chapter 7).

The final chapter (Chapter 8) is a discussion relating the previous topics to each other.

II. General Methods



CHAPTER TWO

GENERAL METHODS

2.1. Introduction

This study incorporates both field and laboratory work to provide information about the ecology, behaviour and aspects of the physiology of C. austriaca. In this chapter the methodology for all aspects of the research are described. These are subdivided into three sections namely: Fieldwork, Laboratory work and Analysis.

One part of the section on the laboratory work describes the methods and results of an experiment to study the effects of attachment of radio-transmitters on the behaviour of snakes using time-lapse video analysis. The results are presented here since this is an investigation into the effect of the methodology itself, rather than an investigation into the biology of the species.

2.2. Fieldwork

2.2.1. Site mapping

To accurately assess home ranges and movement rates it is necessary to determine the position of animals in the field with a high degree of precision. To this end, a series of markers (details below) were put out at each of the study sites. These markers were accurately positioned relative to each other by measuring a distance and a bearing, by triangulation (using cross bearings) or a combination of these methods. Once positioned in the field each marker location was transcribed onto graph paper. An arbitrary ten figure grid-system was assigned to each site, allowing locations to be positioned to the nearest 10 cm by 10 cm square. Thus, a unique grid reference could be given to each marker. This grid system allowed the position of an animal to be described relative to nearby markers (again by measurement of a distance and a bearing or by cross-

bearings). A ten figure grid reference for each sighting was later calculated either by plotting on graph paper or with the aid of a simple computer program. Additionally, it was simple to incorporate any extension to the marker system as it became necessary during the fieldwork.

Two marker systems were employed. The open nature of the habitat at Site Two allowed a ten by ten metre grid system to be marked directly in the field (using silver tape attached to vegetation or wooden pegs flattened flush with the ground on rides and paths). Further markers and landmarks were positioned relative to this grid. Site One provided a 'mosaic' of habitat, with much dense woodland and, as such, marking a grid on the ground was not feasible. Here individual trees and fence posts, etc., were marked by attaching a small circle of blue plastic to them with a drawing pin and positioning each marker relative to others on the site. No such marker system was used at Sites Four to Ten, snake sightings here were described using 1:10,000 Ordnance Survey maps to assign a grid reference.

2.2.2. Snake capture and processing

Regular field visits searching for snakes were made between early March and late October during the 1984 and 1985 field seasons with a shorter period of intensive study, between early March and early August, being employed in 1986. Only occasional visits to the main study sites (Sites One and Two) were made thereafter, although fieldwork at other sites where an experiment to investigate habitat preference was being undertaken (see section 2.2.5.) continued into early October 1986.

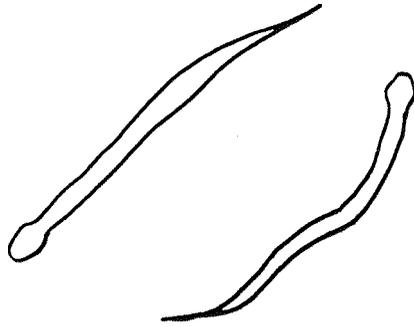
The methods for sampling and processing the snakes outlined below follow very closely the methods previously used and described by Goddard (1981).

When located, smooth snakes were captured by hand and no other methods of capture (eg. traps or drift fences) were employed. Snakes were usually seen basking or moving in the

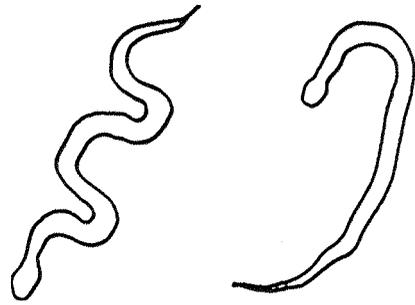
vegetation or found below cover objects, e.g. tin sheeting, concrete tiles that had been positioned around the sites to take advantage of the fact that smooth snakes, and indeed other reptiles, are often found taking refuge below such objects. Prior to capture, the behaviour of the snake was noted and if it was basking the bask posture was assigned a value between one (when fully stretched out) and six (when the snake was very tightly coiled), as illustrated in Fig. 2.1. The time of location (BST throughout) was noted. Immediately upon capture the rectal temperature (hereafter referred to as body temperature) was taken, by inserting a quick acting 'Shultheis' type thermometer into the animal's cloaca. The still, shaded air temperature (taken at 1.5 m above the ground, in the experimenter's shadow and shielded from any wind) and the temperature at the site of location of the snake, but shielded from direct sunlight, were taken. These values were termed shade air temperature (T_A) and bask site temperature (T_{BS}) respectively. The overhead cloud cover was recorded as a value between 0 and 1, with intermediate values scored in eighths.

Upon capture snakes not previously encountered were marked. This involved clipping half of the posterior edges from pairs of ventral scales with fine scissors in a combination that is unique to that snake, as outlined by Prestt (1971). Small snakes of less than 8 g body weight or 26 cm total length were not clipped for fear of causing injury, as recommended by Goddard (1981).

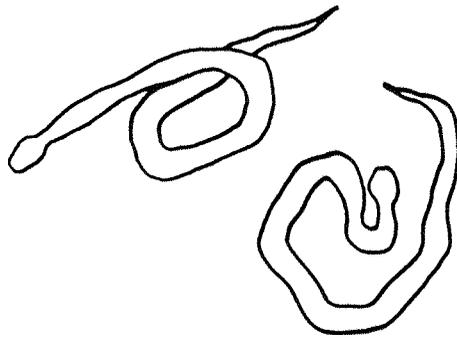
The snake was weighed, to the nearest 0.1 g, using a 100 g 'pesola' balance and the snout-to-vent length (SVL) and tail length (TL) were measured by gently holding the outstretched snake against a tape measure, recording this data to the nearest 1 mm. The pairs of subcaudal scales were counted. The snake was sexed by a combination of relative tail length, number of subcaudal scales and tail shape; males having relatively longer and broader tails, often with a slightly swollen base, and also have a greater number of pairs of subcaudal scales than do females (see chapter 3).



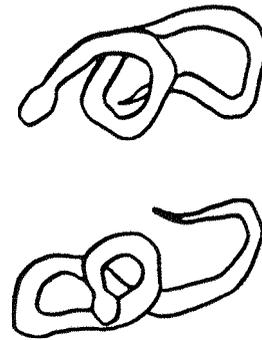
Posture 1



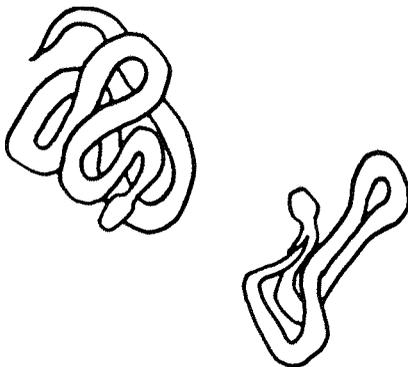
Posture 2



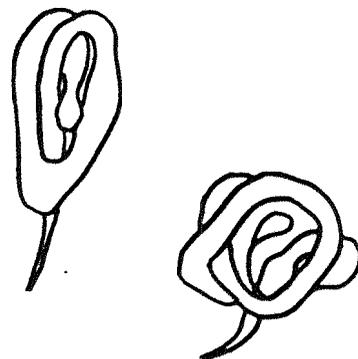
Posture 3



Posture 4



Posture 5



Posture 6

Fig. 2.1 : Examples of Basking Postures Demonstrated by *C. austriaca*.

Postures described range from being fully stretched out (1), through increasing degrees of coiling, until tightly coiled with almost no gaps between the loops of the body (6).

Feeding condition was assessed by palpation, and the feeding status of each animal was later assigned to one of three categories, as follows: i. snakes that had recently fed and contained a large item of food in the gut (typically over 2 cm in length), ii. those specimens that had a small item of food in the gut that could be detected by feeling along the length of the snakes body (typically between 0.5 and 2 cm in length) and iii. snakes that did not appear to have any food in the gut (or had only the presence of food items less than 0.5 cm in length). These categories were termed 'recently fed', 'having a small item in the gut' and 'unfed' respectively. No attempt to force regurgitation to identify food items was made. It was considered more important to obtain movement data for animals in a variety of feeding conditions rather than collecting more information on feeding ecology; this aspect already being well documented (Goddard 1981, Corbett *in* NCC 1983). Regurgitation would effectively render the snake in an unfed condition. However, any faeces voided or food regurgitated was collected.

The slough condition was classified as follows: i. 'post-slough', where the snake had recently shed its skin. ii. 'mid-slough', stages between i. and iii. where the skin no longer had the sheen of a newly shed animal but was not in a stage just prior to shedding. iii. 'pre-slough' in stages prior to skin shedding characterised by the skin becoming darker and the eyes being cloudy. iv. 'shedding', where the skin was visibly loose (with the eyes having cleared again after phase iii.), splitting at the nose or being shed from the body.

Breeding condition was assessed by palpation and recorded as presence or absence of a penial swelling in males, with the former category being subdivided as 'slight' and 'pronounced' on a subjective basis. In females whether the specimen was pregnant or not was assessed and, where applicable, the number of embryos present were counted. Juvenile and immature snakes were classified as 'immature'.

The location of the snake in the habitat was described using the system of markers described above (usually by a distance and bearing or by cross bearings) and assigned a grid reference later. Vegetation within an approximate 0.25 m² (50 cm by 50 cm) quadrat was assessed qualitatively and structurally, as described in Section 2.2.4.

At subsequent locations, the snake was re-weighed and the slough, feeding and breeding statuses assessed. Location and vegetation data were collected and all weather data and body temperatures were taken. The SVL, TL and the number of subcaudal scales were usually only re-measured if a period in excess of one month had elapsed since the previous location.

Details of weights and lengths of specimens captured are given in Chapter 3.

2.2.3. Radio-tracking

a. Transmitter design and attachment

Small 173 MHz (type SS-1) transmitters (Biotrack Ltd., Wareham, Dorset) weighing about 1 g, excluding battery, were used during the study. These had previously been used in work on the ecology of sand lizards, Lacerta agilis (Dent 1986). The short rigid wire aerial used in that study was replaced by a flexible, nylon coated, trace (whip) aerial of about 15 cm in length. Experiments to assess the most suitable method of attachment and shape of transmitter were carried on captive garter snakes, Thamnophis sirtalis, in a semi-natural vivarium prior to use in the field. This species was chosen as it was easily available during the winter and was of similar overall dimensions to C. austriaca.

Smooth snakes often inhabit structurally complex vegetation and thus it was important to design a transmitter package that minimised snagging whilst the animal was moving. After

laboratory investigation, it was found that the most suitable design for the transmitter was a streamlined and slightly rounded package being built around the original transmitter and attached battery with epoxy resin ('araldite', Ciba-Geigy Plastics, Cambridge, England), see Plate 4. The lower side which attached along the dorsum of the snake was concavely rounded with flanges of 'araldite'. These extended slightly around the sides of the animal (see Fig. 2.2) and helped reduce lateral movement of the transmitter when the animal moved. The transmitter was attached (using a plastic, surgical tape, 'Sleek' (T.J. Smith and Nephew, Hull and Welwyn Garden City, England)) to the top of the tail of the snake about 2 cm beyond the cloaca. A thin band of tape (1.0- 1.5 cm wide) was placed around the tail of the snake initially, with a further length (about 2 cm long and 0.75 cm wide) extending posteriorly from this band of tape and along the back. These two pieces of tape provided a point for attachment of the transmitter and also protected the scales against physical abrasion by the transmitter.

A layer of tape was adhered to the underside of the transmitter overlapping slightly (about 1 mm) at the sides of the anterior end. A longer band of tape, about 5 cm long and 1 cm wide, was then attached around the anterior end of the transmitter adhering to the small overlap of tape on the underside. This ensured that the transmitter was firmly joined to the tape used in attachment. Excess tape, resulting from the angled anterior of the transmitter, was cut away ensuring a smooth front end to the unit. A further length of tape was glued (using 'Loctite Super glue 3', Loctite Holdings Ltd., Welwyn Garden City, England) to the underside of the transmitter providing an adhesive base to it.

The transmitter was then attached to the tape already positioned on the snake by initially fixing the adhesive underside of the transmitter to the tape along the dorsal side and gently winding the longer tape around the snakes tail to give a firm, but not tight, fit. The two ends of



Plate 4 : Radio-transmitters showing shaped araldite potting.



Plate 5 : Specimen of C. austriaca with radio-transmitter attached.

Type SS-1 Biotrack Radio-transmitter

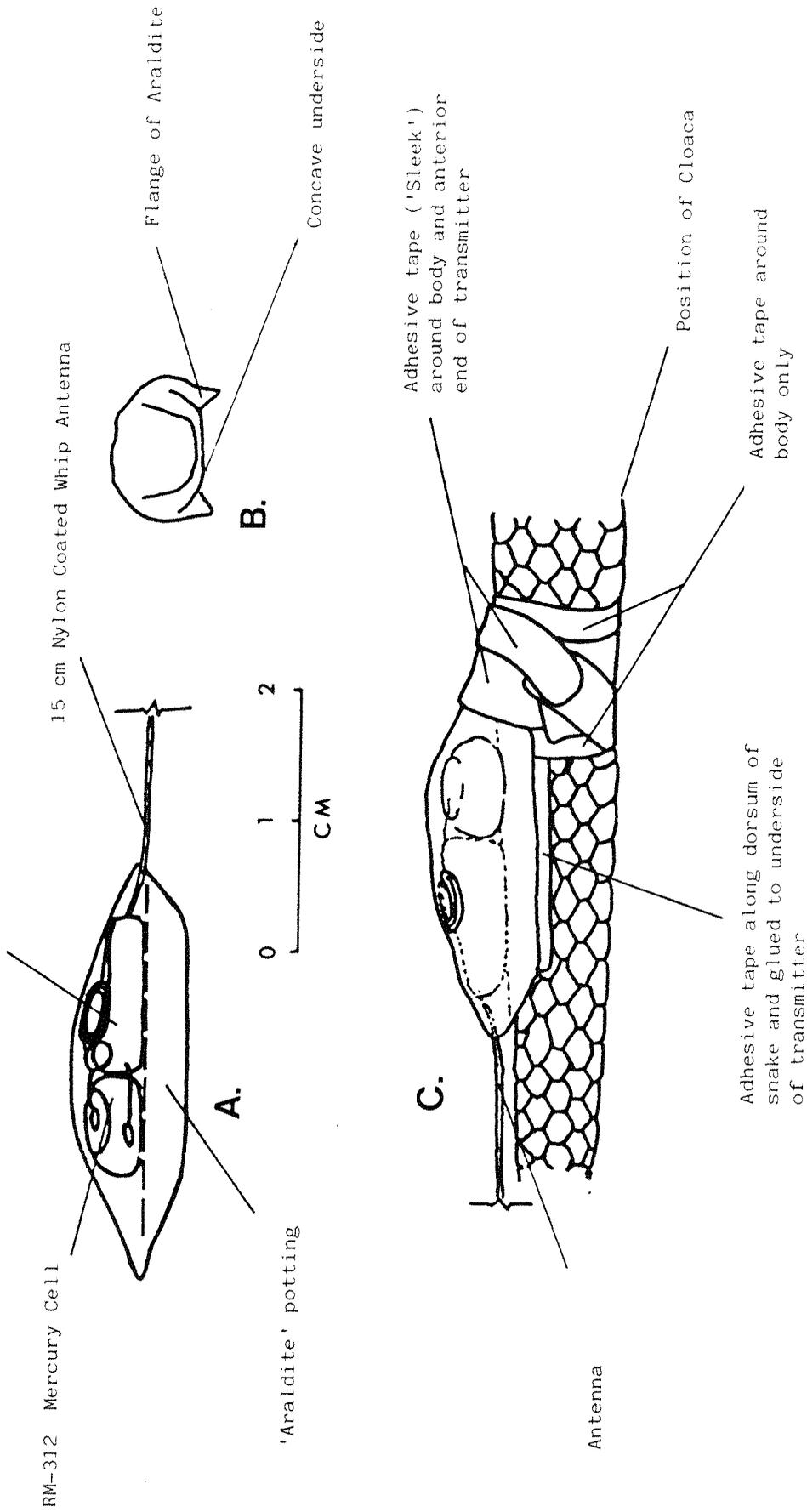


Fig.2.2 : Transmitter Design showing A. Side Elevation, B. Front View and C. Method of Attachment to the Snake.

the tape band were overlapped giving a strong tape to tape attachment. A final narrow band (about 0.5 cm wide) of tape was then taped over the very anterior of the transmitter and the tape around the body. This held the front of the transmitter down and prevented vegetation, etc, catching below it. The transmitter was attached to the snake by the anterior end as this was observed to reduce lateral movement of the package when the animal moved which, in turn, decreased the likelihood of the transmitter snagging. Transmitters that were attached to females had an additional layer of tape on the concave underside ensuring a better fit on their narrower tails. A smooth snake with a radio-transmitter attached is shown in Plate 5. The transmitter units at attachment weighed about 2.5 to 3.0 g inclusive of battery and tape attachment. MacDonald (1978) suggested an arbitrary weight limit for transmitters as not exceeding 5% of the animal's body weight from studies mainly on mammals. Although the weight of transmitters (within reason) was regarded as being a less serious handicap than the physical bulk of the device (due to the nature of snakes movement), transmitters were not attached to snakes weighing less than 30 g, i.e. such that the radio-tag was always less than 10% of the body weight. Transmitter life was generally in excess of two weeks, but they were not left attached to the animal for more than ten days to ensure transmitter recovery and minimise stress to the animal and interference to the animals behaviour. Range of transmitters varied between habitats but was usually from about 20 metres to in excess of 200 metres.

Radio-tagged snakes were located using a Mariner 57 'Biotag' receiver and a three element 'yagi' antenna (directional aerial), (Mariner Radar Ltd., Lowestoft, Suffolk) that indicated the direction of the strongest signal. Animals were tracked until their exact position was located, where possible by visual location.

b. Field data

Animals were located at approximately two hour intervals

(between 1.0 and 3.0 hours) but noting the exact time when the position was finally fixed. The time interval between locations was chosen to allow maximum data to be collected whilst minimising disturbance to the animal which would adversely affect estimates of its movement rates, etc. A two hour time interval not only allowed several snakes to be tracked at any one time but gave sufficient time for other areas of the site to be searched for other animals. The two hour intervals were kept as accurately as possible so that it was valid to compare series of movement data. The behaviour of the snake was noted, as before. The vegetation was qualitatively and structurally assessed in a hypothetical 0.25 m² quadrat centred on the location of the snake, as described in Section 2.2.4. This quadrat was not accurately measured to reduce disturbance to the radio-tagged snake.

Weather variables were recorded, including cloud cover, shade air and bask site temperatures. The animal was disturbed as little as possible during radio-tracking, even viewing it through binoculars where possible, and thus the bask site temperature was usually recorded at a nearby location resembling the position of the snake as closely as possible with respect to vegetation, slope, shade, etc.

Weight, feeding and slough conditions, SVL and TL were recorded prior to the attachment of the transmitter and again after the transmitter was removed. Changes in weight and feeding condition provided useful information about the effect of the transmitter on the snake. Any obvious effects of the transmitter on the animal, e.g. scale loss or scarring, were noted (see Chapter 8, section 8.2).

c. Continual activity recording

Movement activity of radio-tagged animals can be detected by changes in signal strength resulting from differences in the orientation of the transmitting unit relative to the receiving equipment, these changes in signal strength being detectable when the output from the receiving equipment is

recorded on a chart recorder. Traces obtained from moving animals are erratic and uneven whilst those obtained from stationary specimens are regular and even. Examples of such traces (obtained from the present study) are presented in Plate 6. Monitoring of movement activity in this way has been used in many studies of terrestrial vertebrates (e.g. roe deer, Capreolus capreolus, mountain hares, Lepus timidus (Cederlund and Lemnell 1980), and woodcock, Scolopax rusticola (Hirons and Owen 1982)). Primarily with the view to determining emergence and submergence times and for investigating the possibility of nocturnal behaviour, several short periods of continual monitoring were undertaken during June and July 1986.

The receiving equipment (Mariner receiver and antenna, as above) was connected to a portable chart recorder (model CQ95, WPA Scientific Instruments, Saffron Waldon, England) powered by a 12 volt car battery. To permit long periods of continual use the receiver was also powered by a 12 volt car battery rather than using the smaller (9 volt) internal power supply. The chart recorder was set to a speed of 1 mm per minute which was found to yield sufficient resolution for observing movement behaviour without generating excessive lengths of chart. The most suitable writing instrument for the chart at this speed was found to be a ball-point pen refill (Parker Ltd., England). The receiver, chart recorder and two car batteries were housed in a purpose built container consisting of a metal tray, measuring 50 cm by 60 cm, on which the equipment was placed and a metal box, with a slightly angled lid, which covered the whole apparatus. Thus the equipment was kept dry in the event of rain. The exterior of the container was camouflaged to reduce the likelihood of interference from members of the public.

The antenna was placed in top of the vegetation adjacent to the receiving equipment, this usually being about 50 cm above the ground, and pointed towards the location of the study animal. The equipment was checked throughout the day whilst other fieldwork was being undertaken and the

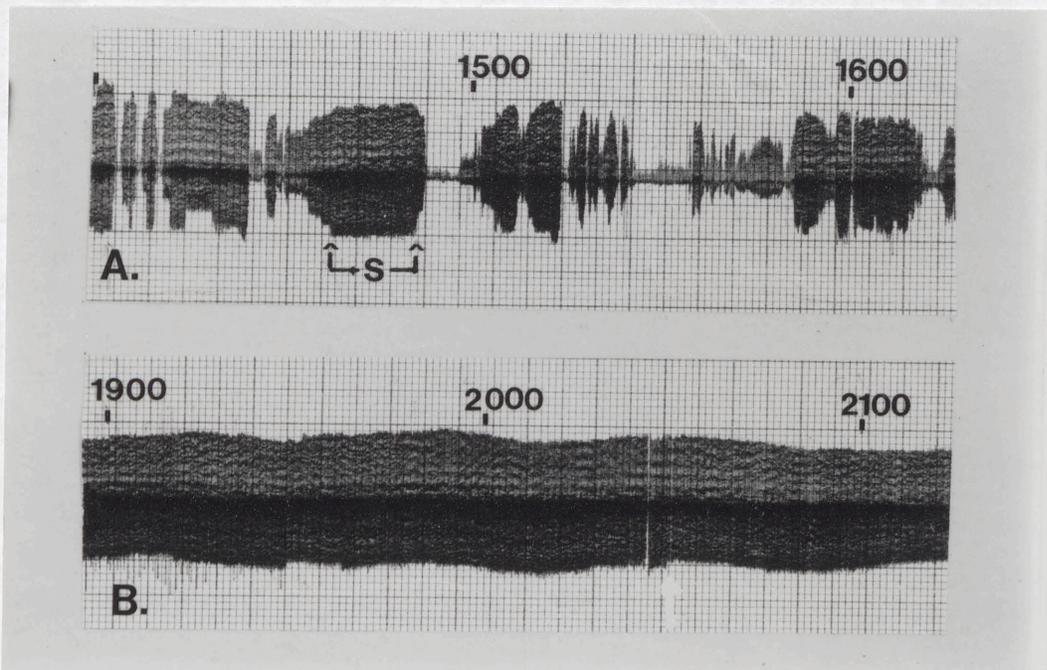


Plate 6 : Examples of traces obtained from continual activity monitoring: a) trace obtained from a moving animal b) trace obtained from a stationary animal. Times (in hours BST) are shown above the traces. A period where the animal was stationary in a) is indicated by 's'.

receiving antenna occasionally moved to ensure a strong signal was being received. Simultaneously, shade air and ground temperatures were automatically recorded each hour using a Grant's temperature recorder.

Initially data collection was interrupted during the day at intervals when the receiving equipment was required for radio-location of the study animal(s), but during the latter part of the field season a second receiver was available, permitting continuous recording throughout the day.

The method was confounded by several problems, most notably the chart roll often becoming snagged during recording, which prevented the collection of as much data as had been hoped. Nonetheless, useful data were collected over nine days which collectively gave information over five 24 hour periods. However, only one complete continuous 24 hour period of data was collected during these experiments.

2.2.4. Quantification of biotic components of habitat

In order to assess the habitat requirements of C. austriaca, it was necessary to quantify the components of the biotic habitat in which the study animals were located. From this type of information it was possible to investigate elements within that habitat that are selected by the study animals and hence try to identify the features that are important to the species as a whole. For a ground living carnivore, such as C. austriaca, both the floral and faunal components of the biotic habitat may be expected to be important in influencing the animal's behaviour. To this end, both vegetation and faunal components of the habitat were described and quantified.

a. Vegetation

At each location of a specimen of C. austriaca the vegetation immediately surrounding the animal was assessed to investigate the habitat preferences of the species. To

this end, the vegetation was qualitatively described by visually estimating the percentage cover of each plant species, vegetation litter and bare ground to the nearest 5% (unless a vegetation type occupied less than 5% in which case its cover was estimated to the nearest 1%) in a hypothetical 0.25 m² (50 cm x 50 cm) quadrat, centred on the location of the snake. Ground layer vegetation only was described in this way and hence the vegetation species composition was assessed by being viewed from the experimenter's shoulder height.

Vegetation categories were subsequently assigned to each sighting, defining each as occurring within a distinct plant community depending on the proportion of the dominant plant species found in each quadrat. These categories are described in Appendix I.

During the 1985 and 1986 field seasons, vegetation structure was also described by estimating the percentage cover of vegetation in each of 16 different height groups (0 cm, 0 to 5 cm, 5 to 10 cm, 10 to 15 cm, 15 to 20 cm, 20 to 30 cm, 30 to 40 cm, 40 to 50 cm, 50 to 60 cm, 60 to 70 cm, 70 to 80 cm, 80 to 90 cm, 90 to 100 cm, 100 to 150 cm, 150 to 200 cm, >200 cm) directly above the animal for the 0.25 m² quadrat (defined above). This height estimation included all vegetation above the animal and hence estimation of height and species composition employed slightly different methods in their calculation. This difference was noticeable when the snake was located below tall, overhanging vegetation.

Data for each site were totalled, but were kept separate for each sex and for the two methods of location (visual location and radio-tracking) to allow investigation of possible differences between these categories.

To assess habitat selection it was necessary to quantify the occurrence of vegetation types throughout the study sites. To this end, 100 random grid references obtained from a random number generator on an electronic calculator

were plotted on 1:10000 scale maps of each of the two major study sites (Sites One and Two). The limits to each study area were defined by a convex polygon linking the outer most sightings of C. austriaca at each site. The randomly selected points were then related to the grid marker system (described in section 2.2.1) and located in the field using both distance and bearing. At each point the plant species composition, vegetation community type and height structure were recorded within a 0.25 m² quadrat as above. This aspect of vegetation examination was undertaken in June 1986, it being necessary to leave such sampling until the final field season when the boundaries of each study area could be defined.

The use of the habitat demonstrated by C. austriaca was then compared against the observed abundance of each vegetation type at each site. Thus it was possible to investigate whether smooth snakes demonstrate a use of their environment that would indicate selection of certain vegetation types or whether each type is merely used in proportion to its relative abundance within the habitat.

b. Faunal components

C. austriaca is a carnivore and is known to take small mammals and reptiles as prey (Goddard 1981, NCC 1983) and, as such, the abundance and distribution of potential prey species was investigated. Two methods were employed.

In order to identify the most productive types of habitat for small mammals two short periods of live trapping were undertaken using Longworth small mammal traps during the first field season (1984). These were done early summer (14th to 17th May) and late summer (20th to 25th August) with trapping periods lasting between three and five days in duration. Three trap lines were set up at Site One each on different vegetation types, namely 'mature dry heath', 'wet heath / Molinia grassland' and 'mature, pure Corsican pine (Pinus nigra) plantation', but were otherwise identical in design. Each line consisted of five rows of 10

traps, placed singly at five metre intervals, with each row being five metres away from its neighbour. Thus each trap line consisted of 50 traps. There was no 'pre-bait' period, this being regarded as unnecessary during such short periods of trapping, and the traps were set immediately. Traps were provided with straw bedding and grain and semi-dry cat food as food for rodents and shrews respectively. Traps were checked twice daily (0700 and 1900 hours) and any animals captured were identified to species, weighed and sexed and the breeding condition noted. Animals were marked by fur clipping prior to release to allow recognition should they subsequently be captured. Totals on each site were calculated and the results used to compare the abundance of potential mammalian prey on each of the very different habitat types.

The location of all potential prey species observed whilst searching for C. austriaca at Sites One and Two were described, relating their position to the markers in the field, and a grid reference later assigned to each sighting. Thus distribution maps of all potential prey species could be produced. This provided the most suitable method of assessing reptile distributions, however it does not allow for comparisons between sites, etc., due to the inconsistency of sampling effort.

The possibility of competition between C. austriaca and V. berus has been suggested (Spellerberg and Phelps 1977) and, as such, the location of all snake species were also described as above. These too were used to produce distribution maps at the main study sites investigate the possibility of interactions between the species. Similarly predators may also be important in affecting the behaviour and range use of smooth snakes and hence any sightings of likely predators (e.g. kestrels, Falco tinnunculus, buzzards, Buteo buteo, foxes, Vulpes vulpes, stoats, Mustela erminea, etc.) were noted. However, due to the large range sizes occupied by these animals only their general location was described.

2.2.5. Habitat selection experiment

Further to describing the vegetation types in which C. austriaca were observed, an experiment to objectively investigate vegetation preferences, and additionally quantify these, was undertaken during the final field season. In this experiment the relative abundance of this species within different, defined vegetation categories was investigated. Three sites (Sites Four, Nine and Ten) offered a variety of vegetation types within a relatively small distance of recent sightings of smooth snakes and these sites were therefore selected for use in this experiment. At each site different categories of vegetation were defined. These categories were sampled in a consistent manner on each site thus permitting direct comparisons to be made between each of the different vegetation categories identified at each of the three sites. However the three sites were not all sampled with constant effort, consequently comparisons between vegetation types were restricted to those found within any one site.

Small pieces of tin sheeting (about 30 cm x 30 cm) were placed in equal grids, totalling between six and seven pieces of tin at 10 to 15 m intervals, at each defined vegetation category at each site. A total of eight vegetation types (with 8 x 6= 48 tins) were used at Site Four, six (with 6 x 7= 42 tins) at Site Nine and seven vegetation types (with 7 x 6= 42 tins) were described at Site Ten.

These categories differed with respect to vegetation community and/or age but were otherwise as similar as possible (e.g. with respect to slope, aspect, proximity to known smooth snake sites). Transects were sampled as often as possible throughout the season and usually about once per week. Upon capture specimens of C. austriaca were weighed and measured and previously uncaptured individuals marked by scale clipping.

A particular objective of this aspect of the study was to

investigate the effect of burning of the dry heathland on smooth snake populations and hence several of the habitat categories selected were dry heathland of different ages. Five categories of post-burn heathland were recognised: immediately post-burning, 'pioneer phase', 'building phase', 'mature' and 'degenerate phase' (sensu Gimingham 1972) and tins were placed on as many of these categories as possible at each site. The other vegetation categories sampled were wet bog (Molinia/Sphagnum/Myrica dominated), wet/humid heath (Erica tetralix/Molinia dominated), bracken and pine woodland. Details of the vegetation community categories used at each site, and the plant species composition of these categories, are presented with the results to this experiment in Chapter 5 (section 5.3.2 d).

Ideally more habitat types would have been included, therefore providing a more complete survey of habitat use. However, attempts were made to replicate each experiment where possible thus reducing bias from selecting unrepresentative areas, e.g. due to them having a low, or non-existent, population of snakes regardless of the habitat suitability. Consequently it was impractical to attempt to sample a larger number of vegetation categories.

There was also the additional problem of placing out many pieces of tin sheeting on land with public access, since this could lead to interference with the tins and the possibility of illegal collection of C. austriaca and other reptiles. This practically was the reason why this method had not been employed prior to the final field season. Therefore tins were placed in areas that were less often frequented by members of the public, thereby reducing the risk of any such tampering.

To further diminish the possibility of interference, only small pieces of tin were used and these painted to afford some degree of camouflage. Tins were also left out for the shortest possible time, from just prior to the field season (early March) to the end of September. The grids were irregular in shape, and tins were positioned so that they

were as inconspicuous as possible.

This aspect of field work allows a simple comparison to be made between the abundance of C. austriaca in different vegetation communities. This was permissible as the standardised sampling technique employed on each vegetation type, avoids the bias of simply finding snakes where the investigator searches which, in turn, tends to favour areas where snakes are assumed to be abundant or easily located. These relative abundances can be related to various other parameters including vegetation height, structure and biomass for each habitat. Prey species relative abundance was also objectively assessed, by recording the frequency of sightings of other species on the transects and below the tin sheeting. Estimation of relative abundance of other elements of the food chain, by mammal trapping and arthropod sampling (pitfall trapping or 'D-Vac' suction sampling) were considered, it being of interest to see how these relate to the reptile fauna. These, however, were not undertaken due to the likelihood of public interference and shortage of time particularly in the light of the low numbers of C. austriaca that were encountered during the experiments.

2.2.6. Continuous temperature records

With the view to investigating the diurnal and seasonal variation in temperatures between different locations within the habitat, continuous temperature recording was undertaken during the final field season. Temperature records were obtained from six different positions within the environment so that an indication of the range of temperature regimes potentially available to specimens of C. austriaca could be studied. The temperature recorder was custom made at Southampton University (C. Hawkins, Biology Department) and was able to measure temperatures from upto eight 'Grant' temperature recorder probe wires at anyone time. Recording intervals were determined by an electronic timer and a selection of time intervals of 7.5, 15, 30 and 60 minutes were available. Data were stored in 'memory

chips' and read, via a computer program, using a BBC micro-computer. Mean daily temperatures and mean temperatures for each hourly interval over the recording period were additionally calculated via this software. Accuracy of measurement was to the nearest one degree celsius, a level deemed sufficient for measurement of environmental temperatures.

The temperature recorder was powered by four 1.2 volt Ni-Cad rechargeable batteries. The complete unit and power supply was housed in a small plastic food container (20 cm by 12 cm). During field measurements the recorder was placed in a polythene bag and housed in a wooden box to provide additional protection from the weather. Recording intervals were commenced and finished by the insertion and removal of a jack-plug and the relevant start and stop dates and times noted.

Temperature records were made during each of the months May to October 1986 inclusive, for periods of between five and eight days. Temperatures were measured at 60 minute intervals at each of six locations. Further details of the locations within the habitat that were used, and the results obtained, are given in Chapter 6, section 6.3.10 (b.).

2.3. Laboratory work

2.3.1 Respirometry

The smooth snake is an ectotherm and as such habitat selection is likely to be influenced by the thermal requirements of the species. Body temperature will in turn affect the animal's metabolism and therefore an understanding of the effect of temperature upon the metabolism of C. austriaca will be useful in interpreting the use of the thermal environment in the wild. To this end, the rate of oxygen consumption ($\text{ml O}_2 \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$) was determined at different temperatures and this parameter used to investigate the variation of standard metabolic

rate with temperature. Oxygen consumption rate was measured using a closed system respirometer (Fig. 2.3). The apparatus consisted of two 500 ml boiling flasks, clamped in a water bath maintained at a constant temperature, and connected to each other by a manometer tube. The tops of the flasks were made gas tight using vaseline. At the junctions between the manometer tube and the tops of the flasks there were three way taps. The manometer was partially filled with Evans blue solution from a reservoir syringe at the bottom of the tube via a three way tap.

Bags of silica gel and soda lime were placed in each side of the apparatus to remove water vapour and carbon dioxide respectively. A specimen of C. austriaca was weighed, the system flushed with oxygen and the animal then introduced into one of the chambers. The tops of the flasks were secured but at this stage the taps were set so that the system was open to the atmosphere. A third flask was also placed in the water bath containing a Yellow Springs Instrument Co. (YSI) telethermometer probe so that the ambient temperature experienced by the snake could be accurately determined.

Once the animal had been placed in the flask and the joints sealed with vaseline, the system was covered with a cloth to reduce visual disturbance and to promote a true resting state. The apparatus was then left for three hours at the first test temperature prior to measuring the rate of oxygen consumption. This period allowed the animal to cease exploratory behaviour. The three-way taps were then closed so that the two flasks and the manometer formed a closed system. A stop clock was started upon closing the taps. After a suitable change in the height of the fluid in the manometer was detected, the fluid was returned to the original levels by injecting oxygen into the system via the three-way tap above the animal chamber using a 1 ml syringe, connected to the tap by narrow gauge rubber tubing. The amount of oxygen required to level the fluid and the time elapsed were recorded and the stop clock was reset. The first reading was discarded, since this value

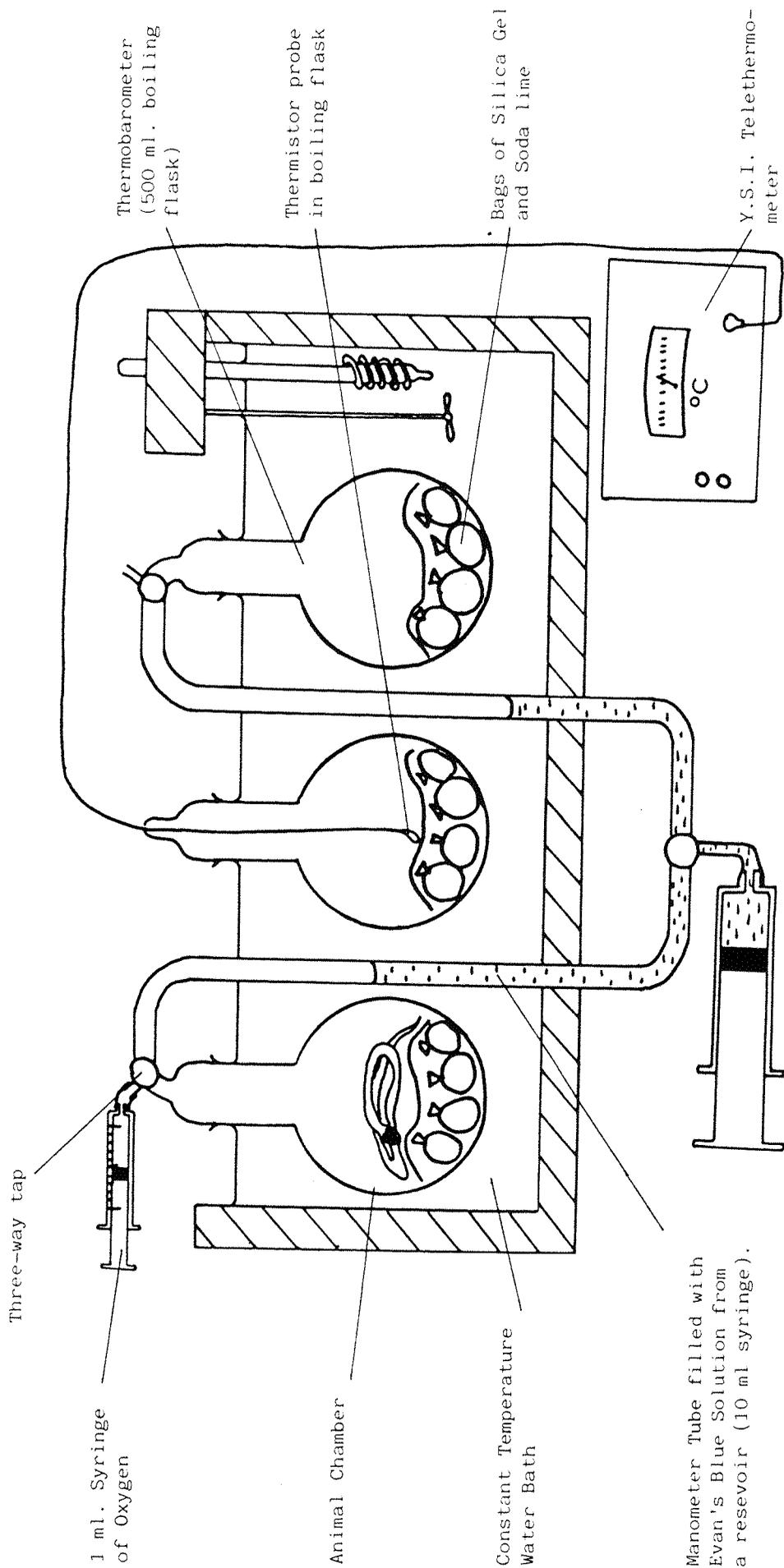


Fig. 2.3 : Closed System Respirometer

may have been affected by residual carbon dioxide upon closing the system, and the procedure repeated until about ten readings were obtained. Those readings that suggested movement had occurred were rigorously discarded as these would not be representative of resting metabolic rate (Bennett and Dawson 1976).

The four lowest, but consistent, values were used to calculate the rate of oxygen consumption per minute, these being regarded as a true reflection of the resting animals metabolic rate (Al-Sadoon 1983). The values were converted to standard temperature and pressure (STP), i.e. 0°C and 760 mmHg (1013.25 mB), and then divided by the animal's body weight to give oxygen consumption (ml) per gramme per hour at STP. Values of weight-specific oxygen consumption rate ($\text{ml O}_2 \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$) are affected by the body weight of the animal, with larger animals using less oxygen per unit mass than do smaller specimens (Bennett and Dawson 1976). To compensate for this values of oxygen consumption rate can be 'weight corrected' to give a value representing the standard resting metabolic rate of a hypothetical 1 g animal based upon the metabolic rate - body weight regression equations. Within the specimens used, however, no clear relationships were observed between the metabolic rate and body size throughout the range of temperatures tested and, consequently, no weight correction equation could be derived for the species. Further, the range of body masses encountered was not large and consequently there was little need for weight correction to permit the intra-specific comparisons for which the data were intended (details of regression calculations and weight of study animals are furnished in Chapter 7).

Temperature coefficients (Q_{10} values) were calculated for the whole range of readings and for separate 5°C intervals (for equation see Section 7.3.1).

Once a complete set of data was obtained for one temperature the water bath was set to a new temperature by either decreasing or increasing the thermostat by 5°C. The

apparatus was left for a minimum of two hours after the new temperature had been attained to ensure that the snake had become rested at the new temperature before taking any oxygen consumption readings.

2.3.2. Selected body temperatures (Voluntary temperature range)

The selected body temperature range is the range of body temperatures maintained by an ectotherm in a laboratory temperature gradient, or equivalent apparatus, that provides conditions which permit an animal to extend its body temperature above and below the activity temperature range (Pough and Gans 1982). Hence the apparatus simulates environmental conditions that would permit active temperature regulation. In the thermal gradient animals are allowed to thermoregulate and will therefore display temperatures between the voluntary minimum and the voluntary maximum temperatures. The arithmetic mean of these values, the mean selected temperature, can be calculated. These data can then be extrapolated to try to explain the observed use of the animal's thermal habitat in the field.

A thermal gradient, consisting of a large metal tank (215 cm by 38 cm and 38 cm high) with a false floor covering heating and cooling elements (hot plates and Grant cooling coils, respectively), was set up. Even illumination along the length was provided by alternate 40 and 60 watt light bulbs above the apparatus. The false floor was covered with a thin layer of 'vermiculite', a substratum that allowed the animal to burrow without snagging the thermistor transmitter, and also offered some insulation. A strip of hardboard 15 cm wide and supported 1.5 cm above the substratum by small wooden blocks, ran the full length of the gradient and provided cover for the snake. The surface temperatures of the gradient chamber were monitored on a Yellow Springs Instrument Co. (YSI) telethermometer via a series of YSI thermistors that were held flush with the floor by adhesive tape. Slight alteration of the

thermostats on the hot plates could therefore be used to maintain a gradual temperature gradient ranging from about 5° to over 40°C at the surface of the false floor along the length of the chamber.

Body temperatures were measured by telemetry using adapted SS-1 type radio-transmitters (Biotrack Ltd, Wareham, Dorset) with a thermistor probe attached. The thermistor probe was inserted into the animal's large intestine, via the cloaca, to a depth of 2 to 3 cm, and held in place with surgical adhesive tape, 'Sleek'. The transmitter was further secured by tape to the snake's tail. The pulse rate of the transmitter was proportional to the temperature of the thermistor probe and hence changes in the body temperature were detected as an increase or decrease in the number of beats recorded per unit time. Radio signals were detected using a Mariner 57 'Biotag' receiver, via a wire aerial that ran the length of the gradient chamber, and then recorded on a chart recorder (Model CQ95, WPA Scientific Instruments, Saffron Waldon). Both the receiver and chart recorder were powered by 12 volt car batteries, which allowed the former to run continually. The chart recorder was activated for a period of 20 seconds each hour by a timer and thus the body temperature was sampled at discrete periods throughout the day. The snake was introduced to the chamber at least 2 hours before attaching the thermistor tag which allowed a period for it to become familiar with the apparatus. Snakes were left in the thermal gradient chamber for varying periods of time, ranging from 36 to 75 hours. During the experiment the animals were exposed to a light:dark cycle that approximated natural conditions at the time the experiments were undertaken. The light:dark periods were 11:13 (n= 2), 13:11 (n= 4) and 16:8 (n= 1). Lighting was controlled by a time switch. The gradient tank was covered by a net curtain to ensure diffuse, even lighting along the gradient and also reduce disturbance from movement outside the tank.

The hot plates and cooling coils were switched on at least 24 hours before introducing the animal to the chamber to

allow the gradient of temperatures to become established. Transmitters were calibrated prior to and after each experiment, and an 'average' calibration curve used to calculate body temperature.

The snakes used were in a variety of slough and feeding conditions. One male (B4) had recently fed although it regurgitated during the experiment and a female (L1) possibly had food in its gut. The other specimens were in an unfed condition. Most animals were either in mid-slough (n= 3) or post-slough condition (n= 3) although one male (H27) was in a pre-slough state. One of the three female snakes (S3) was pregnant. No subdivisions into slough, feeding or breeding conditions were made when analysing the results of this experiment, although these parameters are likely to affect the selected body temperature, on account of the small sample sizes in each group. Data were, however, separated for each sex.

2.3.3. Critical thermal minimum (Critical minimum temperature)

The critical thermal minimum is not physiologically lethal to an animal (cf. lethal minimum temperature) but is the temperature at which the locomotory activity of the animal becomes disorganised and the animal loses its ability to escape (Pough and Gans 1982). This temperature can therefore be regarded as ecologically lethal since an ectotherm cooled to this body temperature would be unable to avoid any conditions that would be fatal, e.g. predators or a further reduction in temperature. This parameter was investigated in this study as smooth snakes would be expected to seek shelter well before their body temperatures fell to this critical value. Body temperatures above this value would permit at least a limited capacity of movement and hence permit the animal to seek a more suitable environment.

Critical minimum temperature levels were investigated by slowly cooling snakes, which were retained in a small metal

tin that provided a flat substratum and offered little insulation, in a deep freezer. Body temperatures were continually recorded using a fine YSI thermistor probe inserted into the animal's cloaca and a telethermometer until such a time that the snake was just unable to turn itself upright after successively turning it onto its back. At this temperature the animal was regarded as having just lost its ability to move and this body temperature was taken as the critical minimum.

2.3.4. Maximum tolerated temperature

This parameter is the body temperature at which an ectotherm moves away from undercover in response to increasing temperature to actively seek a cooler site and hence represents the maximum body temperature that that animal will tolerate. It therefore has direct application to interpreting thermal site selection in the field by defining the upper extreme of temperature tolerated by the snakes. To investigate this aspect of the thermal biology of C. austriaca, a snake with a fine YSI thermistor probe inserted into its cloaca was placed beneath a small square of tin sheeting in the centre of a small wooden arena containing a thick 'vermiculite' substratum. The thermistor probe was connected via a YSI telethermometer to a continual chart recorder. A 275 watt heat lamp was clamped 60 cm above the tin square which was turned on as soon as the animal was settled below the tin. The increasing body temperature of the animal was recorded until it moved from under cover. The body temperature at which the animal had moved completely from under the tin was recorded and this value was termed the Maximum tolerated temperature.

2.3.5. Determination of the effect of radio-transmitters on snake behaviour using video analysis / Observation of behaviour using video analysis

Radio-location of smooth snakes tagged with miniature transmitters was an important aspect of the field work during the present study. Consequently it was necessary to

investigate whether the attachment of these transmitters affected the animals behaviour. Any observed effect would have implications on the interpretation of the results obtained from the field.

A short laboratory study was devised to investigate whether changes in the behaviour of C. austriaca could be determined following attachment of radio-transmitters by watching behaviour of tagged and untagged individuals over a period of several days using time-lapse video analysis. Simple arenas were used and as such only changes in movement rates and the proportion of time the animals assigned to each of certain defined behaviours were investigated.

Two animals were observed during each of two separate experiments, in early June and early July 1986. A further aspect, namely the use of structurally complex 'vegetation', was also investigated during the second pair of experiments by a slight alteration to the arenas.

a. Methodology

A metal and brick vivarium was divided centrally into two identical arenas each measuring 168 cm by 109 cm and 61 cm high. The floor of the arenas were made of concrete and covered with a generous layer of fine sand. Each arena was identically equipped with a 250 watt heat lamp positioned at the centre of one side (and 30 cm above the ground), a centrally positioned wooden board as a refuge and four petri-dishes of water. Additionally, half of each arena was covered with slightly folded 5 cm mesh chicken wire to simulate vegetation during the second set of experiments. A video camera was positioned centrally so that the entire floor area of both arenas could be filmed at the same time (see Fig. 2.4).

One snake was introduced to each arena and left for at least 24 hours to allow the animals to adjust to their surroundings. Each snake was then removed from the arenas

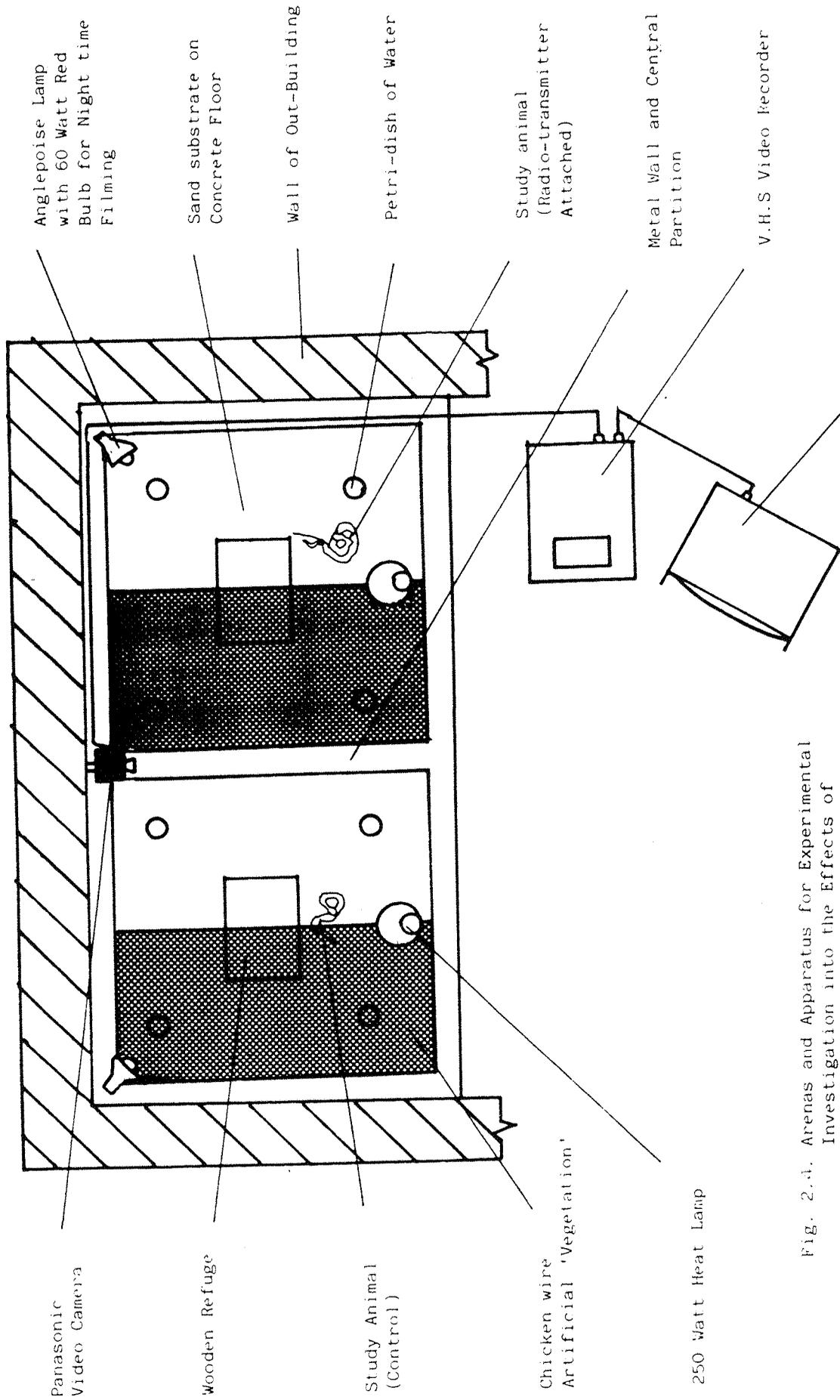


Fig. 2.4. Arenas and Apparatus for Experimental Investigation into the Effects of Attachment of Radio-transmitters on the Behaviour of C. austriaca.

and processed as on first capture in the field (i.e. weighed, SVL and TL measurements taken, subcaudal scales counted and slough, breeding and feeding conditions assessed). A radio-transmitter was then attached to one of the snakes and both animals released back into their respective half of the vivarium. The time lapse video recorder, set to record ten days data per 3 hour video tape, was then started. The length of time spent in the arena may effect the behaviour of the study animals. For the purpose of investigating this aspect this first period of filming was termed Trial One.

Following a period of between two and three days both snakes were removed from the arenas and both 'processed' as before. The transmitter was removed from the tagged snake and attached to the previously untagged individual. Both snakes were then released back into their respective arenas for a further two to three days during which time their behaviour was video-recorded, this period being referred to as Trial Two.

Any weight changes that occurred during a trial were converted to a mean rate per day. Differences in rate of change in weight of radio-tagged animals (when compared with a control animal) provides an additional parameter by which the effect of attachment of radio-transmitters on the study species can be assessed.

During the period of filming, the animals were disturbed as little as possible so that the behaviour observed was influenced minimally by outside distractions. The vivarium was housed in a small, brick out-building. Lighting was controlled by time-switches and was provided by an overhead fluorescent strip (between 0500 and 2100 hours BST) and by the heat lamps (between 0745 and 1645 hours BST). Natural light was excluded using wooden shutters. Two red 60 watt light bulbs were continually left on so that filming was possible overnight (between 2100 and 0500 hours BST). Air temperatures in the vivarium varied between 15 and 25°C although temperatures below the heat

lamp attained greater maximum values during the day (upto 36°C).

The transmitter was attached first to one animal and then to the second, in preference to having both snakes either tagged or untagged at the same time, as this compensated for any inherent, climatic or acclimatisation related, etc., effects of length of time in the arena on behaviour.

Ideally, very similar animals would have been used on both sides of the arena during both experiments to reduce any variation between the test animals. During the first pair of experiments this was possible and two male snakes (D2 and L2) of similar size (SVLs= 466 mm and 455 mm respectively) were available. However the second pair of experiments used one male (B7) and one female snake (S10) with a not inconsiderable difference in size (SVLs= 438 mm and 564 mm).

b. Analysis

The behaviour of radio-tagged and untagged smooth snakes was compared by observing the proportion of time assigned by each to five previously determined behaviours. These behaviours are:

i. Below Cover- the snake was assumed to be inactive and was placed in this category if greater than 95% of the body was below the central refuge.

ii. Inactive in Open- any non-movement behaviour where 5% or more of the body was outside the central refuge that was not classed as thermoregulating.

iii. Active- any movement behaviour where 5% or more of the body was outside the central refuge that was not classed as thermoregulating.

iv. Movement Thermoregulating- any movement behaviour where all or part of the body was exposed in a circle where the ground temperature was greater than normal surface temperature as a result of the influence of the heat lamp.

v. Non-Movement Thermoregulating (Basking)- any non-movement behaviour where the body was exposed in a circle where the ground temperature was greater than normal as a result of the influence of the heat lamp.

Prior to any video recording, the diameter of the circle in which the heat lamp was deemed to have an effect upon the ground temperature was determined. This was measured using a Grant recorder via a series of thermistor probes placed along the ground at 25 cm intervals, with the first of these probes being directly below the heat lamp. Half hourly measurement of temperature were taken at each of these positions and hence the area affected by the heat lamp could be determined throughout the day. An acetate overlay was produced, that described the extent of this area (and its successively diminishing diameter with time after the heat lamp had been extinguished), and was placed over the screen of the monitor. This allowed the extent of the warm area to be defined, and consequently whether the snake was 'thermoregulating' or not to be determined, whilst reviewing the video tapes. Brief spells of behaviour, lasting less than one minute, were discounted.

Total time spent on each behaviour per hour were recorded and pooled into six 4 hourly time periods. The six time periods were selected to coincide with the artificial lighting and approximated periods of the day as follows: 05-0900 hr= dawn, 09-1300 hr= morning, 13-1700 hr= afternoon, 17-2100 hr= evening, 21-0100 hr and 01-0500 hr= night.

Time budget data were analysed pairwise for each behaviour type, using the Mann-Whitney U-test to test for

differences in time spent on each behaviour between tagged and untagged animals and, additionally, between first and second trials within each time period. The latter comparison was undertaken to assess whether or not, or to what extent, behaviour differed with time spent in the arena.

The effect of a radio-transmitter upon movement rates of C. austriaca was investigated by assessing the total distance moved per hour. Movement was traced onto an acetate overlay placed over the screen on the video monitor, following the movement of the mid-point of the body and measuring the trace produced with a map measurer. The mid-point of the body was chosen as a reference point thus avoiding an overestimate of the animal's movement which would result from following either of the extremities of the snake, e.g. through movement of the head whilst looking around. Hourly movement rates were pooled into 4 hour and 24 hour periods as above and mean values compared between radio-tagged and untagged individuals using the Student's t-test.

The effect of the radio-transmitter on the behaviour and movement of C. austriaca with respect to vegetation was investigated in two ways using the data from the second pair of experiments only. Three vegetation types were defined these being : 'vegetation' (more than 50% of the body within the area covered by chicken wire), 'open' (50% or more of the body outside the area covered in chicken wire) and 'cover' (95% or more of the body below the central refuge). The proportion of time spent in each of these vegetation categories was compared between tagged and untagged animals, for the 4 hour and 24 hour periods as above, using the Mann-Whitney U-test. The effect of time in the arena on 'vegetation use' was also investigated by testing data for Trial One against data for Trial Two for each time period using the Mann-Whitney U-test. Movement rates within the two non-cover vegetation types ('vegetation' and 'open') were analysed for differences that could be attributed to the attachment of

a radio-transmitter using the Student's t-test within each 4 hour time period and over the whole day.

c. Results

The proportions of time spent on each activity during the six 4 hour time periods and over the whole day for radio-tagged and untagged animals are summarised in Fig. 2.5. A very similar pattern in the division of time between different behaviours was observed between animals with transmitters and those without. Both groups demonstrated a decreased use of cover during the morning (up until 1300hr), reaching a minimum during the afternoon and rising again to a maximum overnight. Activity was at its greatest in the early morning (05-0900 hr) with low levels during the afternoon and during the night. Non-movement thermoregulating was the dominant activity during the period in which the heat lamp was on and particularly so during the afternoon.

Mann-Whitney U-tests demonstrated a significant difference between tagged and untagged animals in only two behaviour categories. These were the proportion of time the animals were active during the 05-0900 hr time period and the proportion of time spent below cover in the same time period. During that time radio-tagged snakes used cover more frequently (29.7% compared with 15.0% of the time) ($U=584$, $n_1=40$, $n_2=40$, $p<0.05$) and were less active (32.8% compared with 49.1% of the time) ($U=570$, $n_1=40$, $n_2=40$, $p<0.05$) than snakes without radio-transmitters attached.

It was concluded that the attachment of radio-transmitters only affected the behaviour of C. austriaca to a small extent during these experiments with respect to time budgetting and their activity patterns throughout the day.

Behaviour patterns were also found not to vary between the first and second trials for 4 hourly time periods nor over the whole day with the exception of two instances. A larger proportion of time (82.8% compared with 61.5%) was

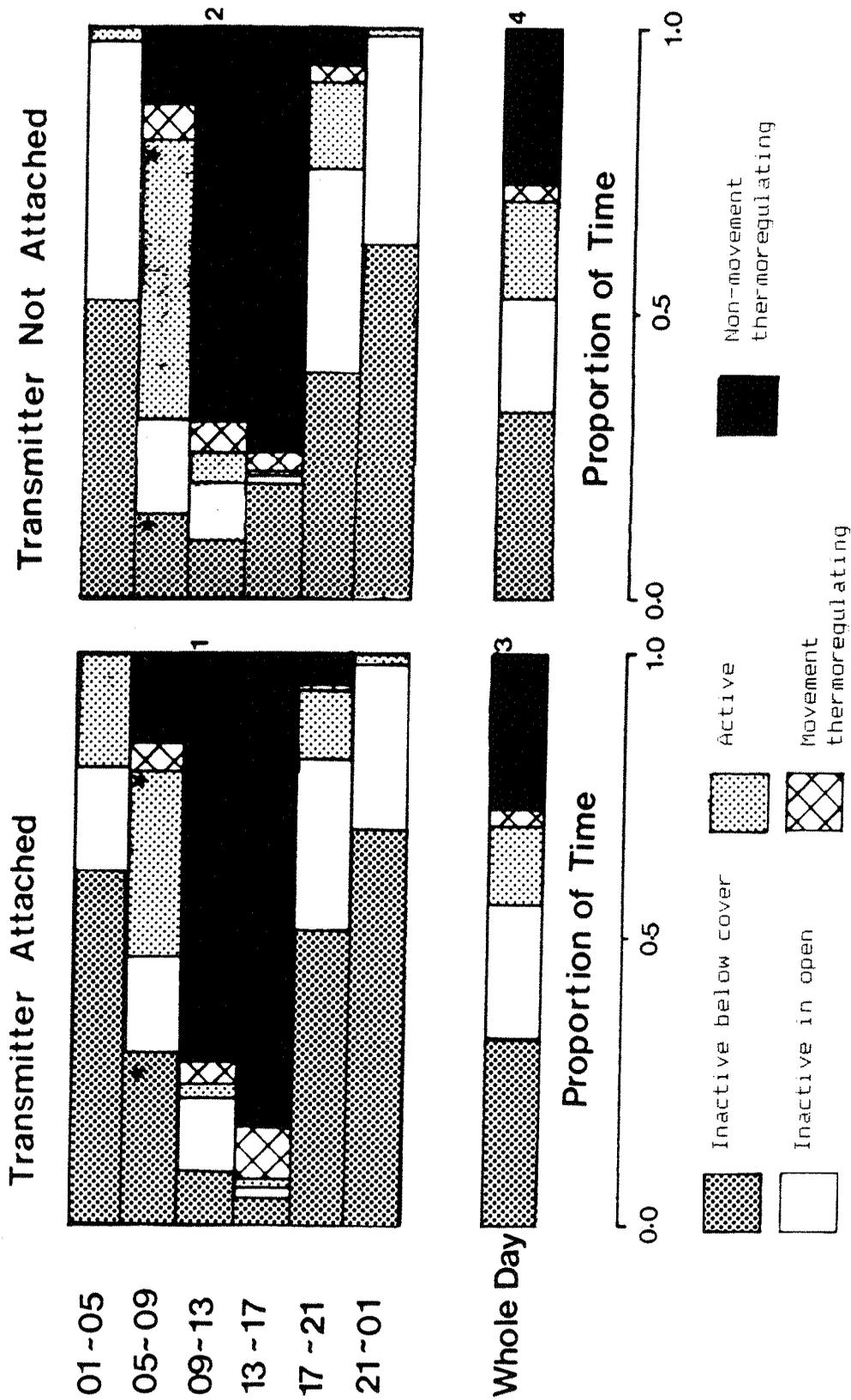


Fig. 2.5 : Proportion of time assigned to each behaviour during six 4-hour time periods and over the whole day by *C. austriaca* with radio-transmitters attached and not attached as determined by video analysis. Four animals were used for between two and three days; n= 40 hourly observations in all cases except **1** where n= 37 hourly observations, **2** where n= 36 hourly observations, **3** where n= 237 hourly observations and **4** where n= 236 hourly observations.

★ denotes a significant difference at the 5% level.

devoted to non-movement thermoregulating between 09-1300 hr during Trial One than Trial Two ($U = 369$, $n_1 = 42$, $n_2 = 31$, $p < 0.05$) and less time (72.6% compared with 84.6%) in the 13-1700 hr period during Trial One than Trial Two. Thus there is a slight indication that the snakes were basking later during the later trials than during the earlier ones.

Movement rates were highly variable within each time period but yielded a very similar pattern between radio-tagged and untagged animals. Intermediate levels of activity were observed before the commencement of the light period and activity increased to a maximum value during the dawn period. Lowered levels of movement were observed during the morning and, after a slightly increased movement rate during the afternoon, again in the evening. Minimum movement occurred during the first half of the night. These observations are presented in Table 2.1. No significant differences in movement rates were observed between radio-tagged and untagged animals during any time period or over the whole day (values obtained from t-tests are presented in Table 2.1).

It was concluded that transmitters do not seem to affect the movement rates of C. austriaca in simple, artificial arenas.

The study animals demonstrated a similar use of each of the two defined vegetation types ('vegetation' and 'open') and of 'cover' within each time period and over the whole day whether transmitters were attached or not, with one exception. Untagged animals were observed inactive in the open for a significantly larger proportion of time than were radio-tagged specimens (30.8% compared with 17.7% of the time) between 05-0900 hr ($U = 185$, $n_1 = 16$, $n_2 = 16$, $p < 0.05$) (see Fig. 2.6).

Cover is used for the greatest proportion of time during the first half of the night, decreasing during the remainder of the dark period to yield low values between

<u>Time</u>	<u>Transmitter Attached</u>			<u>Transmitter Not Attached</u>			<u>Significance</u>	
	<u>Mean</u>	<u>s.d.</u>	<u>n</u>	<u>Mean</u>	<u>s.d.</u>	<u>n</u>	<u>t</u>	<u>d.f.</u>
01-05	38.30	81.8	40	25.55	60.5	40	0.793	78
05-09	115.63	163.3	40	155.48	182.1	40	1.030	78
09-13	28.30	53.4	37	16.84	23.3	38	1.210	73
13-17	58.28	103.8	40	30.80	69.7	40	1.390	78
17-21	35.38	82.4	40	26.50	49.6	40	0.584	78
21-01	3.43	17.7	40	1.13	4.6	40	0.795	78
Total	46.78	100.7	237	42.93	100.1	238	0.045	473

Table 2.1: Mean hourly movement rates (cm/ hr) for C. austriaca with radio-transmitters attached and radio-transmitters not attached during 4 hour periods and over the whole day, together with the t-test values. All values of 't' are not significant at 5% level.

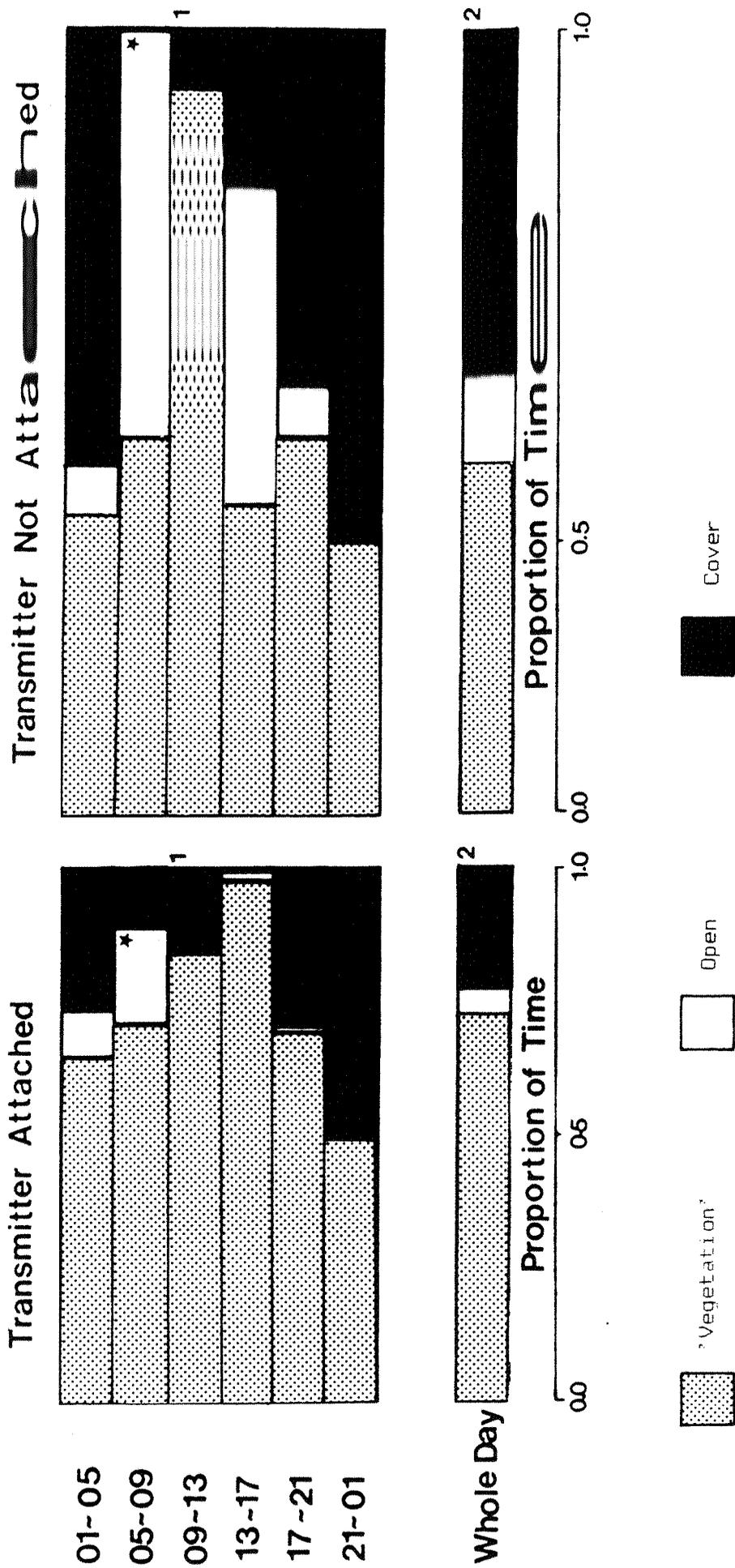


Fig. 2.6 : Proportion of time spent in each 'vegetation' type and below cover during six 4-hour time periods and over the whole day by *C. austriaca* with radio-transmitters attached and not attached as determined by video analysis. Two animals were used each for two days; n= 16 hourly observations in all cases except **1** where n= 14 hourly observations and **2** where n= 94 hourly observations. denotes a significant difference at the 5% level.

dawn and late afternoon. Use of cover then increases again during the evening following the heat lamp being turned out. Periods with the smallest proportion of time below cover were 05-0900 hr for untagged animals and 13-1700 hr for radio-tagged specimens. Throughout the day both tagged and untagged animals spent most time in 'vegetation' with the exception of the first half of the night when equal proportions of time were spent in 'vegetation' and below cover. Use of the 'open' ground occurred mostly during the early morning (between 05-0900 hr) for both radio-tagged and untagged specimens. However, open ground is also used during additional periods in the second half of the night (01-0500 hr) and during the afternoon (13-1700 hr) and evening (17-2100 hr) by both tagged and untagged animals. Even though snakes without radio-transmitters attached spend a larger proportion of time in 'open' ground than those with radios attached during these latter three time periods, these observed differences are not statistically significant. In conclusion radio-tagged specimens of C. austriaca showed a similar use of vegetation within the artificial arenas as those without transmitters attached.

Use of vegetation by the snakes varied with time in the arena only during the 05-0900 hr period. Animals used 'vegetation' more (79.9% compared with 59.3% of the time) ($U = 182$, $n_1 = 16$, $n_2 = 16$, $p < 0.05$) and 'open' ground less (8.0% compared with 39.8% of the time) ($U = 210$, $n_1 = 16$, $n_2 = 16$, $p < 0.002$) during the second trial when compared with the first. Generally, and when looking at pooled data, vegetation use does not vary between trials One and Two.

A significant effect of the attachment of a transmitter was observed only on movement rates of C. austriaca through 'vegetation' in the 13-1700 hr period, when animals with transmitters moved more (mean 89.4 cm/hr ± 117.7 compared with 11.1 cm/hr ± 18.2) ($t = 2.630$ with 30 d.f., $p < 0.02$) than those without. However no differences were observed during other time periods or when all the movement data in 'vegetation' were pooled over the 24 hour

period, (see Table 2.2).

Mean movement rates in the 'open' category showed significant heterogeneity between tagged and untagged snakes during 05-0900 hr and for the pooled data over the 24 hour period, (see Table 2.2). Transmitters appear to cause a reduction in movement rates in the open resulting in a mean value of $43.6 \text{ cm/hr} \pm 75.0$ compared with $292.8 \text{ cm/hr} \pm 238.1$ for untagged animals during the dawn period ($t= 3.993$ with 30 d.f, $p<0.001$) and $12.1 \text{ cm/hr} \pm 39.2$ and $69.3 \text{ cm/hr} \pm 167.7$ respectively for the 24 hour period ($t= 2.662$ with 187 d.f, $p<0.01$).

In conclusion the attachment of radio-transmitters seemed only to have a small effect on activity patterns and time budgetting of captive smooth snakes and that effect was limited to only a few time periods during the day. Movement rates were highly variable but were also not significantly affected by the transmitters in the artificial arenas. Analysis of 'vegetation' use was limited to only a small number of observations and this data were collected using two very different individuals (a large pregnant female snake and a medium sized male snake). The results suggested a similar use of open and vegetated ground by tagged and untagged animals over most of the day, however, when movement rates were analysed separately for different vegetation types a slight effect following the attachment of a radio-transmitter was detected. Movement rates were greater for radio-tagged animals than untagged animals during one time period (13-1700 hr) in the rough vegetation, which appears contrary to what may have been expected. Snagging of transmitters would perhaps have been expected to reduce, rather than increase, movement rates in this vegetation type. All other time periods yielded no significant difference between movement rates in the structurally complex vegetation type. Reduced movement rates in the open following the attachment of radio-transmitters are also hard to explain, particularly as movement rates during the first pair of experiments (in which there was no simulated

A. VEGETATION

Time	Transmitter Attached			Transmitter Not Attached			t	d.f.	sig.
	Mean	s.d.	n	Mean	s.d.	n			
01-05	80.8	97.2	16	48.0	117.8	16	1.114	30	NS
05-09	209.2	172.7	16	335.8	272.3	16	1.570	30	NS
09-13	35.5	73.5	14	9.6	12.2	15	1.347	27	NS
13-17	89.4	117.7	16	11.1	18.2	16	2.630	30	p<0.02
17-21	29.8	84.2	16	112.6	209.8	16	1.465	30	NS
21-01	6.9	27.8	16	0.0	0.0	16	0.993	30	NS
<u>Total</u>	76.1	123.0	94	87.0	187.8	95	0.470	187	NS

B. OPEN

Time	Transmitter Attached			Transmitter Not Attached			t	d.f.	sig.
	Mean	s.d.	n	Mean	s.d.	n			
01-05	15.0	32.6	16	47.8	133.8	16	0.922	30	NS
05-09	46.3	75.0	16	292.8	238.1	16	3.993	30	p<0.001
09-13	0.0	0.0	14	0.0	0.0	15	-	-	-
13-17	9.2	36.8	16	1.4	5.8	16	0.837	30	NS
17-21	3.6	7.8	16	69.7	181.7	16	1.454	30	NS
21-01	0.0	0.0	16	0.0	0.0	16	-	-	-
<u>Total</u>	12.1	39.2	94	69.3	167.7	95	2.662	187	p<0.01

Table 2.2: Mean hourly movement rates (cm/ hr) for C. austriaca with radio-transmitters attached and animals with transmitters not attached during 4 hour periods and over the whole day, divided into the two vegetation categories ('Vegetation' and 'Open'), together with t-test values and significance values.

vegetation, and hence the entire arena could be regarded as being 'open') yielded no differences in movement rates for tagged and untagged specimens.

It is likely that the highly variable data and small measured distances involved make such comparative studies unreliable on such small samples; conclusions drawn from such data clearly must be advanced tentatively. However the overall similarity in the results from video analysis on time budgetting, activity patterns, movement behaviour and vegetation use between radio-tagged and untagged snakes suggests that the attachment of such a device has only a small affect on the behaviour of C. austriaca. Although it is often unwise to try to extrapolate the results of laboratory studies to field conditions, the above experiments do indicate that data collected by radio-tracking in the field are likely to be a reflection of true behaviour and not be an artefact of the method. Further, this similarity suggests that it is reasonable to pool the data collected during the video experiments and use these data in their own right to provide additional information about the behaviour of the species. Results from the combined experiments are presented in Chapter 4, section 4.3.10.

Weight changes, expressed as g/ day, are presented in Table 2.3 for each animal. Mean rate of change in weight of captive smooth snakes was -0.325 g/ day ± 0.442 ($n= 4$) in animals with transmitters attached and -0.578 g/ day ± 0.889 ($n= 4$) in untagged snakes. The difference between these two values is not statistically different ($t= 0.513$ with 6 d.f, $p>0.05$). Thus, although the sample sizes and sample periods are small, there seems to be no effect of transmitter attachment upon weight changes in C. austriaca. No significant difference was observed between the weight change of snakes during the first and second trials with mean values of -0.270 g/ day ± 0.438 ($n= 4$) and -0.633 g/ day ± 0.865 respectively ($t= 0.749$ with 6 d.f, $p>0.05$).

Code	Sex	Expt.	TRIAL ONE		TRIAL TWO	
			Wt.Change <u>g/day</u>	Transmitter	Wt.Change <u>g/day</u>	Transmitter
D2	M	1	-0.41	ON	-1.72	OFF
L2	M	1	-0.78	OFF	-0.81	ON
S10	F	2	+0.26	ON	+0.34	OFF
B7	M	2	-0.15	OFF	-0.34	ON

Table 2.3: Mean rate of change in weight (g/ day) for C. austriaca during Trials One and Two of the video recording experiment, indicating whether transmitters were attached (ON) or not (OFF).

2.4. Analysis

Field data on newly captured C. austriaca were transcribed onto record cards and subsequent locations described on 'subsequent record' sheets that were attached to the original sightings record card. Radio-tracking data were recorded on separate radio-tracking schedules. All locations of C. austriaca were subsequently stored as 38 character strings (giving information on date, time and grid reference of location, the behaviour and body temperature of the snake, weather variables (cloud, shade air and bask site temperatures) and details of the snake's slough, feeding and breeding status as well as an identifying code relating to the sex, site and identification number of that snake and the method used to locate it) in 'data' files on the ICL 2976 computer at Southampton University. Movement data were derived from these data via a program that calculates distance, direction of movement and the time difference between successive sightings (where the observations are from the same day) and also the rate of movement. Mean cloud cover, shade air and bask site temperatures over the movement interval are also calculated. These data were stored in separate 'results' files depending on whether the data was obtained by visual location or radio-tracking. Daily movement rates were also calculated using radio-tracking data where five or more sightings (see Chapter 4, section 4.3.2) were recorded in a day by summing the total distances between successive sightings for that date. Locations of other species were recorded initially on 'other species' location sheets and later stored as 20 character strings (detailing date and time of location, species and sex of the animal and the grid reference of the sighting). These data were used to produce distribution maps.

Analyses of movement data were restricted to those obtained by radio-location. Home range analyses, however, incorporated data collected by all methods. Home range areas were calculated using a series of BBC microcomputer

programs, the 'Ranges suite' (Kenward 1987).

The statistical analyses used in each section are described in the relevant results chapter although a general outline of the methods employed shall be given below. The tests employed are named and the statistic produced from the test given in parentheses. Where different authors give different statistics alternative names are given and the authority quoted. Where mean values are presented in the text of this report the degree of variability is indicated by ± 1 standard deviation, whilst in figures the reliability of the mean is illustrated by error bars ± 1 standard error, unless stated to the contrary.

Where samples indicate normality, parametric statistical procedures were favoured as these operate on absolute magnitudes of the data and hence offer the most powerful statistical tests. Non-parametric statistical tests, on the other hand, are more robust and do not require the data to be continuous and normally distributed since they operate on relative magnitudes (ranked data). Thus where the data indicated discontinuous or skewed distributions non-parametric procedures were employed. Median values are presented either with or in lieu of mean values where the data do not satisfy parametric assumptions. These 'middle values' are more representative of the population since they are not affected by extremes in the data.

For the comparison of two samples t-tests were employed when the data was assumed to meet the requirements that would permit parametric statistics. The homogeneity of the variances were tested prior to employing this test via the F_{max} test (yielding a value for ' F_{max} '). Where the data indicated homogeneity the Students t-test was employed but for heterogeneous data a t-test employing separate variance estimates was favoured (the statistic in both cases being 't'). Where the requirements for parametric statistics were unlikely to be met, the Mann-Whitney U-test was employed (statistic= 'U'). The Wilcoxon/ Mann-

Whitney pairs test (statistic= z) was used in lieu of the Mann-Whitney U-test in later statistical analysis, this being the equivalent non-parametric test in the 'Statgraphics' package.

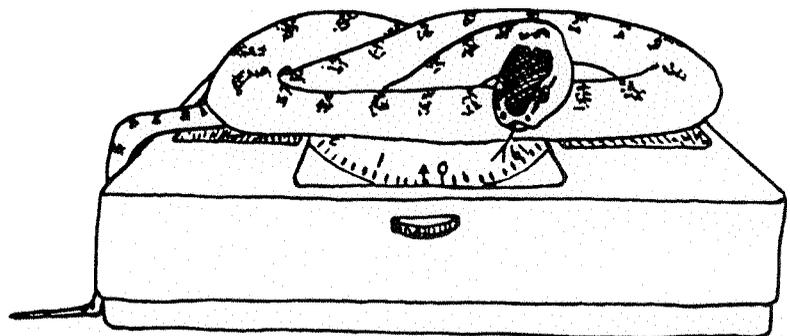
Where comparisons between more than two independent samples were undertaken one-way analyses of variance (ANOVA) were used where for data that was assumed to be normally distributed (yielding the ratio 'F'). Heterogeneity of the variance were tested prior to employing this test via the Bartlett-Box F test (producing a value for 'F'). Where data were heterogeneous ANOVA were still employed but the conclusions treated with caution. For non-parametric data the Kruskal-Wallis test was employed (which yields a value for chi-squared).

Relationships between two independent variables were tested via the Pearson correlation coefficient (r) and the Spearman rank correlation coefficient (r_s) for parametric and non-parametric data respectively. These relationships were described by calculating regression equations. Further relationships between one variable with two other variables were described using multiple regression equations. Frequency distributions were compared via Kolmogorov-Smirnov two sample tests (yielding the statistic D (Sokal and Rohlf 1981) or z (SPSS Inc 1983)). G-tests were employed where comparisons between observed and expected frequencies were required (statistic= 'G').

Much of the statistical analyses of these data were undertaken using the updated Statistical Packages for the Social Sciences (SPSS-X) programs (SPSS Inc. 1983) on the ICL 2976 computer and the procedures for these are described in SPSS Inc. (1983). Other statistical analyses were undertaken using the 'Statgraphics' package, Version 2.0 (STSC Inc. 1986) on an Amstrad PC-1512 computer. Additional statistical tests follow the procedures listed in Siegel (1956) and Sokal and Rohlf (1981). The level of significance used in the statistical analyses in this report is 5% (i.e. $p = 0.05$). Computational facilities were

provided on the ICL 2976, Honeywell 6080, PDP 11/45
mainframe computers and BBC and RM 380Z-D microcomputers
at Southampton University and the Amstrad PC-1512.

**III. The Study Species:
Aspects Of General Biology, Morphology
And Populations**



CHAPTER THREE

THE STUDY SPECIES

ASPECTS OF GENERAL BIOLOGY, MORPHOLOGY AND POPULATIONS

3.1. Introduction

The smooth snake, as a component of the British herpetofauna, was introduced in Chapter One (section 1.1) where its classification and its distribution were discussed. In this chapter the morphology of the species is described, referring to data collected during the present study as well as the literature. The general biology, including annual cycles, longevity and breeding biology and the diet of the species is also outlined below and data on the population biology (size and structure) of the study populations is presented. Where data on lengths and weights (collected during this study) are presented, a single mean value for each parameter was calculated for each animal. These were then pooled for all sites and used collectively to describe the New Forest smooth snake population. This, however, meant that data for some animals incorporated information collected over more than one season and clearly a single value would necessarily omit any information on growth rates. Using a single value to represent each animal was regarded as being most useful for illustrating the range of 'typical sizes' of the animals found in the study populations. This was particularly so because there was a considerable amount of variation in the number of times each animal was captured and measured (with many animals only yielding a single set of measurements whilst one individual was measured 13 times and weighed 27 times during the study period). The exception to this method was the estimation of population age structures using snout to vent lengths to assess the age of each animal. These were calculated separately for each year in which the animal was captured (see Section 3.4.2).

3.2. General Description

Coronella austriaca is a fairly small snake with a slim, cylindrical body and a rather small head with a poorly defined neck. The species is characterised by having a distinctive, dark 'coronet' on the head and a dark stripe running usually from the nostrils, through the eye and backwards to the neck. The eye is small and golden, with a round pupil. The body coloration of the smooth snake varies from grey or brown to a reddish brown with darker spots, blotches or even bars along the back. The ventral scales are lighter but again variable, usually being a lighter shade of the dorsal colour. There appears to be no sexual dimorphism in coloration (Goddard 1981, Personal observation) despite Street's (1967) suggestion of slight differences between the sexes in this regard. The scales are without keels and their polished appearance and smoothness to the touch gives rise to the species' common name.

Adults are typically up to 600 mm in total length. The longest specimen recorded in Britain was a female measuring 725 mm (BHS 1985) although specimens of 830 mm and 920 mm have been recorded in Sweden and Russia respectively (Andren and Nilsen 1976). Total body lengths (TBL, i.e. the SVL and TL combined) of C. austriaca, including juveniles, recorded in the present study ranged from 135 mm to 677 mm with a mean value for all specimens captured being 466.0 mm \pm 118.7 (n= 123). The majority of animals captured were adults with TBLs between 450 mm and 575 mm (see Fig. 3.1). Sexual dimorphism in overall body length is a phenomenon described for many species of snake (e.g. Vipera berus (Prestt 1971), Acrochordus arafurae (Shine 1986)), but this has not been reported for C. austriaca. The data from the present study suggested no difference in the frequency distributions of size categories (total body length) between the two sexes (as illustrated in Fig. 3.1) when tested using a Kolmogorov-Smirnov two-sample test ($D=$ 0.1329, $n_1=$ 72, $n_2=$ 42). Mean values for TBL for male and

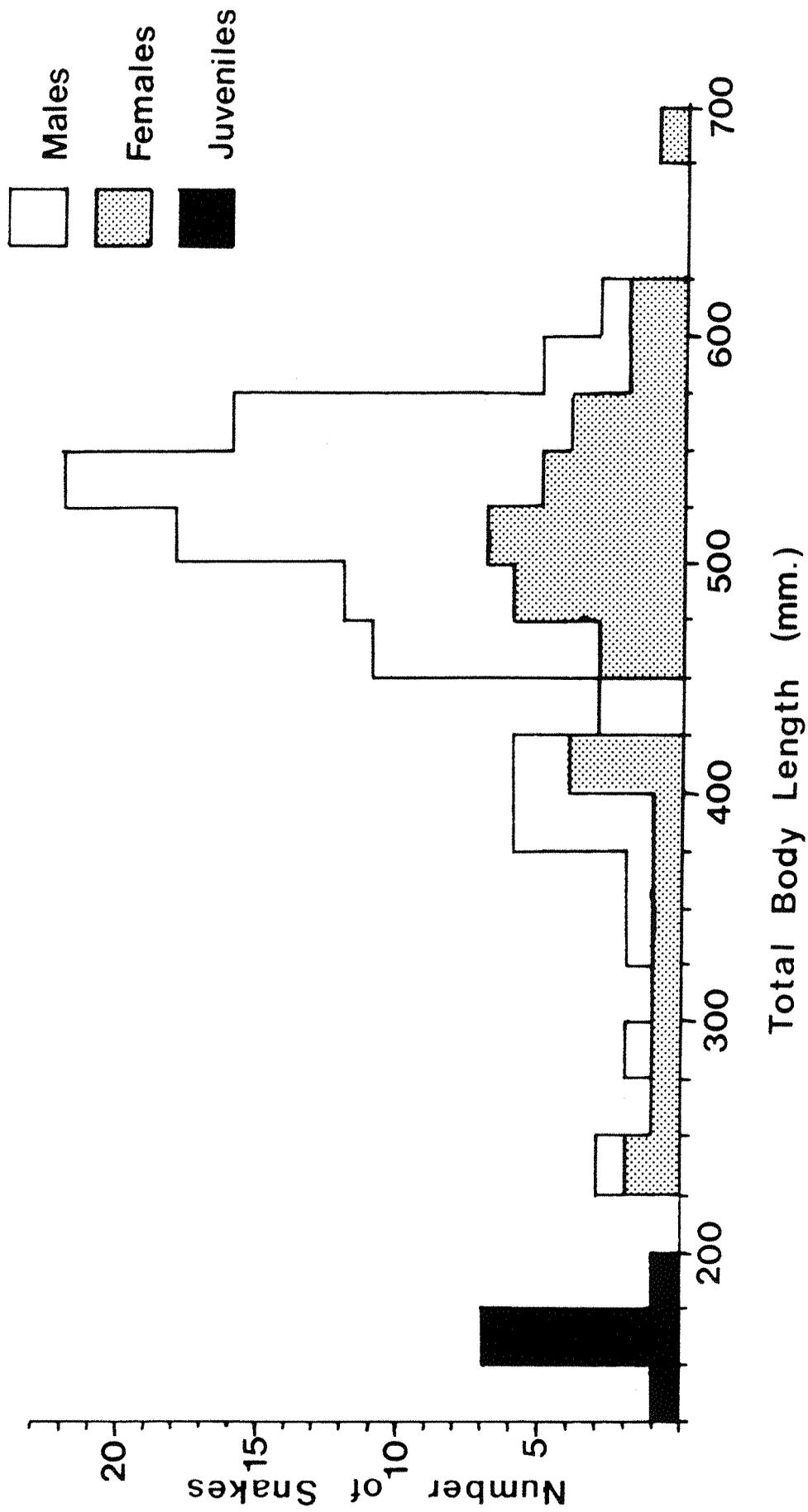


Fig. 3.1 : Mean Total Body Lengths of Specimens of *C. austriaca* captured on all sites during 1984 and 1986 inclusive. Males (n=72), females (n=42) and juveniles (n=9) are indicated by different shading.

female snakes were $497.6 \text{ mm} \pm 71.2$ ($n= 72$) and $476.8 \text{ mm} \pm 104.7$ ($n= 42$) respectively. The F_{max} test indicated heterogeneity of variances ($F_{max} = 2.158$, $p < 0.05$) and hence TBLs of male and female snakes were compared via the Mann-Whitney 'U' test. No significant difference was detected between the TBLs of the two sexes ($U = 1674.0$, $n_1 = 72$, $n_2 = 42$, $p > 0.05$).

Males, however, have longer tails relative to total body length than do females (see Fig. 3.2). The regression equations to describe these tail length (TL) against total body length (TBL) relationships are as follows :

$$\text{Males: TL} = 0.26 \text{ TBL} - 18.2$$

(and hence TL is approximately one quarter of TBL)

$$\text{Females: TL} = 0.17 \text{ TBL} + 3.3$$

(and hence TL is between one fifth and one sixth of TBL). Since TL is a component of TBL, direct comparison of the two regression lines is not statistically permissible. The ratio of TL/TBL was calculated as an index of relative tail length and this statistic compared between males and females using a t-test. This index of relative tail length is significantly different for each of the sexes ($t = 15.70$ with 112 d.f., $p < 0.001$). Males also have more subcaudal scales than females (usually in excess of 53, females usually having less than 54) (see Table 3.1 and Fig. 3.3). The mean number of subcaudal scales for male smooth snakes was 57.5 ± 2.36 and for females was 50.37 ± 2.59 (a t-test indicated this difference to be highly significant ($t = 14.83$ with 111 d.f., $p < 0.001$)).

Adult C. austriaca typically weigh between 40 and 50 g (Appleby 1971, Smith 1973, Arnold and Burton 1978). Mean body weights were calculated for each individual captured during the study period and these mean values ranged from 1.8 g to 83.3 g. The mean weight of all specimens captured was $36.2 \text{ g} \pm 17.98$ ($n = 123$) using data from juvenile and

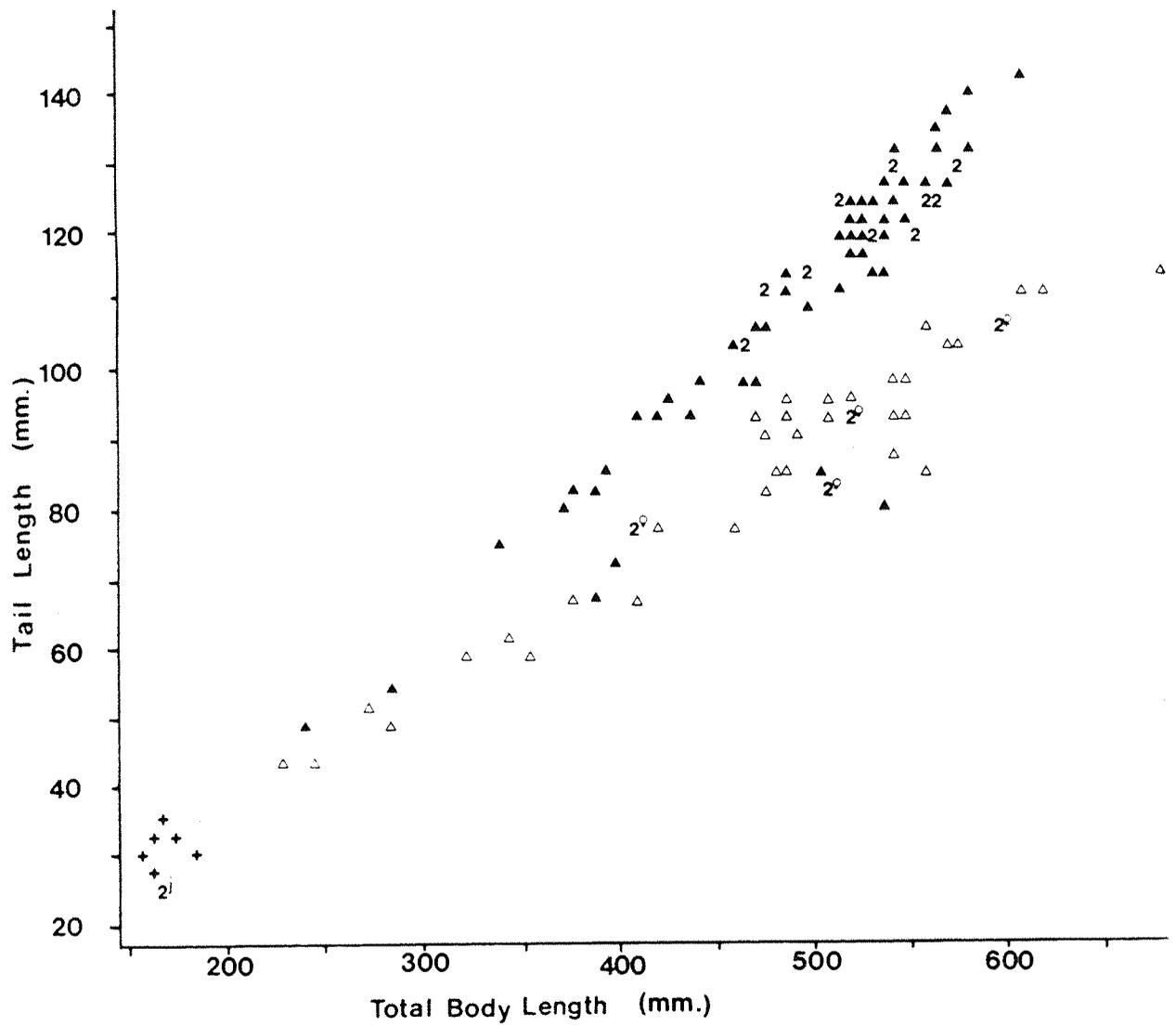


Fig. 3.2 : Relationship between Mean Tail Length and Mean Total Body Length of Male (closed triangles, n=72), Female (open triangles, n=42) and Juvenile (crosses, n=8) *C. austriaca* captured at all sites during 1984 and 1986 inclusive. Numbers indicate points where more than one sample occurs and represent males in all cases except where superscripted by ϕ (females) or j (juveniles).

<u>Study/source</u>	<u>Males</u>	<u>Females</u>
Smith (1951)	54 to 62	44 to 56
Breeds (1973)	51 to 64	42 to 57
Spellerberg and Phelps (1977)	50 to 66	44 to 56
Goddard (1981)	50 to 64	44 to 56
Present study (1984/86)	52 to 64	43 to 55

Table 3.1: Numbers of pairs of Subcaudal scales observed for the two sexes of C. austriaca. Data from present study taken from animals from all sites.

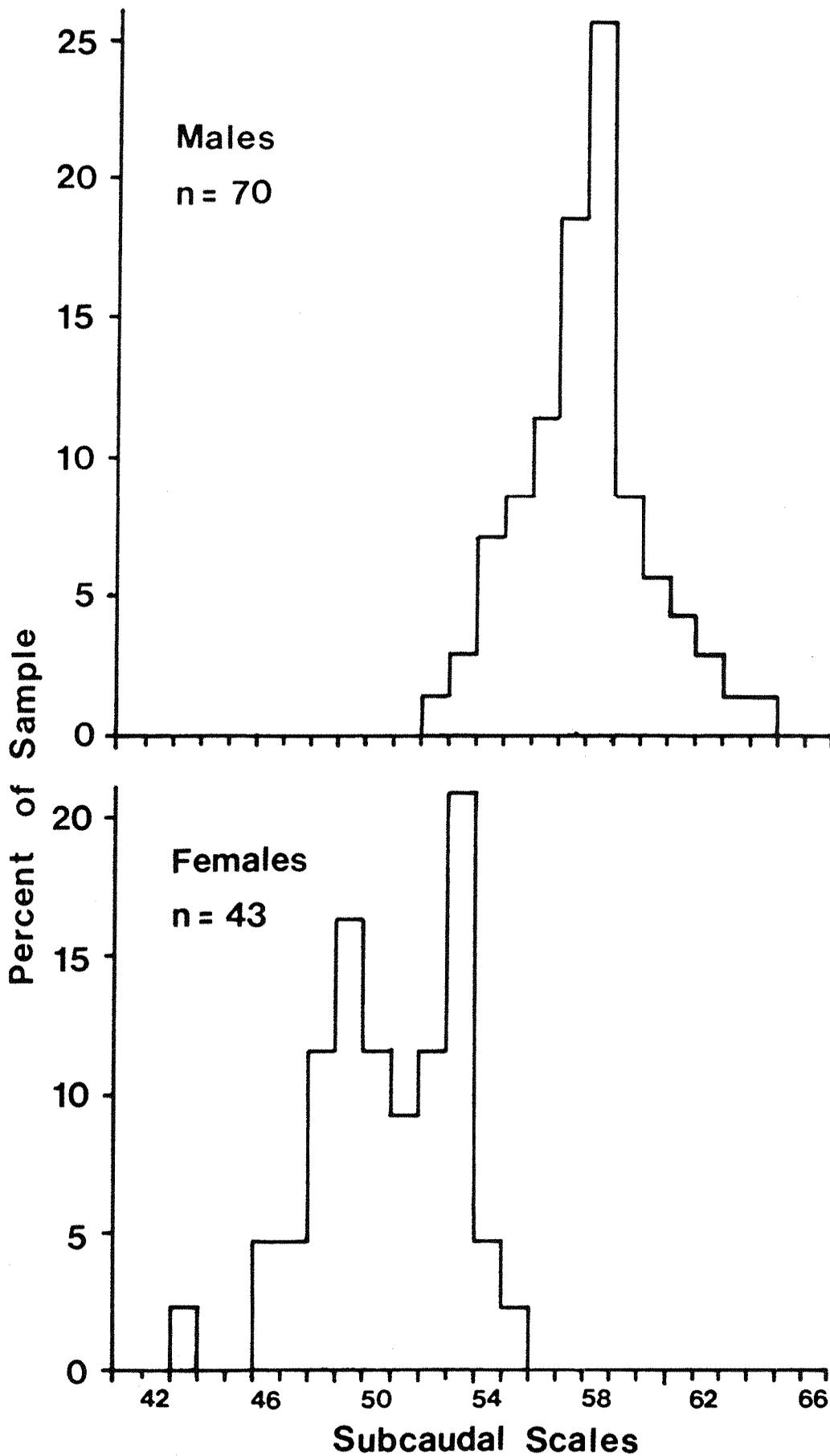


Fig. 3.3 : Number of Subcaudal Scales found on Male and Female *C. austriaca* captured on all sites during 1984 and 1986 inclusive.

adult specimens. The range of mean body weights observed is presented in Fig. 3.4 which illustrates that the majority of specimens captured were adults with a body weight in the region of 35 to 60 g. The mean body weight of female specimens was $40.5 \text{ g} \pm 20.46$ ($n= 41$), for male specimens $37.9 \text{ g} \pm 12.62$ ($n= 73$) and for juvenile specimens $2.5 \text{ g} \pm 0.49$ ($n= 9$). The body weights of male and female smooth snakes showed heterogeneity of variances ($F_{max} = 2.63$, $p>0.01$) and hence comparison between these required non-parametric analysis. No difference in weights were detected between the two sexes via the Mann-Whitney 'U' or Kolomogrov-Smirnov two-sample tests ($U= 1677.0$, $n_1 = 73$, $n_2 = 41$, $p>0.05$ and $D= 0.2028$, $n_1 = 73$, $n_2 = 41$, $P>0.05$ respectively), although the observation that the heavier snakes were female probably related to these specimens being pregnant. Weights of individual animals were, however, very variable throughout a season depending on the feeding condition of the animal and, in females, whether or not the snake was pregnant.

3.3. General biology

3.3.1. Seasonal activity and breeding biology

a. Overwintering

Many temperate species of reptile have a period of inactivity over winter that enables them to avoid the low temperatures associated with that time. The term 'brumation' has sometimes been employed to distinguish winter dormancy in ectotherms from hibernation displayed by endotherms. This terminology, however, but has not been universally accepted (Gregory 1982) and the term 'overwintering' shall be used in the present study to describe this period of inactivity. Several species of reptile have been shown to demonstrate changes in metabolism during winter dormancy (Al-Sadoon and Spellerberg 1985) indicating that this behaviour is not simply a period of torpor induced by low temperatures. Rather, overwintering behaviour entails physiological

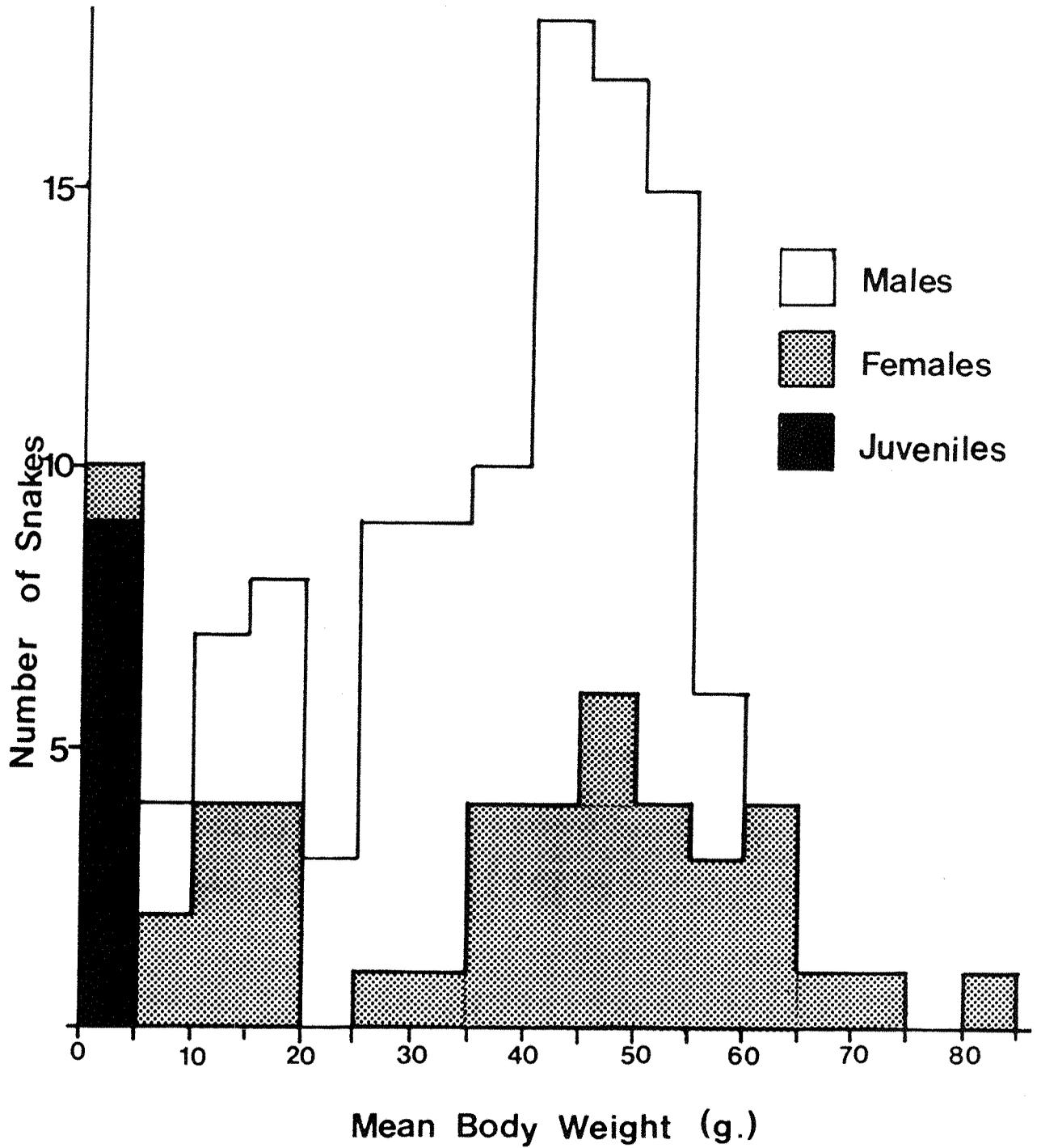


Fig. 3.4 : Mean Body Weight of specimens of *C. austriaca* captured at all site during 1984 and 1986 inclusive. Males (n=73), females (n=41) and juveniles (n=9) are indicated by different shading.

changes that permit reduced energy expenditure, hence favouring the survival of the animal during periods of inclement weather and food shortage.

C. austriaca undergoes such a period of winter dormancy, generally submerging during October and emerging again during March or April of the following year (Duguy 1961, Breeds 1973, Spellerberg and Phelps 1977, Goddard 1981). Goddard considered that air and soil temperatures were the most important environmental cues for determining the start and finish of overwintering and consequently the dates at which these occur will be governed by local weather conditions. Accurate determination of the period of overwintering in the field is not possible due to the secretive nature of the species. Goddard estimated submergence and emergence dates from the final captures of specimens in the Autumn and the initial capture dates of animals in the spring respectively. Although he cautioned the interpretation of these observations, in that the assumption that these dates are indicative of the cessation and onset of activity is somewhat tenuous, he justified the use of these data on the grounds that no more accurate method was available.

To further investigate overwintering behaviour, Goddard's (1981) method was extended to data collected during the present study. Final recapture dates of specimens of C. austriaca during September and October (hereafter referred to as Autumn) are presented in Tables 3.2 and 3.3. Final observations of both male and female C. austriaca occurred throughout the Autumn, with the final observations in 1984 being a female and a juvenile smooth snake on 25th October and a male smooth snake was the last specimen observed in 1985 on 21st October. Although sites were only visited infrequently after July 1986, two female smooth snakes were observed during the 'Autumn' of that year. These observations were on 4th September and 2nd October. In total three male, three female and four juvenile smooth snakes were observed in the month of October, pooling data for 1984, 1985 and 1986.

	<u>1984</u>	<u>1985</u>
Males	21st September 21st September 7th October 18th October	7th September 7th September 8th September 12th September 12th September 21st October
Females	11th September 25th October	3rd September 4th September 8th September 11th September 11th September 11th September 12th September 23rd September
Juveniles	21st September 18th October 18th October 25th October	23rd September 23rd September

Table 3.2: Dates of final capture of specimens of C. austriaca at Site One in Autumn.

	<u>1984</u>	<u>1985</u>
Males	2nd September 3rd September 6th September 8th September 8th September 29th September	11th September 17th September 19th September 20th September 23rd September
Females	3rd September 5th September 7th September 7th September 8th September 24th September 24th September 29th September	8th September 10th September 16th September 17th September 17th September 18th September 19th September 19th September 20th September 23rd September 25th September 10th October
Juveniles	28th September	16th October

Table 3.3: Dates of final capture of specimens of C. austriaca at Site Two in Autumn.

Kolmogorov-Smirnov two-sample tests were employed to investigate differences in submergence behaviour between the two sites and the two sexes. No differences were observed between the males on either site ($D=0.3$, $n_1=10$, $n_2=10$, $p>0.05$) nor between females on either site ($D=0.45$, $n_1=20$, $n_2=10$, $p>0.05$) and, as such, data from the two sites were pooled. The sampling technique also favoured pooling the data from the two sites in that effort was concentrated on each site in turn for distinct periods rather than visiting each alternately with only a short time interval between each visit. Combined data from the two sites indicate that there was no significant difference in the submergence dates of the two sexes (1984: $D=0.1$, $n_1=10$, $n_2=10$, $p>0.05$; 1985: $D=0.15$, $n_1=20$, $n_2=10$, $p>0.05$; 1984 and 1985: $D=0.1$, $n_1=30$, $n_2=20$, $p>0.05$). Goddard (1981), however, suggested that female *C. austriaca* delayed entry into overwintering until later in the year than males, the former still being active well into October whereas the latter tended to submerge in September. He proposed that this difference was related to viviparity in the species. Gravid females would have to remain active later in the year to give birth to their young prior to overwintering. Further, post-partum females may have to forage to replenish their reserves in order to survive the winter. Spellerberg and Phelps (1977), however, suggested that some females may retain their embryos over winter and give birth the following Spring.

Overwintering sites are likely to be cracks, crevices and burrows in the ground and along embankments, and also in hedges or vegetation of similar structure, (Duguay 1961, Spellerberg and Phelps 1977, Goddard 1981) that would allow a seepage of water but that would not be susceptible to waterlogging. Rollinat (*in* Duguay 1961) noted that smooth snakes that overwintered in moister conditions demonstrated a considerably higher survival than those that occupied areas that were too dry.

Many cool temperate species of snake overwinter in large

aggregations, with many individuals migrating to, and overwintering in, a single communal 'hibernacula' (e.g. Vipera berus (Prestit 1971), Thamnophis sirtalis parietalis (Aleksiuk 1976), Coluber constrictor (Brown and Parker 1976), Elaphe obsoleta (Sexton and Hunt 1980), Crotalis viridis viridis (Duval et al 1985)). C. austriaca does not generally exhibit this aggregation behaviour nor do they tend to migrate to distinct winter ranges, as reported for the other species of British snake (Prestit 1971, Spellerberg and Phelps 1977, Phelps 1978, Goddard 1981, Madsen 1984). Several reports of communal overwintering, however, have been published. Spellerberg and Phelps (1977) discovered a clump of bog myrtle, Myrica gale, (about 1 m across) being used by several males and Corbett (in NCC 1983) reported over 60 individuals using the foundations, drains and walls of an area of disused Nissen huts (the size of the area covered by these buildings was not, however, reported).

b. Emergence from overwintering

Although specimens have been recorded as early as 20th February (Spellerberg and Phelps 1977) and 27th February (Goddard 1981), most C. austriaca emerge from overwintering during late March and April (Breeds 1973, Spellerberg and Phelps 1977, Goddard 1981). Emergence dates, defined as the first sighting of each individual in March and April (hereafter referred to as Spring) (as Goddard 1981), at Sites One and Two during the present study are given in Tables 3.4 and 3.5 respectively. Where no captures for a particular group occurred during the Spring period the earliest date of capture are furnished in square parentheses. These latter data were, however, not included for statistical analyses. Data were too few to permit statistical analyses between sites or between years and hence combined observations from each were employed to investigate differences in emergence dates between the sexes, using a Kolmogorov-Smirnov two-sample test.

Specimens of C. austriaca were first observed during late

	<u>1984</u>	<u>1985</u>	<u>1986</u>
Males	11th April	2nd April	[2nd May]
	11th April	6th April	
	11th April	18th April	
	20th April	18th April	
	20th April	24th April	
Females	11th April	6th April	31st March
			28th April

Table 3.4: Dates of initial capture of specimens of C. austriaca at Site One in Spring. Where no observations were made in Spring dates of earliest capture are presented in square parentheses.

	<u>1984</u>	<u>1985</u>	<u>1986</u>
Males	[18th June]	20th April	24th April 28th April
Females	[5th June]	[6th May]	[20th July]

Table 3.5: Dates of initial capture of specimens of C. austriaca at Site Two in Spring. Where no observations were made in Spring dates of earliest capture are presented in square parentheses.

March and early April, with the earliest record being a female on 31st March (1986). The earliest records in 1984 were three males and one female on 11th April and in 1985 one male and one female were observed on 6th April. The earliest sighting of a male snake in 1986 was 24th April. No significant difference in emergence times between the sexes was indicated by the results from the present study ($D= 0.37$, $n_1=4$, $n_2=13$, $p>0.05$), although this may be simply a reflection of the small sample sizes encountered through less intensive sampling over this period. Duguay (1961) indicated that males emerged from hibernation earlier than females in the population studied by Rollinat in central France and, similarly, Phelps' (1978) study revealed that males were the first specimens to be captured in each of the four years of his study at two sites in Dorset. In the latter study females were first observed a few days later. Goddard (1981), however, suggested that there were no differences in emergence dates between the sexes. All studies are in agreement that most specimens emerge during late March and April.

c. Activity period

After emergence from overwintering, smooth snakes undergo a period of basking, during which time they apparently do not feed. This period is likely to be associated with the maturation of the gonads (Duguay 1961). Courtship and mating occur early in the year with males probably seeking out and following receptive females by smell. Although not territorial, males may guard female snakes from other males during this time. Observations of mating are rare, with Breeds (1973) being the only worker in Britain to have reported seeing mating in the wild. Goddard provided evidence of Spring mating by looking for the presence of spermatozoa in the cloaca of female snakes. He thus showed that females had been mated between April and June inclusive. Bont et al (1986) observed mating between two radio-tagged snakes during mid-May in the Netherlands and Rollinat (in Duguay 1961) reported mating between mid-March and early April in France. Rollinat (in Duguay 1961) and

Street (1967), however, reported instances of Autumn mating by snakes in outdoor vivaria. Whether this latter phenomenon occurs in the wild is not known.

As the season progresses daily activity commences earlier (Bont et al 1986), this being associated with the increasing day length and higher day time temperatures. Smooth snakes feed through out the activity period, from mid- to late April and into September or October, although most feeding seems to occur in June (Duguy 1961). The first moult occurs late in April and, subject to suitable weather conditions and ample food, a smooth snake may shed its skin as often as once per month up until the end of August, although snakes more usually molt only two or three times per season (Spellerberg and Phelps 1977).

Smooth snakes give birth to live young, with litter sizes varying between one and 16 (various sources in NCC 1983), during September and October. Estimates of dates of birth can be made from data collected during the present study, where females were captured in a gravid condition and subsequently caught after having given birth. Four such records were obtained. One snake gave birth between 11th and 18th October, a second between 8th and 24th September and a third between 29th August and 7th September. This latter record is particularly interesting as the animal was attached with a radio-transmitter during that time. It was highly likely that this animal gave birth between 3rd and 5th September whilst below ground as a new born snake was captured very nearby on the 5th. A fourth snake was gravid on 27th August and recaptured post-partum on 16th September. Other snakes were last recaptured still pregnant in September and October, with the latest record of a gravid animal being 16th October.

Activity decreases throughout late September and October as the weather becomes cooler and smooth snakes start to enter into their winter retreats. Prior to overwintering snakes will regurgitate any food in their gut which would otherwise decompose inside them over the winter (Duguy

1961).

3.3.2. Diet

The diet of the smooth snake is primarily small vertebrates, particularly lizards (Lacerta spp., Anguis fragilis), small mammals (e.g. Sorex spp.) and the young of small mammals (e.g. Apodemus spp., Clethrionomys glareolus). A wide variety of vertebrate (and possibly invertebrate (O.P. Cambridge, in Smith 1973) prey are taken (Corbett, in NCC 1983). There is some debate about the relative importance of each prey taxon, as earlier workers stressed the importance of reptilian prey, particularly the sand lizard L. agilis, (Duguy 1961, Smith 1973, Andren and Nilsen 1976) whilst Spellerberg and Phelps (1977) and Goddard (1981) suggested that mammalian prey items are predominant in the diet. Goddard resolves this difference of opinion by suggesting that the species is an opportunist and that the prey capture frequency would be dependent on the relative abundance of each prey species within the environment. Both Spellerberg (1977) and Goddard (1981), however, suggest that juvenile C. austriaca demonstrate an innate feeding preference for lizards and propose that this could be related to the risks involved of a small snake attempting to feed on mammals.

The diet of C. austriaca was not investigated as part of this study and no forced regurgitations of food items have been attempted. Two specimens did regurgitate upon capture, however; one yielding two shrews (Sorex sp.), the other the tail of a slow worm (Anguis fragilis).

3.4. Population size and structure

3.4.1. Population size and sex ratio

The total numbers of C. austriaca captured on Sites One and Two and Four to Seven from April 1984 to September 1986 are presented in Table 3.6. No snakes were captured at Sites Eight, Nine or Ten. Data are presented separately for each

<u>Site</u>	<u>Male</u>	<u>Female</u>	<u>Juvenile</u>	<u>Total</u>
Site One	30	16	6	52
Site Two	33	23	3	59
Site Four	6	3	0	9
Site Five	2	0	0	2
Site Six	0	1	0	1
<u>Site Seven</u>	<u>1</u>	<u>1</u>	<u>0</u>	<u>2</u>
Total	72	44	9	125

Table 3.6: Total Number of male, female and unsexed juvenile C. austriaca captured on Sites One and Two and Four to Seven inclusive, April 1984 to October 1986 (Site Three was incorporated as part of Site One).

site and adult and sub-adult snakes (i.e. second year and older) are further subdivided by sex. Juveniles (i.e. new born individuals), for whom reliable sexing was difficult, are presented as a single category. Deviations from an expected equal sex structure were investigated using a G-test.

There were significantly more male C. austriaca captured at Site One than female specimens ($G = 4.329$, 1 d.f., $p < 0.05$) during 1984 to 1986, suggesting an uneven sex ratio there. There was no significant departure from an even sex ratio at Sites Two or Four ($G = 1.795$ and 1.019 respectively, 1 d.f., $p > 0.05$). Data were too few to allow G-tests to be employed on Sites Five to Seven. When the data for all seven sites were pooled however a significant difference was detected ($G = 6.797$, 1 d.f., $p < 0.01$). Goddard (1981) reported even sex ratios on his Sites One, Two and Three. Spellerberg and Phelps (1977), however, suggested evidence existed for an uneven sex ratio caused by a reduction in numbers of female snakes in some populations.

3.4.2. Population age structure

An approximation to age can be derived from snout to vent length measurements (Goddard 1981) and this relationship has been employed to describe the age structure of the populations on Sites One and Two. Using a combination of Goddard's (1981) Figures 4.10 and 4.11, SVLs were grouped to give ten different age classes as follows : SVLs less than 220 mm were classed as being in their first year (1 year), 220 to 300 mm were in their second year (2 years), 300 to 380 mm were in their third year (3 years), 380 to 415 mm were in their fourth year (4 years), 415 to 425 mm were in their fifth year (5 years), 425 to 435 mm were in their sixth year (6 years), 435 to 446 mm were in their seventh year (7 years), 446 to 459 mm were in their eighth year (8 years), 459 to 461 mm were in their ninth year (9 years) and those with SVLs of 461 mm or more were classed as being in their tenth or more year (>10 years). Mean values of SVL were calculated for each year an animal was

captured and these values used to assign each snake to the appropriate age category. The data are presented separately for each site (see Figs. 3.5 and 3.6 for Sites One and Two respectively) and the frequency of each sex in each age category is shown. No significant differences were detected between the population age structures of male and female snakes in any of the three years at either of the sites using a Kolmogorov-Smirnov Two-sample test ($D = 0.267$, $n_1 = 15$, $n_2 = 5$, $D = 0.400$, $n_1 = 15$, $n_2 = 10$, $D = 0.667$, $n_1 = 9$, $n_2 = 6$ for 1984 to 1986 inclusive at Site One and $D = 0.300$, $n_1 = 12$, $n_2 = 10$, $D = 0.283$, $n_1 = 24$, $n_2 = 15$, $D = 0.388$, $n_1 = 9$, $n_2 = 4$ for 1984 to 1986 inclusive at Site Two, $p > 0.05$ in all cases). Although age classes between 3 and 4 years yielded the largest number of captures during the present study, there appeared to be no single dominant age groups within the population with most age classes yielding comparable, low numbers of animals.

The observed frequency distributions of age categories are similar to those reported by Goddard when compared by eye in that he too captured small numbers of snakes in the majority of age classes with no single age group being noticeably dominant. Such discrimination, however, is necessarily very subjective when dealing with small sample sizes. Population age structures were not statistically compared between Goddard's work and the present study as it is likely that the SVLs used to calculate each age category differed slightly between the studies, particularly for older animals where the Age against SVL relationship approaches an asymptote (and thus the range of SVLs for a given age class become very narrow).

Survival of juvenile smooth snakes is believed to be low since these specimens are rarely captured in the wild (Breeds 1973, Spellerberg and Phelps 1977, Goddard 1981) and this assumed high rate of juvenile mortality is believed to be offset by the longevity of the species. Specimens that were assumed to be over ten years old were captured during the present study and during previous research (e.g. Goddard 1981) and Wheeler (1981 in NCC 1983)

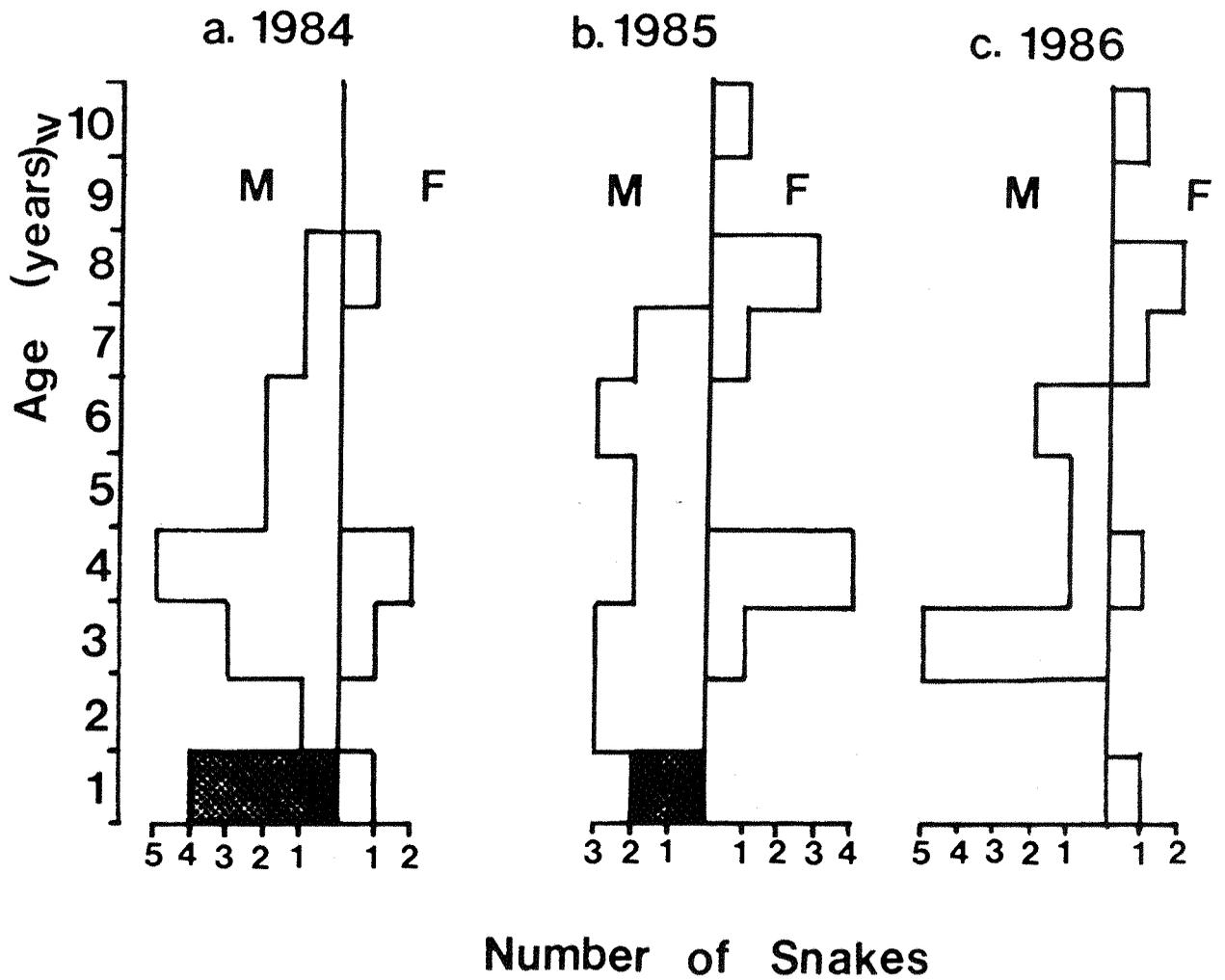


Fig. 3.5 : Population Age Structure of *C. austriaca* at Site
 One for Male (M), Female (F) and Unsexed Juvenile
 (dark shading) Specimens during a) 1984, b) 1985 and c) 1986.

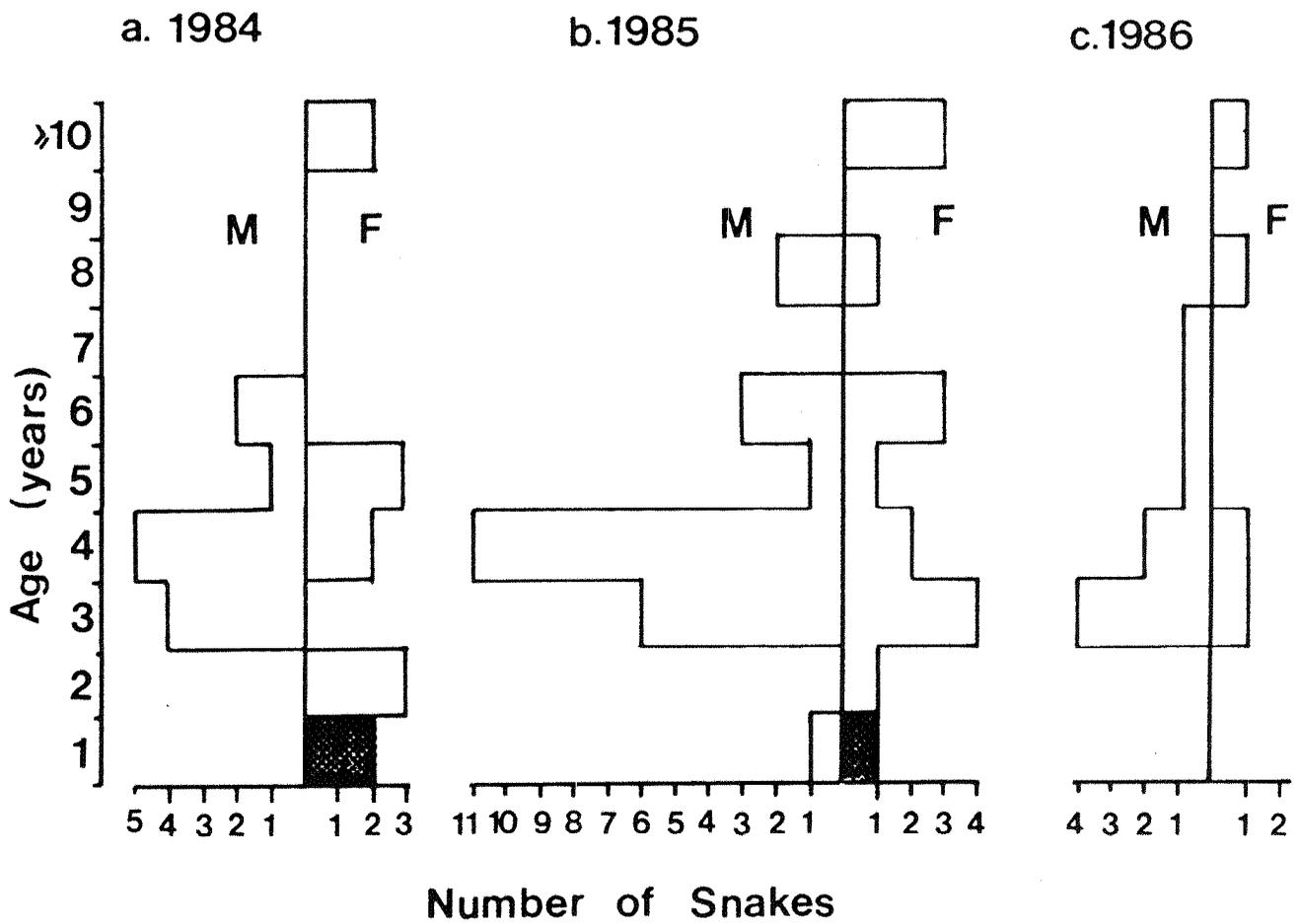


Fig. 3.6 : Population Age Structure of *C. austriaca* at Site
 Two for Male (M), Female (F), and Unsexed Juvenile
 (dark shading) Specimens during a) 1984, b) 1985 and c) 1986.

reports of 3 animals originally marked as adults (and hence over 4 years old at first capture) surviving for at least 19 years and a further specimen for a minimum of 18 years. Goddard however cautions the assumption that high levels of mortality necessarily occur amongst juveniles in that their recapture rate may not reflect their true abundance.

It is likely that smooth snakes fall prey to a variety of terrestrial and avian predators, e.g. foxes Vulpes vulpes, domestic cats Felis domesticus, hedgehogs Erinaceus europaeus buzzards Buteo buteo, kestrels Falco tinnuculus; although little is known about the effect of predators on smooth snakes these animals are known to take other species of snakes and other reptiles (e.g. G.J.M. Hirons pers. comm., Tubbs 1986). Smooth snakes are also likely to be taken by other snakes and, indeed, are cannibalistic (NCC 1983). Although the smooth snake is protected throughout much of Europe (Groombridge 1986) the deliberate killing of C. austriaca but has been reported by several workers in Britain (NCC 1983, BHS pers. comm.) and abroad (e.g. Duguy 1961, Andren and Nilsen 1976, Stumpel 1980). Periods of cold weather may also cause mortality amongst smooth snakes and Spellerberg and Phelps (1977) report of several specimens found dead after unusually cold night early in the year and it is quite probable that many animals, particularly young specimens, succumb during hibernation.

Four dead animals were found during the present study: one appeared to have been attacked (probably by a bird of prey), two had been trampled (one possibly by a human, since it was found where it had probably been basking at the edge of a path, the second by a pony). The fourth specimen had been killed by traffic on a major road (M. Noble pers. comm.). This latter cause of mortality has also been observed elsewhere, e.g. Andren and Nilsen (1976).

3.4.3. Population densities

Population densities at each site can be estimated by dividing the total number of individuals captured by the

total area searched, but this will be subject to a great many inaccuracies (Turner 1977, Spellerberg and Phelps 1977, Goddard 1981, 1984). The total number of snakes recorded in an area at any one time is almost certainly a gross underestimate of the number of animals there, particularly with such a secretive species as C. austriaca, and Turner (1977) estimated that only 40% of the population in any area were available for direct enumeration. Summation of all observations over a long period of time to estimate population size would require the assumption that the species is either fairly immobile or that the study area represents the total range of all individuals within that area. Movement of individuals between the study sites and adjacent sites may cause an over estimate of population density to be obtained, particularly if the species concerned is highly mobile. Expression of density as population per unit area further requires that the study area (used as the denominator in the calculation) should be searched with constant effort and efficiency. In practice search effort was not consistent over the whole study area, with some areas being rigorously searched and frequently visited whilst others were only superficially searched or visited only occasionally. This was partially a consequence of the emphasis placed on radio-tracking as a method of study, this committing effort to areas where the radio-tagged animals were, and also meant that large areas of habitat that was difficult to search systematically (e.g. bog) became incorporated in the study area that would otherwise have been excluded. Uneven search effort was also unavoidable due to differences in the ease of observation and sampling resulting from differences in ground vegetation throughout the study sites. Certain parts of the sites yielded more animals than others whilst some yielded no animals at all and hence it appeared that the density of animals was not uniform throughout the sites. Thus any single estimate of density for a given site will clearly be only an average statistic and will yield underestimates for certain areas whilst grossly overestimating the density in others.

Defining boundaries to the 'study sites' was necessarily somewhat arbitrary, as was the calculation of areas within those sites that were not sampled and, as such, excluded. Calculation of area searched was done by tracing the areas of each site that were sampled from a 1:10000 map. These tracings were photocopied and the areas cut out and weighed. These were compared against a known 'area' of photocopy paper and areas estimated to the nearest 1 ha.

The time spent searching each site should be included in any estimation of density where comparisons between sites are considered. A site that is visited on only a few occasions would be expected to yield a smaller total of animals than a frequently visited area, even if this did not truly represent the density on each site. Therefore as a comparative index of density a figure of population per unit area (ha) per hour's searching may provide the most useful statistic. No record of time spent searching at each site was recorded however, this largely being due to the emphasis placed on radio-tracking as a sampling method. Repeated radio-location of an individual animal meant that time and effort was concentrated on this task and hence visual searching was interrupted. Not only did this reduce the efficiency of visual location (although it was still possible to find other specimens) it also caused an uneven search effort. Thus either to include or exclude radio-location periods in the total time spent searching to give an estimate of capture rate of C. austriaca would be misleading. As such no estimates of capture rate have been calculated.

Notwithstanding the above inaccuracies, densities at Sites One, Two and Four were calculated - expressing the total populations captured as a fraction of the approximate total area searched. Care must be taken in comparisons between sites as Site Four was visited only during the 1985 and 1986 field seasons. Densities at Sites One, Two and Four were 1.89, 1.46 and 0.17 snakes per hectare respectively, (see Table 3.7) suggesting that C. austriaca occur in rather low densities.

Site	Total population size (n)	Approximate total area searched (ha)	Density (n/ha)
Site One	52	27	1.93
Site Two	59	40	1.48
Site Four	9	17	0.53

Table 3.7: Densities of C. austriaca on Sites One and Two (1984 to 1986) and Site Four (1985 and 1986) (Site Three was incorporated as part of Site One).

Previous estimates of smooth snake densities have been given by Spellerberg and Phelps (1977) and Goddard (1981). These densities were highly variable: Spellerberg and Phelps describing low, medium and high density populations of 11, 13 and 17 individuals per hectare respectively. Goddard's estimates for his Sites One, Two and Three were 0.92, 1.99 and 53.33 individuals per hectare.

3.4.4. Estimates of national population size

Several estimates of total populations of C. austriaca have been published, but these are largely anecdotal and are subject to controversy. Prestt et al (1974) estimated a total population of between 1000-3000 adults. The BHS (in NCC 1983) suggested a total population in the region of 2000 individuals and this figure seems now to be accepted by the relevant governmental and conservation bodies. A recent estimate was quoted as being about 8000 individuals (BBC TV 1986 'Living Isles' series). Spellerberg and Phelps (1977) and Goddard (1981) disputed the earlier estimate of Prestt et al, and subsequently (Goddard 1984, Spellerberg 1985) the BHS's figure.

Goddard (1984) proposed an alternative approach to assessing total smooth snake population size by multiplying density figures, obtained from his research, by the total area of habitat likely to be occupied by C. austriaca, for which he used Bibby's (1976) estimate of unburnt, dry heathland area in central Southern England (26,656 ha). Using data from his Sites One and Two (he excluded his Site Three for sampling reasons), he estimated a population size of between 26,656 and 53,312 snakes. Goddard does caution, however, that C. austriaca may not be found in all areas of heathland.

Extending Goddard's method to the results obtained at Sites One and Two in this present study, and using Bibby's estimate of heathland area, yields an estimate of C. austriaca population size in Britain as being between

39,451 and 51,446 animals. Only densities obtained from Sites One and Two were used to calculate these estimates as these areas were the most thoroughly and consistently sampled. (Inclusion of data from Site Four yields a more conservative estimate of 14,127 animals). Although all areas of dry heathland might not be occupied by C. austriaca it is worth mentioning that specimens were located in other habitat types including grassland, bracken, wet heathland and bog and perhaps the areas of suitable habitat should be extended and hence would yield even higher population estimates. Whilst the above method provides an objective method for assessing smooth snake population size, the numbers so obtained are probably considerable overestimates. Density figures at Sites One and Two are likely to be considerably higher than average densities that would occur throughout the southern heathlands since both areas were known to possess good populations of C. austriaca during the study period.

However, once the distribution of C. austriaca in Britain has been accurately established, and the habitat types that are used within this range defined then this method may perhaps be more usefully employed. A realistic and objective estimate of population size could then possibly be obtained.

3.5. Frequency of recapture during the present study

The frequency of recapture of a known individual smooth snake and the length of time over which it is encountered can yield useful information about the movement behaviour and home range of that animal. An animal that is encountered within a study area both frequently and over a long period of time is likely to be resident and have a home range that is mostly within that study area. Conversely an animal that is only encountered on a single occasion or over on a very short period of time, despite regular visits to a site, is likely to occupy a range that is not entirely within the study area or possibly indicate that that animal is not resident to that site and is merely

passing through the area. The proportion of each of these extreme cases found within the study populations can be used to suggest whether the species as a whole tend to be relatively sedentary and occupy small home ranges or whether they disperse over much larger areas. Clearly, with such a secretive species as C. austriaca the apparent absence of an individual at any one time does not necessarily imply that it has moved away, however frequent site visits would probably yield a fair proportion of the animals in an area over a protracted period of time and hence resident animals would be expected to be captured on more than one occasion.

Two methods of investigating recapture rates of C. austriaca were undertaken and both were limited to Sites One and Two as these were regularly sampled over three years. The first of these methods assesses the range use of individuals by observing the number of years in which each was observed; animals that remain within any one area would be expected to occur during all three years of the study whereas animals that move off of the site would be likely to be encountered in only one year. Although most areas of Sites One and Two were searched throughout the three year period, part of Site One was only searched during the latter two years of the study. Thus 14 of the study animals (7 males and 7 females) could only have been encountered for a maximum of two years. Of these only one specimen, a male, was found in more than one year. Juveniles, by definition, could only be found in two years at most (thereafter they ceased to be classified as Juvenile), although as no subsequent captures were made of animals that were originally captured as juveniles this problem of definition presented no complications in the analysis. The encounter rates were similar at each of the sites and for each sex within the sites in that similar proportions were captured in one, two and three years in all cases. The majority of smooth snakes were only captured in one year, this accounting for 81 (73.0%) of the 111 snakes found at the two sites. 25 (22.5%) animals were found in two years and only 5 (4.5%) were observed in all three years of the

study (see Table 3.8) which indicates that the majority of animals move away from the study areas and hence any estimates of home range are likely to be an underestimate in these cases.

The total number of times each individual was captured by hand was also determined. This statistic is also useful for assessing site fidelity in that resident animals would not only be captured over longer periods of time but would also be encountered more frequently. The number of times in which an animal was captured is presented, separately for each site, in Fig. 3.7. Most specimens of C. austriaca (25 (48.1%) at Site One and 28 (47.5%) at Site Two) were only encountered once during the present study. A further 4 (7.6%) and 8 (13.6%) animals were recorded only two times at Sites One and Two respectively and hence estimates for home ranges areas, where a minimum of three sightings are required, could not be obtained in 29 (55.7%) and 36 (61.0%) cases except where these visual locations were backed up with radio-tracking data. Further these observations illustrate the usefulness of radio-tracking as a method of studying these secretive animals. Movement data could not be derived from animals that were located only infrequently and estimates of home range would be unobtainable in the majority of cases, particularly if the Rose's (1982) recommendation of requiring 18 or more sightings to yield reliable home range estimates is adhered to.

		<u>One Year</u>	<u>Two Years</u>	<u>Three Years</u>
Site One	Male	21	9	0
	Female	12	2	2
	Juvenile	6	-	-
	Total	39	11	2
Site Two	Male	22	8	2
	Female	17	6	1
	Juvenile	3	-	-
	Total	42	14	3
Total		81	25	5

Table 3.8 : Number of snakes captured in one, two and three years at Sites One and Two during the present study for male, female and juvenile specimens of C. austriaca.

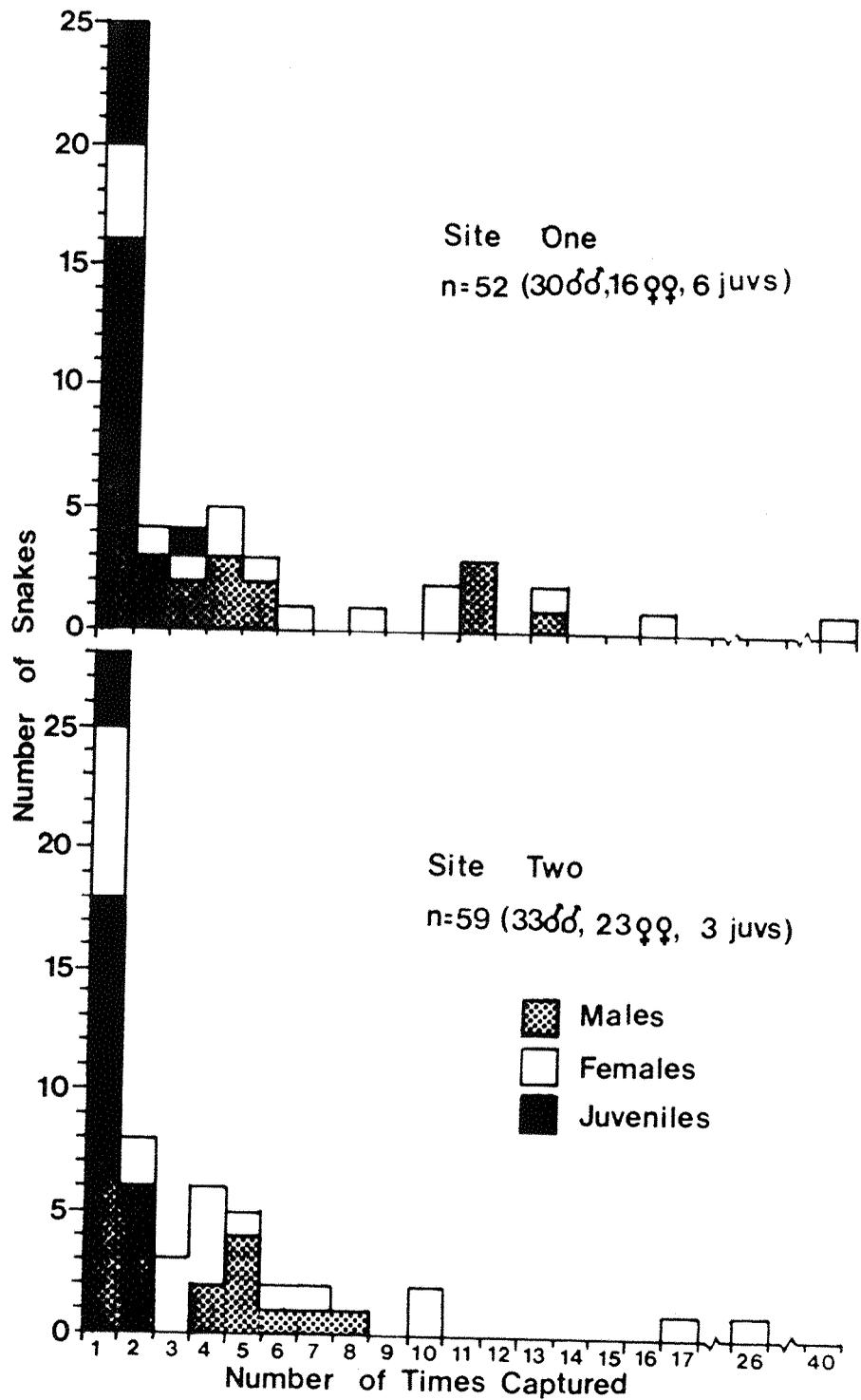
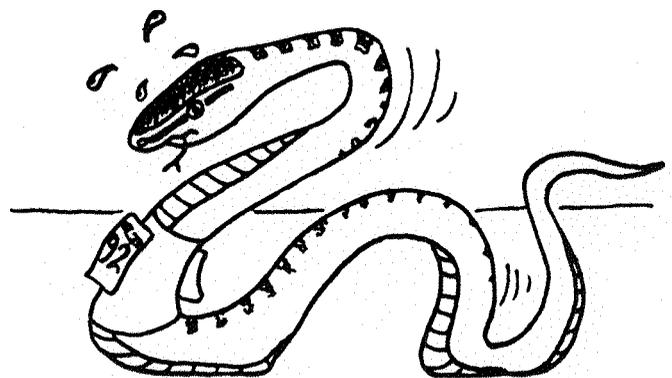


Fig. 3.7 : Number of Times each Animal was Captured by Hand at Sites One and Two during 1984 and 1986 inclusive.

IV. Movement Biology I: Movement Behaviour And Activity Patterns



CHAPTER FOUR

MOVEMENT BIOLOGY I

MOVEMENT BEHAVIOUR AND ACTIVITY PATTERNS

4.1. Introduction

Many studies of the movement behaviour of snakes have been published (e.g. Stickel and Cope 1947, Carpenter 1952, Freedman and Catling 1979), however, compared with other vertebrate taxa, the spatial ecology of the Ophidia is relatively poorly understood (Tiebout and Cary 1987). Snakes are generally secretive animals and the difficulty in being able to relocate individuals consistently has traditionally caused problems. These problems have been classified as 'site bias', where a snake is active but not on the sample transect, and 'technique bias', where an animal may be active but not visible (Cooke 1983 in Tiebout and Cary 1987). Latterly, the advent of small radio-transmitters has meant that many studies are using radio-telemetry as a means of investigating this aspect of snake biology (e.g. Fitch and Shirer 1971, Brown and Parker 1976, Henderson et al 1976, Shine 1979, Reinhert et al 1984, Madsen 1984, Shine and Lambeck 1985, Tiebout and Cary 1987).

The spatial ecology of an animal includes two broad, but closely related aspects of the biology of that animal - namely the movement activity and the way in which it uses its range. Much work has been dedicated to the latter aspect, particularly with regard to home range size and shape and the habitat use within that range; this aspect is investigated and discussed in the next chapter (Chapter 5). In this chapter the movement activity of C. austriaca is investigated by looking at movement rate ('vagility') and activity patterns. Both hourly and daily movement rates were studied, these allowing information on short and longer term dispersal potential to be collected and these were related to extrinsic (e.g. weather) and intrinsic

(e.g. individual condition) factors where appropriate.

Movement activity can be associated with a wide range of behaviour including foraging, searching for mates, site selection for thermoregulation and to avoid extremes of temperature and hibernation. Of these activities the most pronounced movements are associated with movement between summer ranges and overwintering sites, which has been reported for many species of snake (see Brown and Parker 1976) including V. berus in southern Britain (Prestt 1971).

Coronella austriaca is generally regarded as being a relatively sedentary species (Breeds 1973, Spellerberg and Phelps 1977, Goddard 1981, NCC 1983) and is therefore believed to have only a limited potential for dispersal and for colonising new areas. Smooth snakes, additionally, appear not to occupy separate summer and winter ranges (Phelps 1978) and hence would not be expected to show seasonal migration.

Previous research on the smooth snake has, however, been based on recapture experiments, which, due to the secretive nature of the species, do not allow detailed studies of movement behaviour. During the present study, radio-transmitters were attached to smooth snakes which enabled regular and frequent locations of each study animal to be made. Consequently, short term movement behaviour was able to be studied in more detail than had previously been possible. Regular locations also permitted a more systematic study of the behaviour and activity patterns of the species in the wild. In addition laboratory studies, using time-lapse video recording, were undertaken. This latter approach provided additional information about movement rates and activity patterns to supplement the observations made in the field.

4.2. Methods and Materials

4.2.1. Movement behaviour

To allow intensive study periods, and at the same time minimise disturbance to the animal, the movement behaviour of *C. austriaca* was investigated by radio-telemetry. Details of the methodology are given in Chapter 2 (section 2.2.3.). A total of 229.08 days of radio-tracking data were collected in 50 separate periods, each lasting between 0.07 and 9.71 days (mean = 4.60 ± 2.84 days, $n = 50$) between April 1984 and July 1986 (26 of these periods were in 1984, 18 in 1985 and six in 1986). Thirty nine different individuals were radio-tagged (24 males and 15 females) during the three field seasons. Most animals were only radio-tracked on one occasion although seven were radio-tracked twice (four males, three females) and two were radio-tracked on three occasions (both males).

In six cases transmitters were shed by the snakes and in only one of these was the study animal recaptured and fitted with a new transmitter. With the exception of those instances where the transmitter was shed by the study animal, all snakes fitted with transmitters were subsequently recaptured and the transmitter removed; this included all instances where the transmitter ceased to function whilst attached (four occasions). On ten occasions snakes with transmitters became snagged on vegetation or below ground. Although on three of these occasions the animal was freed and the study period continued, seven experiments were consequentially halted. Six cases where the transmitters were shed (3), snagged below ground (2) or ceased to function and yielded less than one day's data have been included in the above total and used in the analysis.

The distance between successive locations of each snake (the Minimum monitored distance) and the bearing of the direction of travel were calculated. For each time interval

where sequential records occurred in the same day (e.g. not overnight), and were separated by an interval of between one and three hours, an hourly rate of movement was calculated, as were the mean shade air and bask site temperatures and mean cloud cover over that period. Daily movement rates were also calculated where six or more radio-locations were made in any one day (see section 4.3.2.). Analyses of these results were undertaken using the SPSS-X statistical package (SPSS Inc.) on the ICL 2976 computer.

4.2.2. Activity patterns

Movement activity of a radio-tagged animal can be detected by changes in signal strength resulting from differences in the orientation of the transmitter and aerial, relative to the receiving equipment. Monitoring movement activity in this way has been used in many studies (e.g Cederlund and Lemnell 1980, Hirons and Owen 1982). Automatic activity recording was only employed during the 1986 field season in the present study. Data were collected from three specimens over nine different days. Hourly measurements of shaded air temperature were recorded simultaneously during activity recording. Details of the methodology are given in Chapter 2 (section 2.2.3 c).

4.2.3. Analysis

Statistical tests used in each analysis are noted along with the significance values in the results section. The analyses carried out in this chapter are summarised below:

a. Hourly Movement rate

Hourly movement rates of C. austriaca were calculated and plotted as a frequency histogram. Movement rates of males and females were compared via the Mann-Whitney U- and Kolmogorov-Smirnov tests. Median and minimum and maximum movement rates were calculated for the whole sample and for the two sexes separately.

b. Daily movement rate

The number of observations required per day to yield a representative daily movement rate was estimated by plotting median movement rates against number of observations per day. Daily movement rates were plotted as a frequency histogram. Male and female daily movement rates were compared via Mann-Whitney U- and Kolmogorov-Smirnov tests. Median, minimum and maximum values were presented for each sex and for both sexes together.

c. Movement rate and environmental temperatures

The relationship of shade air temperature and bask site temperature with hourly movement rate was investigated via linear regression equations and the Spearman's rank correlation coefficient. Median hourly movement rates in each of five degree and two degree intervals of shade air and bask site temperature were plotted as a histogram and compared by the Kruskal-Wallis test.

d. Movement rate and season

Daily and hourly rates of movement were compared between the three defined seasons in which activity occurred, namely Spring, Summer and Autumn, using the Kruskal-Wallis test. Median and minimum and maximum values were presented in each case. Data were analysed for male and female specimens both separately and together. In addition differences in movement rate between the sexes were investigated within each season via the Mann-Whitney U-test.

e. Movement rate and time of day

Hourly movement rates were assigned to the hour interval during which the mid-point of the movement interval occurred in each case. Movement rates in hourly and two hourly time intervals were compared via the Kruskal-Wallis test. The median and minimum and maximum values were

presented in each case. Movement rates in two-hourly time intervals were further studied for variation within each sex separately using the Kruskal-Wallis test and between sexes within each time period using the Mann-Whitney U-test. Hourly movement rates were compared within two hourly time periods, to investigate variations in movement rate across the day, within each of the three defined seasons separately using the Kruskal-Wallis test. This latter analysis was performed on data for the two sexes both separately and together.

f. Movement rate and individual condition

The hourly and daily movement rates of C. austriaca were compared between specimens in different defined feeding, breeding and sloughing states. Where two status categories were defined the Mann-Whitney U-test was employed and where more than two categories were defined the Kruskal-Wallis test was employed. Median, minimum and maximum values for movement rates in each 'status category' were presented.

g. Direction of movement

The direction of each movement record during every radio-tracking period was calculated and assigned to one of eight bearing categories, each of 45° width. The total distance moved in each category was calculated. These totals were compared against an 'expected' movement distance (based on the hypothesis of equal movement in each direction) using the G-test and were plotted as a ray diagram (logarithmic scale).

The net movement for each radio-tracking period, expressed as a distance and bearing, was calculated; this being the displacement between the first and the last radio-locations. As a measure of dispersion, this net movement distance was expressed as a proportion of the total distance moved (the Net/Total ratio). A value for this ratio equal to or above 0.50 was arbitrarily regarded as showing a large displacement for any given total amount of

movement.

h. Activity patterns in the field

Periods in which movement activity was detected by continuous monitoring radio-telemetry were plotted against time of day to create an ethogram. Half hourly time periods were treated as discrete samples and the proportion of observations in which movement was detected within each of these periods was calculated. Temperatures associated with hourly periods in which movement was and was not recorded were compared via a Student's t-test.

The behaviour demonstrated by snakes at the time of location by radio-telemetry was described. The occurrence of each behaviour type was summed and expressed as an absolute and a relative frequency for each of eight 2-hour time periods during the day for each of the three seasons separately and for the study period as a whole. Comparisons between behaviours exhibited at each of the study sites and between the sexes were made using G-tests and Spearman's rank correlation coefficients.

i. Video analysis of movement behaviour

The proportion of time spent on each of five defined activities was determined for captive C. austriaca using video analysis. One-hourly and four-hourly time intervals were investigated and the relative time spent on each behaviour illustrated diagrammatically. Distances moved during one-hourly time periods were measured and hourly and daily movement rates calculated. Median, minimum and maximum values were presented in each case and a frequency histogram presented for hourly movement rate. Frequency histograms of hourly movement rate were also plotted for each of six four-hourly time intervals and median values for each presented.

4.3. Results

4.3.1. Hourly rate of movement

Hourly rates of movement were calculated by dividing the minimum distances (metres) between successive observations by the time interval (hours) between the sightings. Data collected by radio-telemetry only were used in this analysis and, with the view to providing a standardised measure of movement rate, only data where the successive sightings were in the same day and were separated by an interval of less than three hours but more than one hour (i.e. 2 hours \pm 1hour) were used.

Hourly movement rates of male and female snakes were analysed separately. Data from each sex demonstrated a highly positively skewed distribution. As the data were not normally distributed, non-parametric statistics were employed to compare the movement behaviours between the sexes; median values are therefore presented in all cases. The median hourly movement rate for male C. austriaca was 0.57 m/ hr (n= 652). Movement rates ranged between 0.00 and 32.99 m/ hr for male C. austriaca. Female snakes demonstrated a median movement rate of 0.48 m/ hr (n= 422). The minimum recorded movement rate was 0.00 m/ hr and the maximum 44.26 m/ hr for female specimens. No significant difference was detected between the hourly movement rates of the two sexes via the Mann-Whitney U-test (U= 128498.5, $n_1 = 652$, $n_2 = 422$, $p > 0.05$) nor was any difference observed between the frequency distributions of the two sexes when tested with the Kolmogorov-Smirnov test ($z = 1.155$, $n_1 = 652$, $n_2 = 422$, $p > 0.05$).

The similarity of movement rates displayed by the two sexes indicated that the data from male and female specimens could be pooled. Further analysis of the hourly movement rate data therefore incorporates data from both sexes together. A median movement rate of 0.54 m/ hr (n= 1074) was obtained for all specimens of C. austriaca. Movement rates varied between 0.00 and 44.26 m/ hr. The frequency



distribution of hourly movement rates is presented in Fig. 4.1. Hourly movement rates demonstrated a highly positively skewed distribution, and of the 1074 movement records 672 (62.6%) were less than 1.0 m/ hr and 519 (48.3%) were less than 0.5 m/ hr. A rate of 0.00 m/ hr was recorded on 201 occasions (18.7%). Only 41 records (3.8%) demonstrated a movement rate in excess of 10 m/ hr.

4.3.2. Daily movement rates and number of observations per day

Movement behaviour of C. austriaca can also be described as a daily movement rate by summing the individual minimum monitored distances recorded within each day. This method has advantages over the use of hourly movement rate in that this latter method provides a more 'realistic' estimate of dispersal potential and further provides a rate of movement in units that are comparable with many published studies of snake movement behaviour. Rates of movement calculated in this way will be dependent on the number of observations made each day, with an increasing number of movement records yielding an increasing estimate of daily vagility. This is particularly so when only a few movement records are recorded in any one day.

With the aim of selecting the minimum number of movement records that gave a representative estimate of daily movement rate, the median movement rates were calculated for each number of movement records per day (Table 4.1). These medians were then plotted against the corresponding number of movement records (see Fig. 4.2). The minimum representative number of observations per day was regarded as that where the increase in (median) daily movement rate with increasing number of minimum monitored distances stabilised, and hence represented an asymptote on the graph. Although no asymptote could clearly be identified in Fig. 4.2, an arbitrary division could be drawn between estimates of daily movement rate calculated from data from five or less observations and from those movement rates determined using six or more observations. It was decided

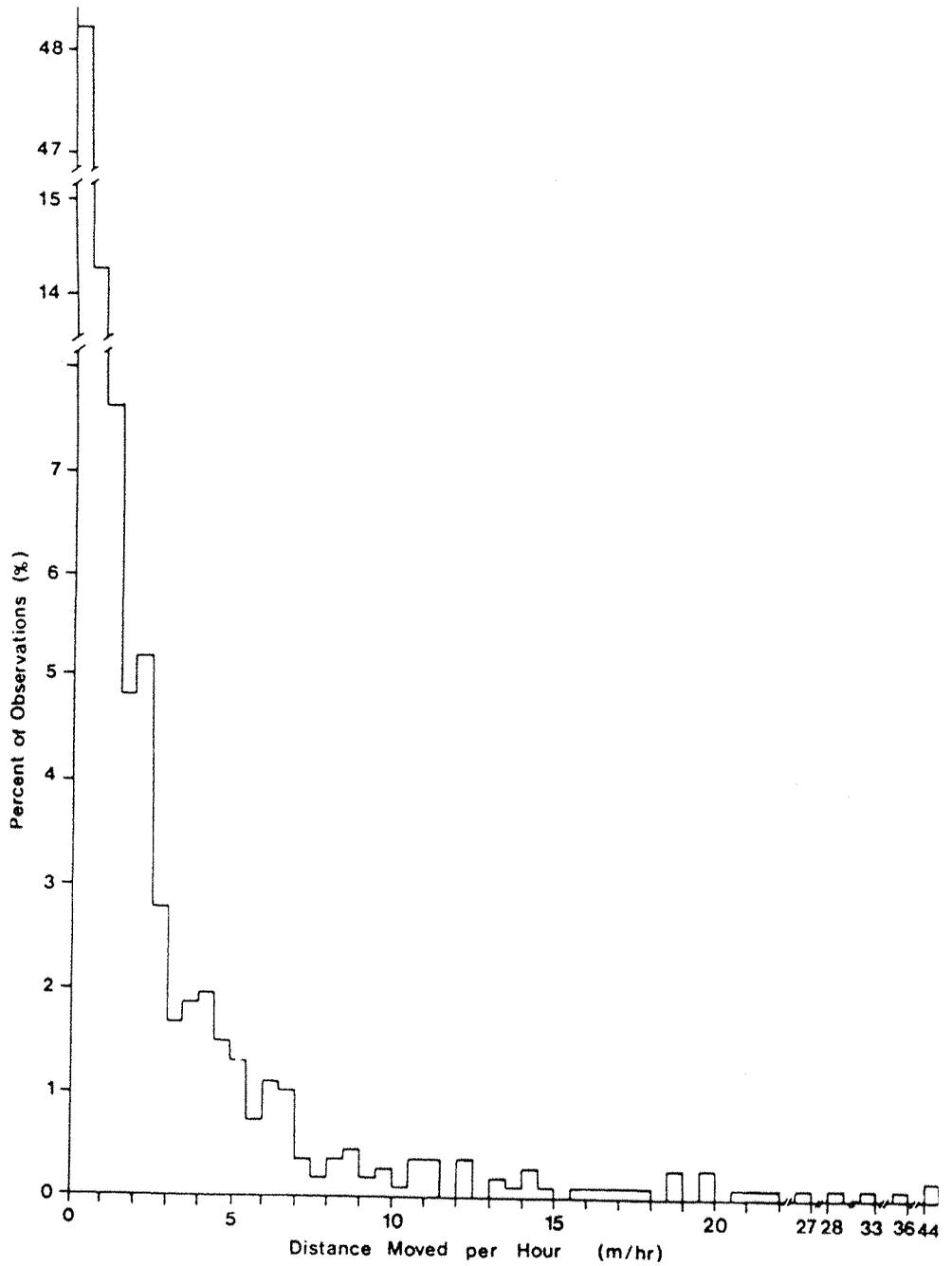


Fig. 4.1 : Distribution of hourly movement rates (m/ hr) of C. austriaca as determined from minimum monitored distances between successive radio-locations (where the time interval was more than one hour but less than three hours) for male and female specimens. Data were collected between April 1984 and July 1986 inclusive (n = 1074 values).

Number of movement records per day	N	Median (m/day)	Min.-Max. (m/ day)
1	8	0.59	0.00- 2.45
2	37	3.06	0.00- 29.35
3	12	4.69	0.70- 28.55
4	23	8.71	0.10-170.92
5	44	7.50	0.00- 91.27
6	61	12.17	1.85-123.25
7	69	13.81	0.00-108.60
8	6	15.00	8.93-166.81
9	2	22.04	15.46- 28.61

Table 4.1: Median (and minimum and maximum) daily movement rates (m/ day) for each number of between sightings movement records (minimum monitored distances) per day's radio-tracking.

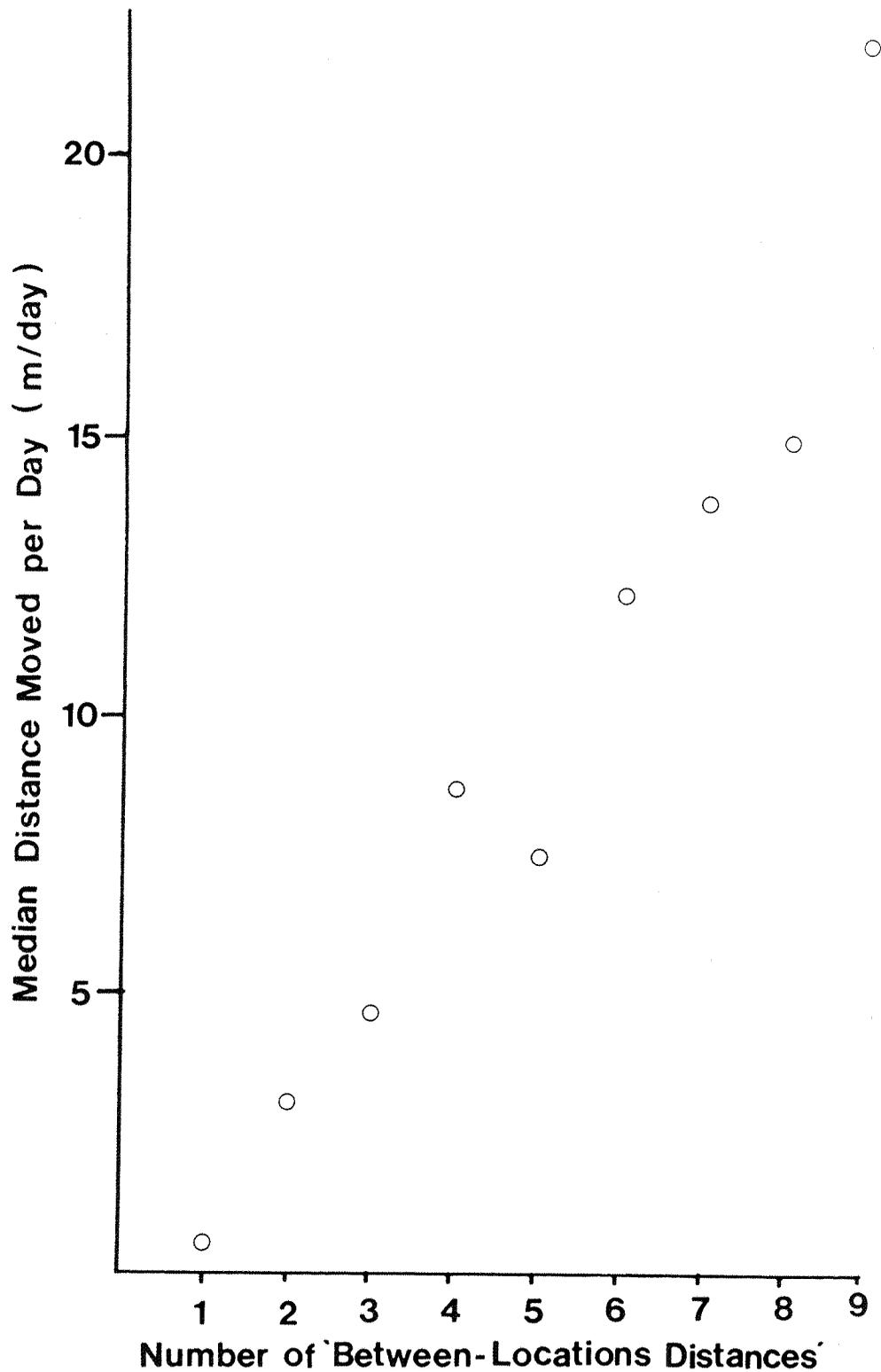


Fig. 4.2 : Median distance moved per day (m/ day) against the number of between locations distances recorded during those days (daily movement rates were calculated from the sum of all between locations distances measured in that day).

that only daily movement rates estimated by summing six or more minimum monitored distances (i.e. seven or more radio-locations of a snake per day) would be used in further analysis. Of 262 'days' radio-tracking data, 138 days had 7 or more observations and were used in further analysis. The remaining 124 days (with between 2 and 6 locations) were discarded from further analysis.

4.3.3. Daily rate of movement

The daily movement rates used in the below analyses are those for which six or more minimum monitored distances were summed to give an estimate of the daily movement rate (see section 4.3.2).

The median daily movement rate of male C. austriaca was 15.13 m/ day (n= 80). Movement rates for male snakes varied between 0.14 to 123.25 m/ day. Female snakes demonstrated a median movement rate of 10.18 m/day (n= 58). The minimum daily movement rate for female C. austriaca was 0.00 m/ day and the maximum 166.81 m/ day. No significant differences were detected between the daily movement rates of male and female C. austriaca when tested via the Mann-Whitney U-test (U= 1890.0, $n_1 = 80$, $n_2 = 58$, $p > 0.05$) or with the Kolmogorov-Smirnov two sample test ($z = 1.122$, $p > 0.05$).

Since no differences were detected between the two sexes, daily movement rates for the two sexes were combined. The frequency distribution for daily movement rates is presented in Fig. 4.3 and this shows a highly positively skewed distribution. Of the 138 values, 24 (17.4%) showed daily movement rates of less than 5 m/ day and 53 (38.4%) were less than 10 m/ day. 75 observations (54.3%) were less than 15m /day. Only 18 values (12.3%) were in excess of 50 m/ day and of these 5 (2.9%) showed movements of over 100 m/day. The median movement rate for all specimens of C. austriaca was 13.30 m/ day (n= 138) with daily movement rates varying between 0.00 and 166.81 m/ day.

Daily movement rates calculated for days in which less than

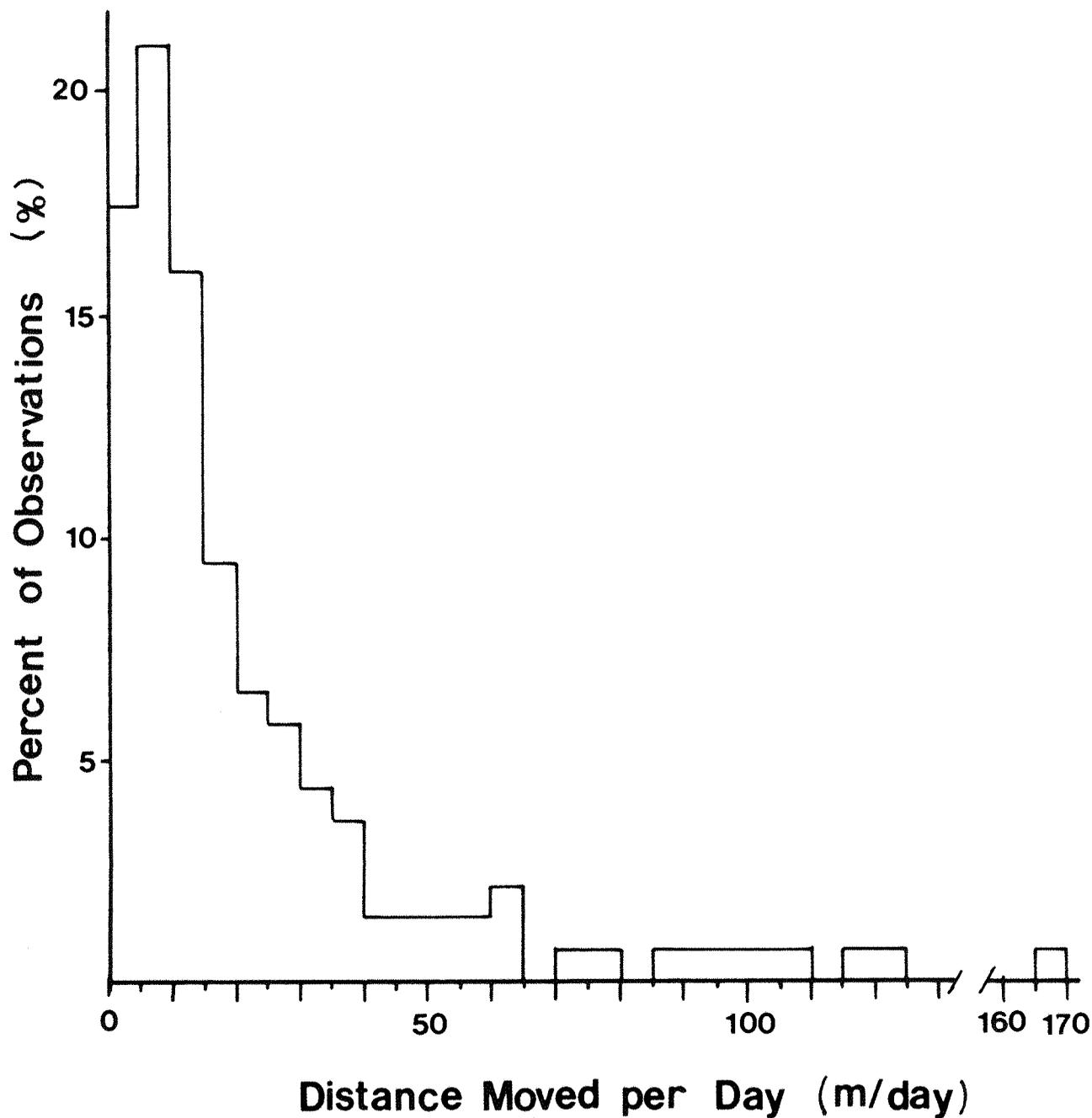


Fig. 4.3 : Percentage frequency distribution of distances moved per day (m/ day) by specimens of C. austriaca during April 1984 to July 1986 inclusive, using daily movement data based on six or 'between locations' distances during each day.

seven radio-locations were made were omitted to ensure some degree of standardisation. The inclusion of these additional daily movement rates yielded a reduced median daily movement rate (8.90 m/ day respectively (n= 262)) and a larger percentage of the data were displaced to the left of the frequency distribution (38% of the observations being less than 5 m/ day, 53.4% less than 10 m/ day and 65.6% less than 15 m/ day). However, data for larger movements were also omitted; four values greater than 50 m/ day, one of which was over 100 m/ day, were discarded. This latter value, of 170.92 m/ day, was obtained from only five observations (four minimum monitored distances) of a female snake, and represents the greatest distance recorded for a daily movement of a specimen of C. austriaca during the present study.

4.3.4. Movement behaviour and its relationship with environmental temperatures

The relationship of movement rate behaviour with environmental variables was confined to an investigation of the hourly movement rates and the corresponding mean shade air and bask site temperatures and cloud cover over the period for which these movement rates were calculated.

Movement rates were tested for correlation with environmental temperatures using the Pearson correlation coefficient. Hourly movement rate was significantly positively correlated with shade air temperature ($r= 0.09$, $n= 1036$, $p<0.002$), that is with increasing temperature increased hourly movement rates were observed (see Fig. 4.4), and the regression equation to describe this relationship is as follows:

$$\text{Movement rate (m/ hr)} = 0.10 \times T_A - 0.032$$

where T_A is shade air temperature in °C.

Movement rate was correlated with bask site temperature ($r= 0.09$, $n= 1036$, $p>0.002$) and, thus, an increased bask site

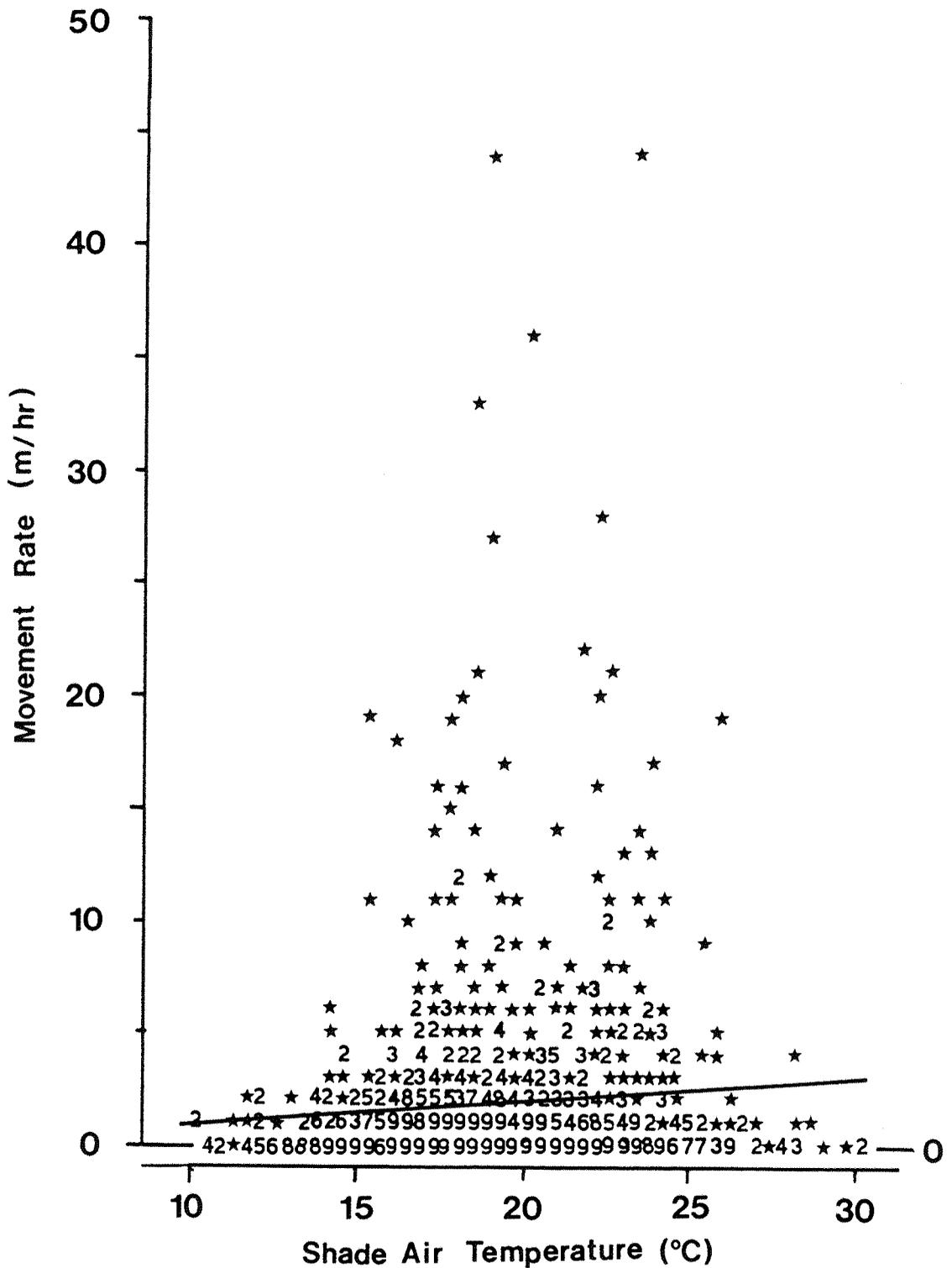


Fig. 4.4 : Movement rate (m/ hr) of specimens of *C. austriaca* against Shade Air Temperature based on radio-tracking data collected between April 1984 and July 1986 inclusive (n = 1036). Numbers indicate where more than one record was obtained with '9' representing nine or more records. Single observations are indicated by a star.

temperature was associated with an increased movement rate (see Fig. 4.5). The regression equation describing this relationship is as follows:

$$\text{Movement rate (m/ hr)} = 0.087 \times T_{\text{BS}} - 0.181$$

where T_{BS} is the bask site temperature in °C. For the purpose of comparison, the above two regression lines are plotted together in Fig. 4.6.

No correlation was detected between movement rate and cloud cover when investigated via the Spearman's rank correlation coefficient ($r_s = -0.011$, $n = 1055$).

Multiple regression equations were calculated for the relationships between movement rate (m/ hr) and shade air temperature with cloud cover and bask site temperature with cloud cover. The equations obtained were as follows:

$$\text{Movement rate (m/ hr)} = (0.15 \times T_A) + (0.12 \times \text{Cld}) - 1.639$$

$$\text{Movement rate (m/ hr)} = (0.12 \times T_{\text{BS}}) + (0.11 \times \text{Cld}) - 1.098$$

where T_A and T_{BS} are shade air and bask site temperatures in °C respectively and Cld is cloud cover in eighths.

To further investigate the effects of environmental temperatures on the hourly movement rate of C. austriaca, median movement rates for two degree and five degree interval categories of shade air and bask site temperatures were calculated. Movement rates in each of the two and five degree categories were tested to see whether temperature affected the movement rate via the Kruskal- Wallis test.

Median hourly movement rates for five and two degree intervals of shade air temperature are presented in Figs. 4.7A and 4.7B and Tables 4.2A and 4.2B respectively. Five divisions of hourly movement rates were obtained when shade air temperatures were divided into five degree interval classes ranging between 10-14.9°C and 30-34.9°C (see

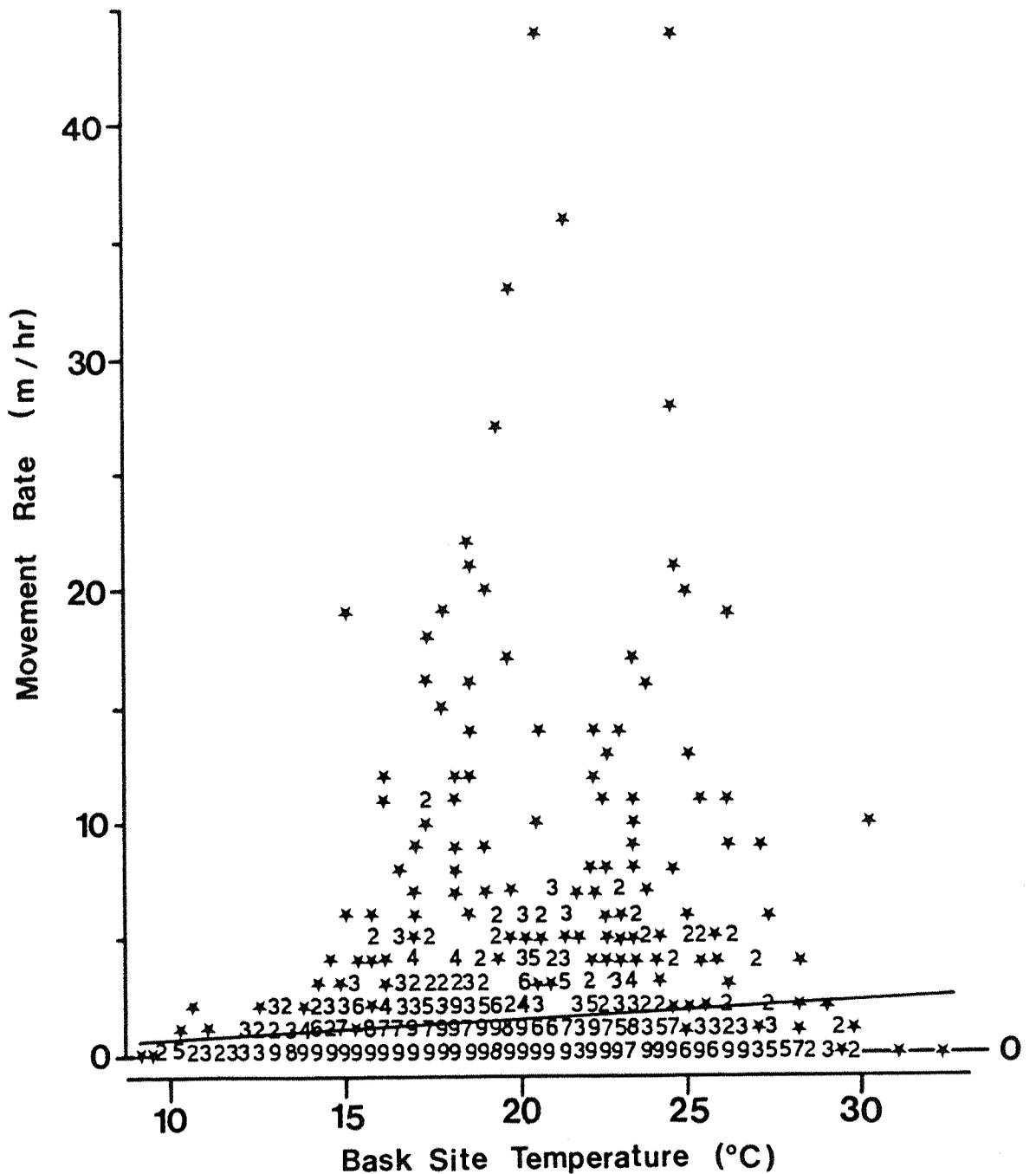


Fig. 4.5 : Movement rate (m/ hr) of specimens of C. austriaca against Bask Site Temperature ($^{\circ}$ C) based on radio-tracking data collected between April 1984 and July 1986 inclusive (n = 1036). Numbers indicate where more than one record was obtained with '9' representing nine or more records. Single observations are indicated by a star.

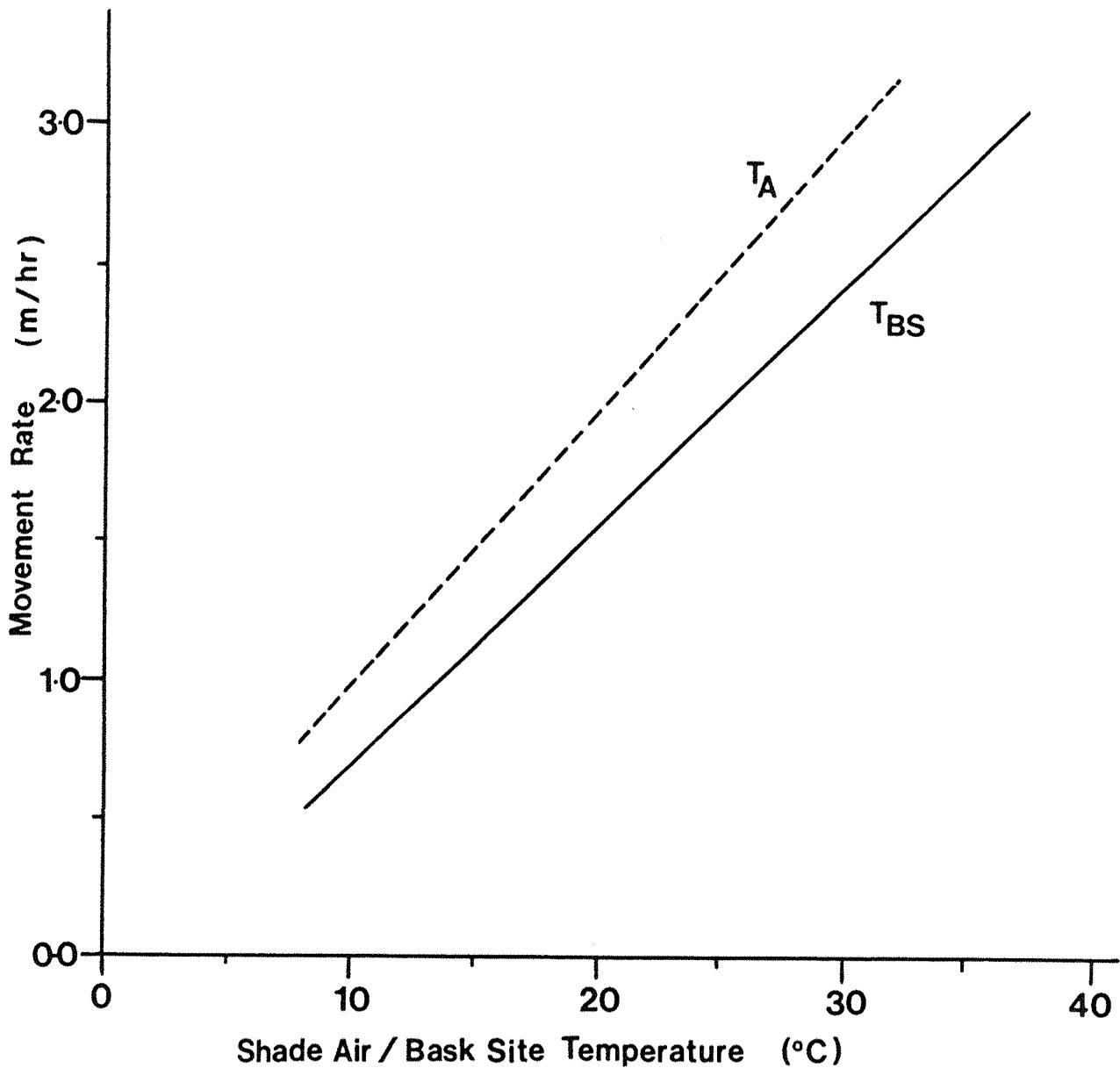


Fig. 4.6 : Regression lines of movement rate (m/ hr) against Shade Air Temperature ($T_A, ^\circ\text{C}$) (dashed line) and against Bask Site Temperature ($T_{BS}, ^\circ\text{C}$) (solid line) for specimens of *C. austriaca* based on radio-tracking data collected between April 1984 and July 1986 inclusive ($n = 1036$ in each case).

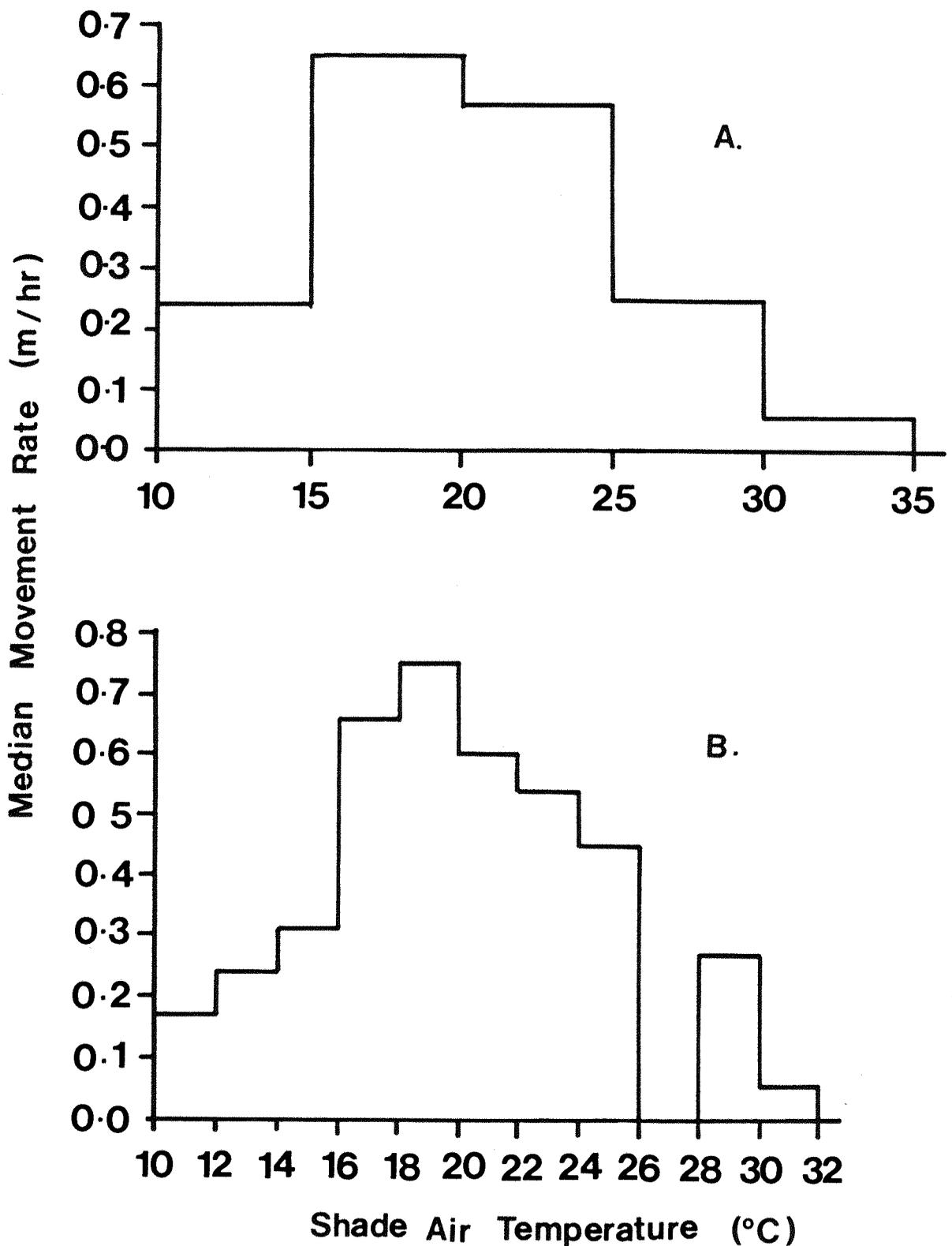


Fig. 4.7 A. and B. : Median movement rates (m/ hr) of specimens of *C. austriaca* within different categories of Shade Air Temperature ($^{\circ}\text{C}$) using A. 5°C intervals and B. 2°C intervals based on radio-tracking data collected between April 1984 and July 1986 inclusive.

<u>A.</u> Temperature (°C)	n	Median (m/hr)	Range (m/hr)
10 - 14.9	127	0.240	0.00 - 5.70
15 - 19.9	503	0.650	0.00 - 44.26
20 - 24.9	349	0.570	0.00 - 44.07
25 - 29.9	55	0.250	0.00 - 18.71
30 - 34.9	2	0.055	0.00 - 0.11

<u>B.</u> Temperature (°C)	n	Median (m/hr)	Range (m/hr)
10 - 11.9	17	0.17	0.00 - 2.37
12 - 13.9	56	0.240	0.00 - 2.41
14 - 15.9	125	0.310	0.00 - 18.79
16 - 17.9	221	0.660	0.00 - 18.82
18 - 19.9	211	0.750	0.00 - 44.26
20 - 21.9	164	0.600	0.00 - 35.72
22 - 23.9	156	0.540	0.00 - 44.07
24 - 25.9	57	0.450	0.00 - 18.71
26 - 27.9	20	0.000	0.00 - 2.00
28 - 29.9	7	0.270	0.00 - 4.05
30 - 31.9	2	0.055	0.00 - 0.11

Table 4.2 A and B: Median Movement rates (m/ hr) within different categories of Shade Air Temperature (°C) for C. austriaca, as determined by radio-tracking during April 1984 to July 1986 inclusive, showing the associated sample sizes and range of values. Shade air temperatures are divided into: A. Five degree intervals and B. Two degree intervals.

Fig.4.7A and Table 4.2A). Temperature had a significant effect on movement rates (chi-squared= 52.54, n= 1036, $p < 0.0001$) with a raised median movement rate occurring in the intermediate temperature categories (15–19.9°C and 20–24.9°C). The maximum median movement rate, 0.650 m/ hr, was recorded during the 15–19.9°C interval and the minimum median movement rate, 0.055 m/ hr, was recorded in the 30–34.9°C division. Minimum movement rates of 0.00 m/ hr were recorded during all five temperature groups. Maximum rates recorded were greatest during the intermediate temperature ranges with maxima of 44.26 and 44.07 m/ hr being observed during the 15–19.9 and 20–24.9°C intervals. The smallest maximum movement rate was 0.11 m/ hr, recorded when shade air temperature was between 30–34.9°C.

Eleven divisions of hourly movement rate were obtained when shade air temperatures were categorised into two degree interval classes between 10–11.9°C and 30–31.9°C (see Fig. 4.7B and Table 4.2B). A highly significant effect of temperature on movement rate was observed (chi-squared= 62.63, n= 1036, $p < 0.0001$). Median movement rate increased with increasing shade air temperature up to a maximum value of 0.750 m/ hr when shade air temperature equalled 18–19.9°C. Thereafter progressively decreasing median movement rates were obtained with increasing shade air temperature. The minimum median movement rate was 0.00 m/ hr recorded for shade air temperatures between 26 and 27.9°C. During all eleven periods, minima of 0.00 m/ hr were recorded. Maxima varied between 0.11 m/ hr and 44.26 m/ hr. Greatest values for maximum movement rates were recorded at intermediate temperatures with values of 44.26, 35.72 and 44.07 m/ hr corresponding to shade air temperatures of 18–19.9, 20–21.9 and 22–23.9°C respectively.

Median movement rates of radio-tagged *C. austriaca* for five degree and two degree divisions of bask site temperature are presented in Figs. 4.8A and 4.8B and Tables 4.3A and 4.3 B respectively. A highly significant effect of bask site temperature on movement rate was observed for the six categories created by dividing the data into five degree

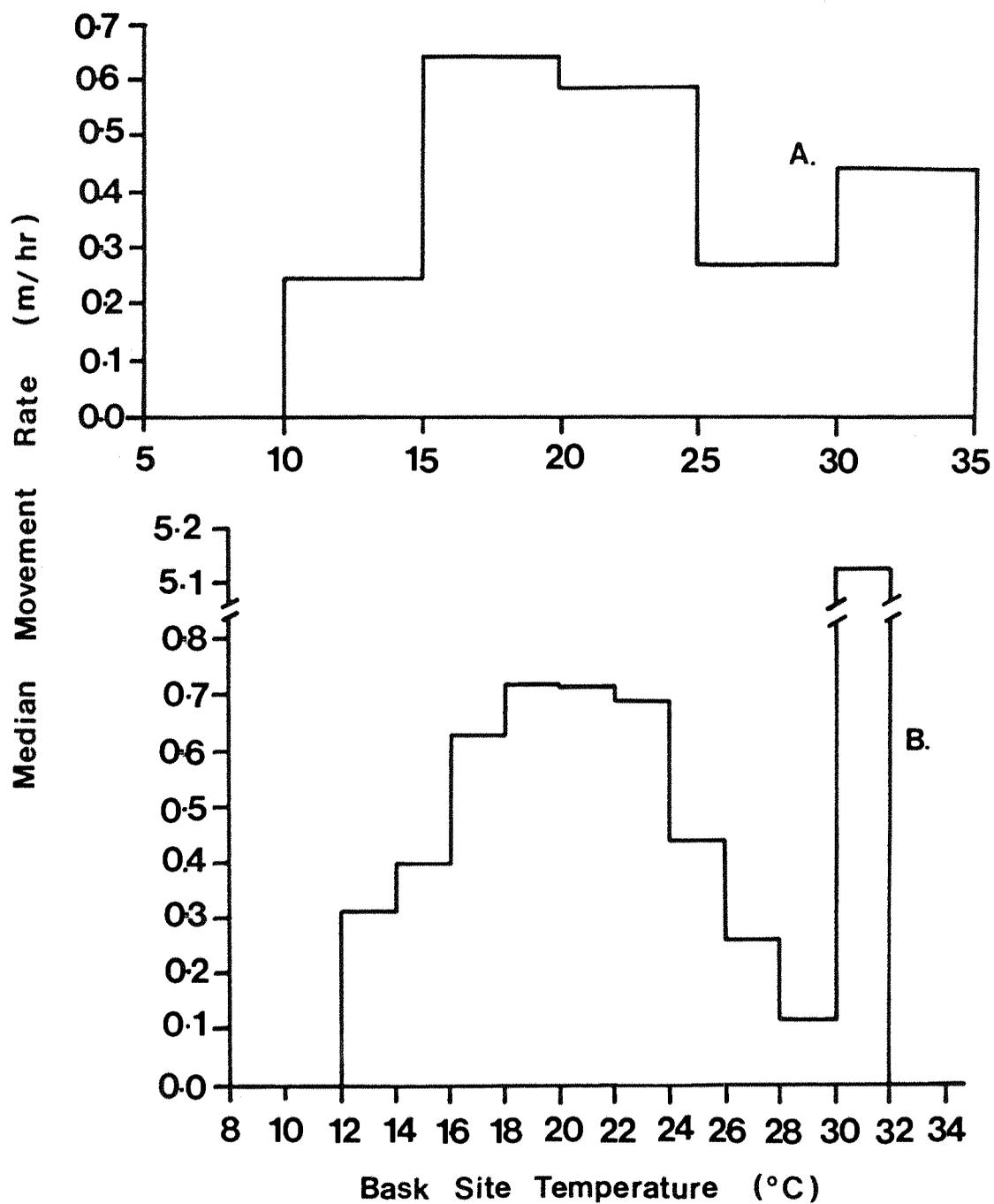


Fig. 4.8 A. and B. : Median movement rate (m/ hr) of specimens of *C. austriaca* within different categories of Bask Site Temperature (°C) using A. 5°C intervals and B. 2°C intervals based on radio-tracking data collected between April 1984 and July 1986 inclusive.

<u>A.</u> Temperature (°C)	n	Median (m/hr)	Range (m/hr)
5 - 9.9	5	0.000	0.00 - 0.69
10 - 14.9	132	0.245	0.00 - 18.79
15 - 19.9	426	0.645	0.00 - 32.99
20 - 24.9	357	0.590	0.00 - 44.26
25 - 29.9	113	0.270	0.00 - 18.71
30 - 34.9	3	0.450	0.00 - 9.81

<u>B.</u> Temperature (°C)	n	Median (m/hr)	Range (m/hr)
8 - 9.9	5	0.000	0.00 - 0.69
10 - 11.9	17	0.000	0.00 - 2.02
12 - 13.9	60	0.315	0.00 - 2.41
14 - 15.9	124	0.400	0.00 - 18.79
16 - 17.9	172	0.630	0.00 - 18.82
18 - 19.9	185	0.720	0.00 - 32.99
20 - 21.9	156	0.715	0.00 - 44.26
22 - 23.9	149	0.690	0.00 - 16.65
24 - 25.9	90	0.440	0.00 - 44.07
26 - 27.9	54	0.265	0.00 - 18.71
28 - 29.9	21	0.120	0.00 - 4.05
30 - 31.9	2	5.130	0.00 - 9.81
32 - 33.9	1	0.000	0.00 - 0.00

Table 4.3 A and B: Median Movement rates (m/ hr) within different categories of Bask Site Temperatures (°C) for C. austriaca, as determined by radio-tracking during April 1984 to July 1986, showing the associated sample size and range of observed values. Bask Site Temperatures are divided into: A. Five degree intervals and B. Two degree intervals.

intervals of bask site temperature (chi squared= 47.52, n= 1036, $p < 0.0001$). These categories ranged from 5–9.9°C to 30–34.9°C (see Fig. 4.8A and Table 4.3A). The maximum median movement rate, 0.645 m/ hr, was recorded where bask site temperatures were in the range 15–19.9°C. The minimum median value was 0.00 m/ hr and corresponded to a bask site temperature of 5–9.9°C. Minimum movement rates of 0.000 m/ hr were recorded in bask site temperature categories. The maxima increased with increasing temperature to a value of 44.26 m/ hr when T_{ms} had a corresponding value of 20–24.9°C. With progressively increasing bask site temperatures in excess of 24.9°C decreasing values were obtained for the maximum movement rates.

Thirteen categories of hourly movement rate were obtained when the associated bask site temperatures were divided into two degree interval classes. These temperature categories ranged between 8–9.9°C and 32–33.9°C (see Fig. 4.8B and Table 4.3B). A highly significant effect of temperature on movement was detected (chi-squared= 63.80, n= 1036, $p < 0.0001$) with a tendency for higher median movement rates to be associated with intermediate temperatures between 18–19.9 to 22–23.9°C. The greatest median movement rate, however, was recorded when the bask site temperature was 30–33.9°C. The lowest median values were obtained when bask site temperatures were 8–9.9 and 10–11.9°C, with values of 0.00 m/ hr being recorded in each case. Minima of 0.00 m/ hr were recorded in all eleven categories. Maximum movement rates increased as bask site temperature increased from 8–9.9°C to 20–21.9°C where the greatest value (44.26 m/ hr) was recorded. Thereafter maxima showed a tendency to decline as bask site temperature increased.

4.3.5. Movement behaviour and its relationship with season

Seasonal variation of the movement behaviour of C. austriaca was investigated by looking at both the daily and hourly rates of movement recorded during radio-tracking in each of three defined seasons (March to May = Spring, June

to August = Summer and September to October = Autumn).

a. Daily rates of movement

No significant difference was detected between the daily movement rates of C. austriaca observed in each of the three seasons (chi-squared= 0.206, n= 138, p>0.05) when tested with the Kruskal- Wallis test. The median movement rate recorded in Spring was 9.64 m/ day with values ranging between 8.54 and 26.55 m/ day (n= 3). In Summer a median movement rate of 12.66 m/ day was obtained and minimum and maximum values recorded were 0.00 and 166.81 m/ day respectively (n= 84). Movement rates recorded in Autumn ranged between 0.55 and 123.25 m/ day with a median value of 14.38 m/ day being obtained (n= 51).

Movement rates within each season were further subdivided into data recorded for both males and females with the aim of investigating whether there were intra-specific differences in seasonal movement behaviour. Movement rates for the two sexes were compared within each season via the Mann-Whitney U-test and Kolmogorov-Smirnov test. No data were available for daily movement rates for females in Spring, and hence no comparisons between sexes were possible in this season. No significant differences in daily movement behaviour were observed between male and female smooth snakes during Summer (U= 667.0, $n_1 = 49$, $n_2 = 35$, p>0.05 and z= 1.180, p>0.05) or Autumn (U= 276.0, $n_1 = 28$, $n_2 = 23$, p>0.05 and z= 0.651, p>0.05). No significant differences were detected in the daily movement rates of male C. austriaca recorded in Spring (median= 9.64 m/ day, range= 8.54 to 26.55 m/ day (n= 3)), Summer (median= 15.46 m/ day, range= 0.14 to 117.47 m/ day (n= 49)) and Autumn (median= 15.09 m/ day, range 1.85 to 123.25 m/ day (n= 28)) when tested via the Kruskal-Wallis test (chi-squared= 0.385, n= 80, p>0.05). Female smooth snakes showed no difference in movement rate between the two seasons for which data were available (chi-squared= 0.546, n= 58, p>0.05). Median movement rates for female specimens were 8.88 m/ day (range= 0 to 166.81 m/ day, n= 35) in Summer

and 12.17 m/ day (range= 0.55 to 91.21 m/ day, n= 23) in Autumn.

b. Hourly rates of movement

No significant difference was detected in the hourly movement rate of C. austriaca in each of three different seasons (defined above in section 4.3.5 a) (chi-squared= 2.765, n= 1074, $p > 0.05$). Median hourly movement rates for all specimens of C. austriaca were 0.43 m/ hr (range= 0.00 to 18.79 m/ hr, n= 111) in Spring, 0.53 m/ hr (range= 0.00 to 44.26 m/ hr, n= 622) in Summer and 0.57 m/ hr (range= 0.00 to 21.02 m/ hr, n= 341) in Autumn.

Hourly movement rates within each season were further divided into categories dependent on the sex of the animals. No differences in hourly movement rates were detected between male and female C. austriaca during Spring ($U = 548.5$, $n_1 = 97$, $n_2 = 14$, $p > 0.05$ and $z = 1.226$, $p > 0.05$) or Summer ($U = 45328.5$, $n_1 = 360$, $n_2 = 262$, $p > 0.05$ and $z = 0.849$, $p > 0.05$) using the Mann-Whitney U-test and Kolmogorov - Smirnov test. Movement rates were significantly different between the two sexes during Autumn ($U = 12379.0$, $n_1 = 195$, $n_2 = 146$, $p = 0.04$ and $z = 1.463$, $p < 0.03$) with median rates of 0.83 m/ hr and 0.435 m/hr for male and female specimens respectively.

Within each sex, no differences in hourly movement rates were found between the seasons when tested via the Kruskal-Wallis test. Male snakes demonstrated a median movement rate of 0.44 m/ hr (range= 0.00 to 18.79 m/ hr, n= 97), 0.54 m/ hr (range= 0.00 to 32.99 m/ hr, n= 360) and 0.83 m/ hr (range= 0.00 to 21.02 m/ hr, n= 195) during Spring, Summer and Autumn respectively (chi-squared= 3.925, n= 652, $p > 0.05$). Median movement rates for female C. austriaca during Spring, Summer and Autumn were 0.38 m/ hr (range= 0.00 to 1.26 m/ hr, n= 14), 0.49 m/ hr (range= 0.00 to 44.26 m/ hr, n= 262) and 0.435 m/ hr (range= 0.00 to 19.67 m/ hr, n= 146) respectively (chi-squared= 1.516, n= 422, $p > 0.05$).

4.3.6. Movement behaviour and its relationship with time of day

Hourly rates of movement of radio-tagged *C. austriaca* were calculated from successive radio-locations (where these locations were between 1.00 and 3.00 hours apart) by dividing the total distance moved (the minimum monitored distance) by the time interval in hours. Each hourly movement rate was assigned to the time corresponding to the mid-point of the interval between the successive radio-locations used for the calculation of the minimum monitored distance. It is against these average time values that the diurnal trends in movement rate are discussed.

a. Diurnal movement rates for all specimens

Movement rates were obtained for times between 07-0759 and 20-2059 hours BST. Throughout this section time intervals will be described by the hour only hence, for example, 0700 will refer to the interval 0700- 0759 hr. Median hourly movement rates for each one hourly time interval (for pooled data from male and female specimens from all seasons) are presented in Fig. 4.9A. Significant variation was observed between these hourly intervals (Kruskal-Wallis chi-squared= 34.629, n= 1074, p=0.001). Median movement rates showed a minimum value of 0.18 m/ hr (range= 0.00 to 5.01 m/ hr, n= 6) at 0700 hrs with a slight increase to 0.20 m/ hr (range= 0.00 to 6.37 m/ hr, n= 15) at 0800 hrs. An increased rate was observed during 0900 with median value of 0.65 m/ hr (range= 0.00 to 16.02 m/ hr, n= 82). The rate decreased slightly between 1000 and 1100 hrs where median values of 0.56 m/ hr (range= 0.00 to 44.26 m/ hr, n= 73) and 0.55 m/ hr (range= 0.00 to 26.77 m/ hr, n= 120), respectively, were observed. During 1200 hourly movement rate increased, with a median rate of 0.76 m/ hr (range= 0.00 to 21.02 m/ hr, n= 88). Median hourly movement rates fluctuated during the afternoon until 1600 hrs; first decreasing at 1300 hr, then increasing at 1400hr and then decreasing again at 1500 hrs prior to increasing to a

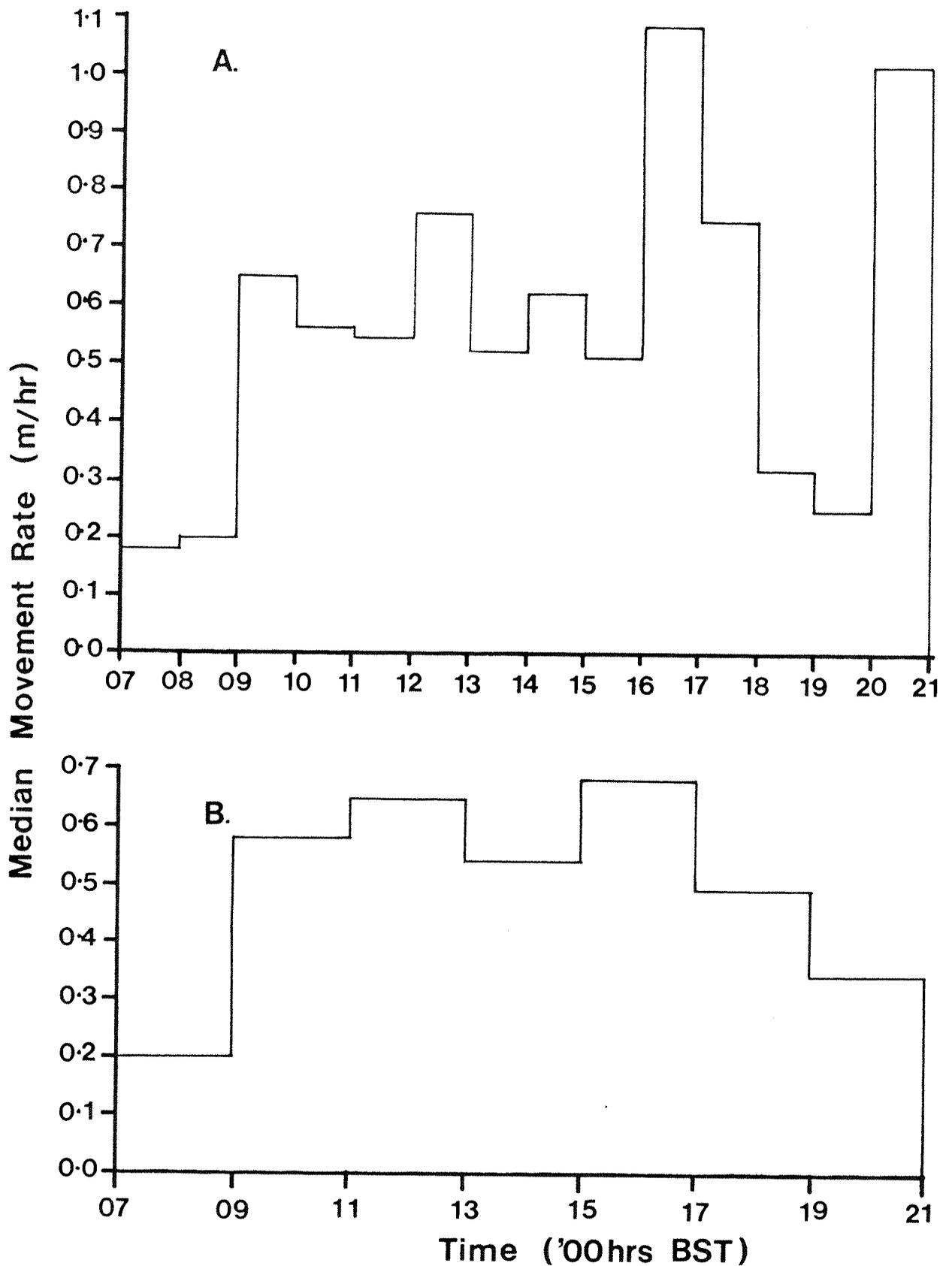


Fig. 4.9 A. and B. : Median movement rate (m/ hr) of specimens of *C. austriaca* during different time periods using A. one-hourly time intervals and B. two-hourly time intervals based on radio-tracking data collected between April 1984 and July 1986 inclusive.

maximum value at 1600 hrs. Median movement rates of 0.52 m/hr (range= 0.00 to 17.79, n= 113), 0.62 m/hr (range= 0.00 to 18.82, n= 95), 0.51 m/hr (range= 0.00 to 44.07, n= 106) and 1.08 m/hr (range= 0.00 to 16.65, n= 88) were observed between 1300 and 1600 hrs respectively. Movement rate decreased after 1700 hrs until 1900 hrs with median values of 0.75 m/hr (range= 0.00 to 35.72 m/hr, n= 115), 0.32 m/hr (range= 0.00 to 20.65 m/hr, n= 92) and 0.25 m/hr (range= 0.00 to 21.95 m/hr, n= 73) respectively being recorded. During the period 2000 to 2059 hrs a median movement rate of 1.02 m/hr (range= 0.00 to 3.42 m/hr, n= 8) was recorded.

Due to the small sample sizes encountered within each hourly division further analyses of the diel variation in movement rates were limited to data pooled into two hourly time blocks. These divisions allowed more confidence to be placed in analyses where the data had to be further subdivided.

Significant variation in movement rates were detected throughout the day by looking at two hourly categories of movement data, for male and female specimens when data from all seasons were pooled, (chi-squared= 16.15, n= 1074, $p < 0.02$). These data are summarised in Table 4.4 and illustrated in Fig. 4.9B. Movement rates were at a minimum during the early morning at 0700- 0859 hrs, where a median value of 0.20 m/hr (range= 0.00 to 6.32 m/hr, n= 21) was obtained. The hourly movement rate increased throughout the morning, with median values of 0.58 m/hr (range= 0.00 to 4.26 m/hr, n= 155) and 0.65 m/hr (range= 0.00 to 26.77 m/hr, n= 208) being observed at 0900-1059 and 1100-1259 hrs respectively. During the middle of the day a lower median movement rate was recorded (with the median at 1300-1459 hrs being 0.54m/hr (range= 0.00 to 18.82, n= 208)) which then demonstrated an increase to 0.68 m/hr (range= 0.00 to 44.07 m/hr, n= 194) during 1500-1659 hrs. Successively lower median movement rates were observed during 1700-1859 and 1900-2059 hrs, with values of 0.49 m/hr (range= 0.00 to 35.72 m/hr, n= 207) and 0.34 m/hr (range= 0.00 to

Time (00 hr)	Median (m/ hr)	n	Range (m/ hr)
0700-0859	0.20	21	0.00 - 6.32
0900-1059	0.58	155	0.00 - 44.26
1100-1259	0.65	208	0.00 - 26.77
1300-1459	0.54	208	0.00 - 18.82
1500-1659	0.68	194	0.00 - 44.07
1700-1859	0.49	207	0.00 - 35.72
1900-2059	0.34	81	0.00 - 21.95

Table 4.4 : Median movement rate (m/ hr) by specimens of C. austriaca during different two-hourly time periods and the respective sample sizes (n) and ranges of observations (m/ hr) as determined by radio-tracking between April 1984 and July 1986.

21.95 m/ hr, n= 81) being recorded.

b. Diurnal movement rate within and between the sexes

Movement rates for male and female smooth snakes in the two hourly time intervals are presented in Table 4.5. Significant variation in movement rate was detected for male snakes throughout the day (Kruskal-Wallis chi-squared= 13.62, n= 652, $p < 0.04$) but such diurnal variation was not detected in female specimens (chi-squared= 6.01, n= 422, $p > 0.05$). No differences were detected between the two sexes when tested pairwise during any of the two hourly time categories (values for the Mann-Whitney statistics (U) are presented in Table 4.5).

Male snakes showed an increased median (and maximum) movement rates during the time periods between 1100 and 1859 hrs, and lower rates of movement at each end of the day (i.e. between 0700-0859 and 1900-2059 hrs). A similar pattern of variation in hourly movement rate was suggested for female snakes, however this was not statistically significant.

For male snakes the highest median and maximum movement rates were obtained between 1500-1659 hrs, these being 0.79 m/ hr and 32.99 m/ hr respectively. The largest median value recorded from female snakes was 0.72 m/ hr and was obtained between 0900-1059 hrs; the maximum movement rate, 44.26 m/ hr was also recorded in this time period.

c. Diurnal movement rate within each season

Hourly movement rates during each two hourly time period were analysed separately for each of the three defined seasons, namely Spring (March-May), Summer (June-August) and Autumn (September-October). Movement rates for each time period in each season are presented in Tables 4.6A, 4.6B and 4.6C respectively. No significant diurnal effects on movement rate were detected during Spring and Summer (Kruskal-Wallis chi-squared= 4.94, n= 111, $p > 0.05$ and

Time (⁰⁰ hrs) (BST)	Males			Females			Mann-Whitney Test	
	Median (m/ hr)	n	Range (m/ hr)	Median (m/ hr)	n	Range (m/ hr)	U	Sig.
0700-0859	0.19	15	0.00- 5.01	0.37	6	0.00- 6.37	35.0	>0.05
0900-1059	0.53	96	0.00-16.02	0.72	59	0.00-44.26	2702.0	>0.05
1100-1259	0.72	123	0.00-26.77	0.45	85	0.00-14.15	4678.5	>0.05
1300-1459	0.62	123	0.00-17.79	0.44	85	0.00-18.82	4514.0	>0.05
1500-1659	0.79	118	0.00-32.99	0.55	76	0.00-44.07	4200.5	>0.05
1700-1859	0.61	123	0.00-19.61	0.43	84	0.00-35.72	4892.5	>0.05
1900-2059	0.36	54	0.00- 5.29	0.21	27	0.00-21.95	654.5	>0.05

Table 4.5 : Median movement rate (m/ hr) of male and female C. austriaca and associated sample sizes (n) and ranges of observed movement rates during different time periods (⁰⁰ hrs BST) as determined by radio-tracking between April 1984 and July 1986.

A. Spring

Time (00 hr)	Median (m/ hr)	n	Range (m/ hr)
0900-1059	0.17	8	0.00 - 0.80
1100-1259	0.87	28	0.00 - 18.79
1300-1459	0.58	26	0.00 - 17.79
1500-1659	0.64	25	0.00 - 6.31
1700-1859	0.39	23	0.00 - 10.77
1900-2059	0.44	1	0.44

B. Summer

Time (00 hr)	Median (m/ hr)	n	Range (m/ hr)
0700-0859	0.20	21	0.00 - 6.37
0900-1059	0.79	95	0.00 - 44.26
1100-1259	0.38	109	0.00 - 26.77
1300-1459	0.52	118	0.00 - 12.41
1500-1659	0.66	108	0.00 - 44.07
1700-1859	0.73	110	0.00 - 35.72
1900-2059	0.36	61	0.00 - 21.95

Tables 4.6A and 4.6B : Title on following page.

C. Autumn

Time (00 hr)	Median (m/ hr)	n	Range (m/ hr)
0900-1059	0.53	52	0.00 - 14.87
1100-1259	0.95	71	0.00 - 21.02
1300-1459	0.70	64	0.00 - 18.82
1500-1659	0.99	61	0.00 - 16.47
1700-1859	0.45	74	0.00 - 19.67
1900-2059	0.00	19	0.00 - 8.69

Tables 4.6A to C : Median Movement Rates (m/ hr) for C. austriaca in different two hour time periods throughout the day during A. Spring, B. Summer and C. Autumn as determined by radio-tracking during 1984 to 1986 inclusive. n = sample size and 'Range' indicates maximum and minimum movement rates obtained.

11.63, $n = 622$, $p > 0.05$ respectively), however significant variation in movement rate was detected during the day in Autumn ($\chi^2 = 15.90$, $n = 341$, $p < 0.01$). During this latter season, median movement rates increased during the morning from 0.53 m/ hr at 0900-1059 hrs to 0.95 m/ hr at 1100-1259 hrs. A slight decrease in median movement rate was observed between 1300-1459 hrs, with a value of 0.70 m/ hr being recorded, prior to the highest median value, 0.99 m/ hr, being obtained at 1500-1659 hrs. During the evening, decreasing values of median movement rate were observed with 0.45 m/ hr being recorded in 1700-1859 hrs and the lowest median value, 0.00 m/ hr, during 1900- 2059 hrs.

The minimum movement rate observed during all time periods in all seasons, where more than one observation was available, was 0.00 m/ hr. The maximum movement rate varied between time periods and seasons, but in all seasons the lowest value of the maximum was either the first (i.e. early morning), as in Spring and Summer, or last (i.e. evening), as in Autumn, observation. The greatest values for maxima were during the morning in all seasons, namely at 1100-1259 hrs during Spring and Autumn and 0900-1059 hrs during the Summer.

d. Diurnal movement rate for each sex within each season

Movement data for each time period were further subdivided within each season by the sex of the study animals. Movement rates are presented for each time period in Tables 4.7A, 4.7B and 4.7C for Spring, Summer and Autumn respectively. No significant differences in movement rate were detected between male and female specimens during any of the time periods in any of the seasons when compared pairwise via the Mann-Whitney U-test (values of the statistic and the corresponding significance level are presented in Tables 4.7a to 4.7C).

No significant variation in movement rate was detected throughout the day for male snakes in Spring or Summer ($\chi^2 = 5.52$, $n = 97$, $p > 0.05$ and $\chi^2 = 8.82$, $n =$

A. Spring

Time (⁰⁰ hrs) (BST)	Males			Females			Mann-Whitney Test	
	Median (m/ hr)	n	Range (m/ hr)	Median (m/ hr)	n	Range (m/ hr)	U	Sig.
0900-1059	0.17	8	0.00- 0.80	-	-	-	-	-
1100-1259	0.87	24	0.00-18.79	0.64	4	0.27- 1.14	44.5	>0.05
1300-1459	0.82	22	0.00-17.79	0.04	4	0.00- 0.65	18.0	>0.05
1500-1659	0.60	22	0.00- 6.31	0.67	3	0.10- 1.26	30.0	>0.05
1700-1859	0.33	20	0.00-10.77	0.39	3	0.00- 0.54	25.5	>0.05
1900-2059	0.44	1	-	-	-	-	-	-

B. Summer

Time (⁰⁰ hrs) (BST)	Males			Females			Mann-Whitney Test	
	Median (m/ hr)	n	Range (m/ hr)	Median (m/ hr)	n	Range (m/ hr)	U	Sig.
0700-0859	0.19	15	0.00- 5.01	0.37	6	0.13- 6.37	35.0	>0.05
0900-1059	0.73	58	0.00-16.02	0.91	37	0.00-44.26	1056.0	>0.05
1100-1259	0.34	61	0.00-26.77	0.40	48	0.00-11.25	1431.0	>0.05
1300-1459	0.50	63	0.00-12.41	0.54	55	0.00-10.78	1724.5	>0.05
1500-1659	0.78	63	0.00-32.99	0.38	45	0.00-44.07	1299.5	>0.05
1700-1859	0.96	61	0.00-19.61	0.53	49	0.00-35.72	1393.5	>0.05
1900-2059	0.36	39	0.00- 5.29	0.28	22	0.00-21.95	365.0	>0.05

C. Autumn

Time (⁰⁰ hrs) (BST)	Males			Females			Mann-Whitney Test	
	Median (m/ hr)	n	Range (m/ hr)	Median (m/ hr)	n	Range (m/ hr)	U	Sig.
0900-1059	0.46	30	0.00-14.87	0.61	22	0.00- 4.13	323.5	>0.05
1100-1259	1.54	38	0.00-21.02	0.71	33	0.00-14.15	458.5	>0.05
1300-1459	1.23	38	0.00-17.17	0.29	26	0.00-18.82	358.0	>0.05
1500-1659	1.10	33	0.00-12.45	0.62	28	0.00-16.47	422.5	>0.05
1700-1859	0.49	42	0.00- 9.80	0.37	32	0.00-19.67	605.5	>0.05
1900-2059	0.12	14	0.00- 3.10	0.00	5	0.00- 8.69	33.5	>0.05

Tables 4.7A to C : Median movement rate of male and female *C. austriaca* during different time periods (⁰⁰ hrs BST) in A. Spring, B. Summer and C. Autumn as determined by radio-tracking between 1984 and 1986 inclusive. n = sample size and 'Range' indicates minimum and maximum values observed.

360, $p > 0.05$ respectively) or for female snakes during Spring, Summer or Autumn (chi-squared= 4.28, $n = 14$, chi-squared= 4.79, $n = 262$ and chi-squared= 3.84, $n = 146$ respectively. $p > 0.05$ in all cases). Significant variation in movement rate throughout the day was detected for male snakes during Autumn (chi-squared= 16.58, $n = 195$, $p < 0.01$). During this latter season, male snakes showed a median movement rate of 0.46 m/ hr during the early morning which increased to 1.54 m/ hr, the highest median value recorded, during 1100-1259 hrs. Median movement rate progressively decreased throughout the afternoon and into the late evening, with the minimum recorded median, 0.12 m/ hr, being observed at 1900-2059 hrs. During all time periods minimum recorded movement rates for male snakes in Autumn were 0.00 m/ hr. Maxima increased in the same manner as the medians, with the greatest value being recorded during the 1100-1259 hrs period and these decreased throughout the remainder of the day with the smallest value being recorded during the evening.

4.3.7. Movement behaviour and individual condition

Movement rates of radio-tagged C. austriaca were related to the condition of the animal. The parameters used to assess individual condition were the slough status, the feeding condition and, in the case of females, the breeding condition. In all cases both the hourly rate of movement and daily movement rate were used in the comparisons between the different individual conditions.

a. Slough condition

Four phases within the sloughing cycle were defined, namely 'post-slough', 'mid-slough', 'pre-slough' and 'shedding' (see Chapter 2, section 2.2.2). Data were analysed in two ways, firstly by comparison between all four categories and secondly where only two categories of slough condition were used (these latter categories being formed by amalgamating the 'post-' and 'mid-slough' and the 'pre-slough' and 'shedding' categories to form two new divisions, termed

'after sloughing' and 'before-sloughing' respectively).

Hourly movement rates were significantly heterogeneous between the four defined slough categories (Kruskal-Wallis chi-squared= 37.00, n= 1073, p<0.001). Median hourly movement rates associated with different phases of the sloughing cycle were as follows: 'post-slough' 0.55 m/ hr (range= 0.00 to 32.99 m/ hr, n= 536), 'mid-slough' 0.65 m/ hr (range= 0.00 to 44.26 m/ hr, n= 447), 'pre-slough' 0.15 m/ hr (range= 0.00 to 2.63 m/ hr, n= 82) and 'shedding' 0.28 m/ hr (range= 0.11 to 0.58 m/ hr, n= 8).

Significant variation in hourly movement rates were also observed when slough condition was divided into two categories (U= 27164.5, n₁= 983, n₂= 90, p<0.001). Snakes in the 'after-slough' state demonstrated a larger median movement rate, 0.61 m/ hr (range= 0.00 to 44.26 m/ hr, n= 983), than that shown by specimens in the 'before slough' condition, 0.18 m/ hr (range= 0.00 to 2.63 m/ hr, n= 90).

Daily movement rates varied significantly between the four defined stages of the slough cycle (Kruskal-Wallis chi-squared= 19.36, n= 138, p<0.001). The largest median movement rate was associated with snakes in 'post-slough' condition and was 15.79 m/ day (range= 0.14 to 123.25 m/ day, n= 73). Specimens that were 'mid-slough' had a median movement rate of 14.38 m/ day (range= 0.82 to 166.81 m/ day, n= 53) and for 'pre-slough' animals a median value of 2.52 m/ day (range= 0.00 to 12.78 m/ day, n= 11) was obtained. A single daily movement was recorded for a snake that was 'shedding' this being 5.51 m/ day (n= 1).

When data were pooled to form two slough categories, the median movement rate for the 'after-slough' category was 15.04 m/ day (range= 0.14 to 166.81 m/ day, n= 126) and for the 'before slough' category 4.02 m/ day (range= 0.00 to 12.78 m/ day, n= 12). These data are significantly different (U= 1324.5, n₁= 126, n₂= 12, p<0.001).

b. Feeding condition

No significant differences were detected between the hourly movement rates when data from snakes in three different defined feeding states (as described in Chapter 2, section 2.2.2) were compared via the Kruskal-Wallis test (chi-squared= 7.74, n= 1006, $p > 0.05$). A significant difference, however, was detected between the daily movement rates of snakes in the three different feeding states (chi-squared= 7.06, n= 133, $p < 0.03$).

Median hourly movement rates for 'unfed', 'small item of food in the gut' and 'recently fed' snakes were 0.47 m/ hr (range= 0.00 to 44.25 m/ hr, n= 712), 0.79 m/ hr (range= 0.00 to 19.58 m/ hr, n= 148) and 0.62 m/ hr (range= 0.00 to 26.77 m/ hr, n= 146) respectively. Daily movement rates yielded median movement rates for the three feeding conditions as follows: 11.04 m/ day (range= 0.00 to 123.25 m/ day, n= 98), 14.36 m/ day (range= 0.55 to 90.43 m/ day, n= 20) and 26.66 m/ day (range= 8.92 to 108.60 m/ day, n= 15) respectively.

c. Female breeding condition

No significant effect of breeding condition was observed on the movement rate of female smooth snakes when the hourly and daily movement rates were compared between pregnant and non-pregnant individuals ($U = 7292.0$, $n_1 = 358$, $n_2 = 41$, $p > 0.05$ and $U = 153.0$, $n_1 = 51$, $n_2 = 6$, $p > 0.05$ respectively).

Pregnant specimens demonstrated a median hourly movement rate of 0.49 m/ hr (range= 0.00 to 44.26 m/ hr, n= 358) whilst non-pregnant specimens had a median movement rate of 0.69 m/ hr (range= 0.00 to 14.15 m/ hr, n= 41). Median daily movement rates were 10.17 m/ day (range= 0.00 to 166.81 m/ day, n= 51) and 14.54 m/ day (range= 0.82 to 21.27 m/ day, n= 6) for pregnant and non-pregnant specimens respectively.

4.3.8. Direction of movement

The direction of travel for each minimum monitored distance was calculated as a bearing (between 0 and 359 degrees) and subsequently these bearings were assigned to one of eight, 45° width, bearing categories (NE= 22.6 to 67.5°, E= 67.6 to 112.5 °, SE= 112.6 to 157.5°, S= 157.6 to 202.5°, SW= 202.6 to 247.5°, W= 247.6 to 292.5°, NW= 292.6 to 337.5° and N= 337.6 (through 0) to 22.5°). For each radio-tracking period, total distances moved within each bearing category were summed. Total distances moved during each radio-tracking period were obtained (from the sum of the distances moved within the eight bearing categories) and from this an 'expected' movement distance was calculated for each direction category, based on the assumption of equal movement in each direction (i.e. total distance moved divided by eight). Observed movement rates were compared with these 'expected' values via a G-test where the expected movement rates were greater than or equal to 5 m (i.e. where total distances moved were 40 or more metres).

Total distances moved in each direction category and the total distance moved together with the significance values for the G-test are presented separately for each sex on each site as follows: females on Site One (Table 4.8), males on Site One (Table 4.9), females on Site Two (Table 4.10) and males on Site Two (Table 4.11), these movement distances are illustrated in Figs. 4.10 A to D respectively, where a logarithmic scale is used due to the wide range of values obtained.

In all cases where statistical analysis was possible highly significant deviations from the 'expected' movement distances (i.e. equal movement in each direction) were observed ($p < 0.001$ in all cases).

As a further measure of dispersion the ratio between net displacement (i.e. distance between first and last radio-locations) and total movement was calculated. These are presented for all cases where more than two radio-locations

FEMALES, SITE ONE

Snake	N	NE	E	SE	S	SW	W	NW	Total	Sig.	. Net Movement .		Net/Total ratio
											Distance	Bearing	
FM02	8.6	5.2	3.1	2.1	3.2	10.0	0.0	11.0	43.2	***	12.6	313	0.29
FM08	0.0	0.0	0.2	1.4	0.9	0.6	4.6	5.4	13.1	N/A	8.1	269	0.61
FM13a	4.0	8.7	1.0	7.8	1.3	2.3	11.1	18.2	54.4	***	16.9	315	0.31
FM13b	17.4	3.2	29.6	9.3	6.9	24.4	39.6	10.2	141.4	***	31.3	238	0.22
FM17	1.2	1.5	3.3	6.8	2.2	2.0	4.7	5.1	26.8	N/A	1.6	150	0.06
FM26a	16.5	5.3	9.4	0.0	0.2	8.8	0.0	0.0	40.2	***	11.3	29	0.28
FM26b	0.2	11.7	0.0	2.0	21.9	2.3	0.0	0.0	36.1	N/A	15.9	166	0.44

Table 4.8 : Total distances moved (metres) in each of eight defined direction categories by Female C. austriaca at Site One as determined by radio-tracking between April 1984 and July 1986 inclusive. Total distances moved (metres) and the level of significance obtained from G-tests are presented (***) indicates $p < 0.001$, N/A indicates that the total distance moved was too small for statistical analysis) based on the hypothesis of equal movement in each direction. Net movement distance (metres) and bearing (degrees) show movement between first and last sighting and net/total ratio express net movement distance as a proportion of the total distance moved during each radio-tracking period. Where any animal was radio-tracked more than once, successive radio-tracking periods are indicated by lower case letters.

MALES, SITE ONE

Snake	N	NE	E	SE	S	SW	W	NW	Total	. Net movement .			Net/Total ratio
										Sig.	Distance	Bearing	
MM03	7.0	5.6	6.3	0.0	0.4	1.1	0.5	2.0	22.9	N/A	14.0	34	0.61
MM06	15.7	18.0	64.8	24.6	2.0	8.1	9.7	5.2	150.1	***	76.8	97	0.51
MM07a	5.4	7.4	1.9	0.7	1.3	0.0	2.3	2.4	21.4	N/A	11.0	31	0.51
MM07b	8.6	0.5	0.8	5.7	6.0	5.2	1.7	2.9	31.4	N/A	3.9	219	0.12
MM09	5.7	1.4	2.1	0.0	4.4	0.4	1.3	0.0	15.3	N/A	5.7	216	0.37
MM10	11.4	0.2	0.4	0.7	10.6	18.8	64.1	45.1	151.3	***	115.0	281	0.76
MM11	16.5	3.4	2.3	2.2	5.0	6.8	24.0	41.3	101.5	***	69.9	305	0.69
MM12	37.6	82.8	0.5	1.2	0.7	2.3	5.4	17.0	147.5	***	126.6	17	0.86
MM16a	42.5	14.7	24.4	17.0	0.0	0.9	1.4	11.5	112.4	***	66.4	41	0.59
MM16b	53.3	25.2	10.8	0.2	3.4	1.0	0.0	3.9	97.8	***	74.4	15	0.76
MM16c	11.5	19.8	6.5	3.8	10.1	35.2	46.6	17.9	151.4	***	56.4	263	0.37
MM19	8.9	49.1	3.0	4.9	20.6	1.4	2.9	0.0	90.8	***	41.6	72	0.46

Table 4.9 : Total distances moved (metres) in each of eight defined direction categories by Male C. austriaca at Site One as determined by radio-tracking between April 1984 and July 1986 inclusive. Total distances moved (metres) and the level of significance obtained from G-tests are presented (***) indicates $p < 0.001$, N/A indicates that the total distance moved was too small for statistical analysis) based on the hypothesis of equal movement in each direction. Net movement distance (metres) and bearing (degrees) show movement between first and last sighting and net/total ratio express net movement distance as a proportion of the total distance moved during each radio-tracking period. Where any animal was radio-tracked more than once, successive radio-tracking periods are indicated by lower case letters.

FEMALES, SITE TWO

Snake	N	NE	E	SE	S	SW	W	NW	Total	Sig.	Net Movement		
											Distance	Bearing	.Net/Total ratio
FH01	0.6	0.2	1.1	0.4	0.0	0.9	0.0	3.9	7.1	N/A	4.2	322	0.59
FH03	25.2	0.7	10.9	0.0	13.9	21.4	3.8	199.4	275.3	***	203.4	278	0.74
FH09a	3.1	0.2	1.8	2.1	2.1	0.1	19.1	103.5	132.0	***	118.5	273	0.90
FH09b	10.3	3.1	39.9	109.1	109.7	0.2	0.0	4.7	277.0	***	195.2	129	0.70
FH11	25.5	0.6	3.5	5.6	2.1	2.0	14.4	38.5	92.2	***	60.1	296	0.65
FH12	1.2	2.3	26.0	5.7	21.0	10.5	50.4	45.4	162.5	***	66.1	248	0.41
FH13	0.5	0.0	73.8	24.9	0.0	0.4	80.4	11.1	191.1	***	5.3	84	0.03
FH37	0.0	0.4	6.4	0.6	2.2	0.4	16.3	9.8	36.6	N/A	14.4	268	0.39
FH39	0.0	0.5	1.3	0.0	10.7	8.9	4.6	11.0	37.0	N/A	18.0	216	0.48
FH44	0.7	0.5	0.8	2.6	0.5	0.0	13.7	6.0	24.8	N/A	15.8	269	0.64
FH56	28.0	6.3	39.0	13.3	2.5	1.0	42.6	53.3	186.0	***	58.7	295	0.32

Table 4.10 : Total distances moved (metres) in each of eight defined direction categories by Female *C. austriaca* at Site Two as determined by radio-tracking between April 1984 and July 1986 inclusive. Total distances moved (metres) and the level of significance obtained from G-tests are presented (***) indicates $p < 0.001$, N/A indicates that the total distance moved was too small for statistical analysis) based on the hypothesis of equal movement in each direction. Net movement distance (metres) and bearing (degrees) show movement between first and last sighting and net/total ratio express net movement distance as a proportion of the total distance moved during each radio-tracking period. Where any animal was radio-tracked more than once, successive radio-tracking periods are indicated by lower case letters.

MALES, SITE TWO

Snake	N	NE	E	SE	S	SW	W	NW	Total	Sig.	. Net Movement .Net/total		
											Distance	Bearing	ratio
MH02	6.0	14.8	87.2	7.4	23.5	22.5	5.7	12.8	179.9	***	81.9	88	0.45
MH04	2.5	0.0	5.9	1.1	0.0	0.0	0.4	1.3	11.2	N/A	6.8	31	0.61
MH06a	6.5	10.2	11.6	0.0	6.8	0.0	0.0	12.5	47.6	***	23.7	360	0.50
MH06b	0.0	0.4	12.8	9.1	0.0	12.6	0.0	11.2	46.1	***	11.9	133	0.26
MH10a	3.1	4.4	1.0	2.8	3.1	8.1	27.3	67.9	117.7	***	88.7	279	0.75
MH10b	29.2	2.6	32.2	3.1	0.4	40.0	21.9	35.4	118.2	***	49.4	304	0.42
MH10c	3.2	14.1	33.4	10.2	10.0	2.5	2.5	2.3	78.2	***	47.6	77	0.61
MH17	0.0	0.0	0.0	0.9	0.0	0.0	0.0	7.8	8.7	N/A	6.9	302	0.79
MH22a	6.3	1.5	0.0	6.7	2.9	3.0	10.1	9.0	39.5	N/A	17.7	252	0.45
MH22b	0.0	0.0	0.0	0.0	3.8	0.0	0.0	0.9	4.7	N/A	3.0	150	0.64
MH29	46.3	7.5	21.9	2.0	7.2	9.2	1.9	21.9	117.9	***	52.5	359	0.45
MH33	41.2	62.7	73.9	15.0	1.1	41.8	42.7	39.5	317.0	***	75.8	340	0.24
MH38	0.0	0.0	74.6	38.1	66.5	36.0	16.1	0.3	231.6	***	168.6	137	0.73
MH42	39.8	0.8	6.6	2.2	15.1	3.7	48.2	36.1	152.2	***	89.6	281	0.59
MH49	0.0	0.0	0.0	34.2	104.9	46.8	0.6	4.0	190.5	***	156.3	163	0.82
MH5B	3.1	13.2	5.0	11.5	17.3	1.4	0.0	1.0	52.5	***	25.0	95	0.48

Table 4.11 : Total distances moved (metres) in each of eight defined direction categories by Male C. austriaca at Site Two as determined by radio-tracking between April 1984 and July 1986 inclusive. Total distances moved (metres) and the level of significance obtained from G-tests are presented (***) indicates $p < 0.001$, N/A indicates that the total distance moved was too small for statistical analysis) based on the hypothesis of equal movement in each direction. Net movement distance (metres) and bearing (degrees) show movement between first and last sighting and net/total ratio express net movement distance as a proportion of the total distance moved during each radio-tracking period. Where any animal was radio-tracked more than once, successive radio-tracking periods are indicated by lower case letters.

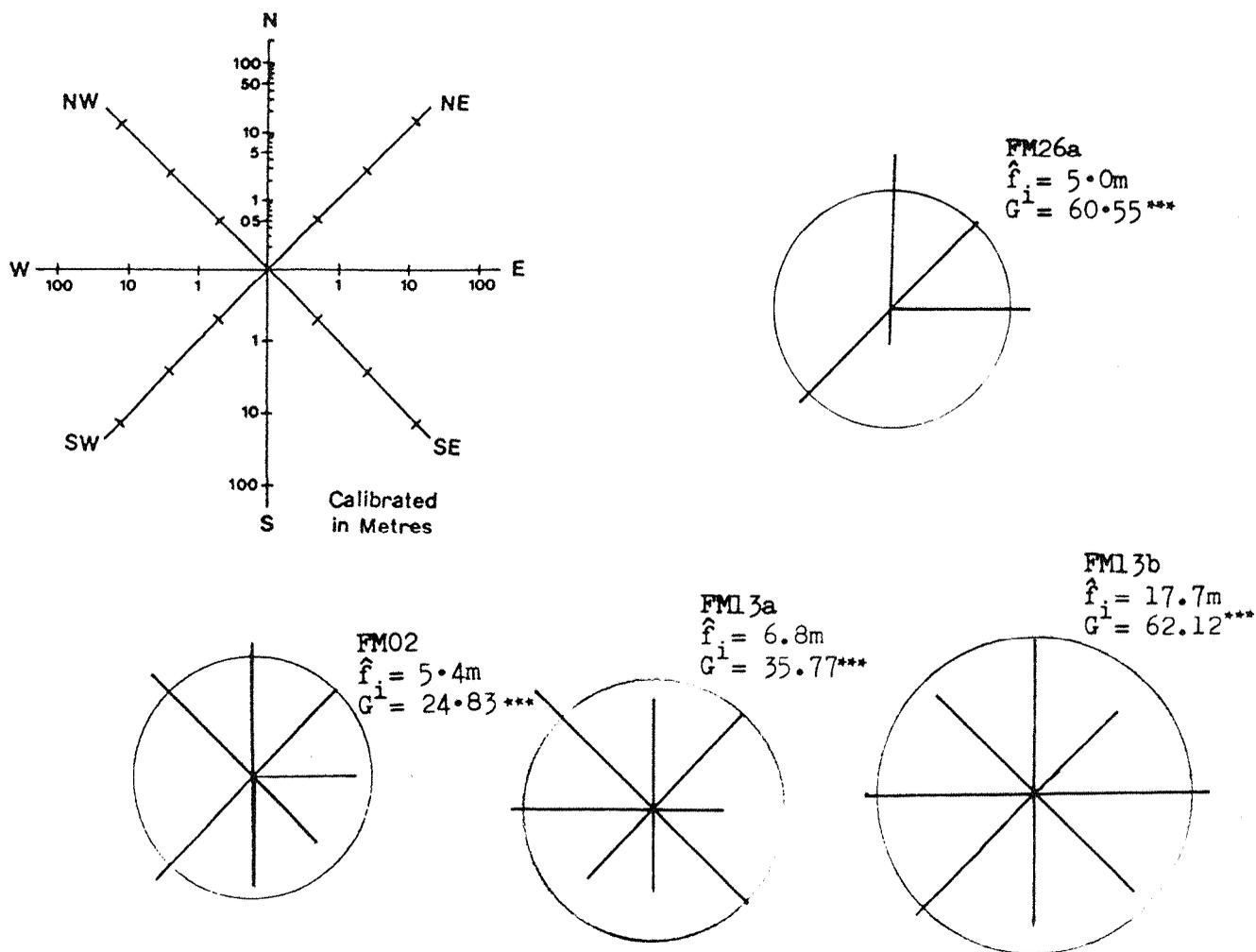


Fig. 4.10 A. : Female specimens at Site One.

Figs. 4.10 A. to D. : Logarithmic plot (Log_{10}) of total distance moved (m) by specimens of C. austriaca in each of eight defined direction categories during each radio-tracking period between April 1984 and July 1986 for A. Female specimens at Site One, B. Male specimens at Site One, C. Female specimens at Site Two and D. Male specimens at Site Two. 'Expected' movement distances for each direction, calculated by dividing the total distance moved by eight, are given (\hat{f}_i) (and represents the diameter of the circle drawn in each case) as are the value of G and the associated probability based on the hypothesis of equal movement in each direction ($*** = p < 0.001$). Successive radio-tracking periods for any specimen are indicated by lower case letters after the four character identification code for that specimen.

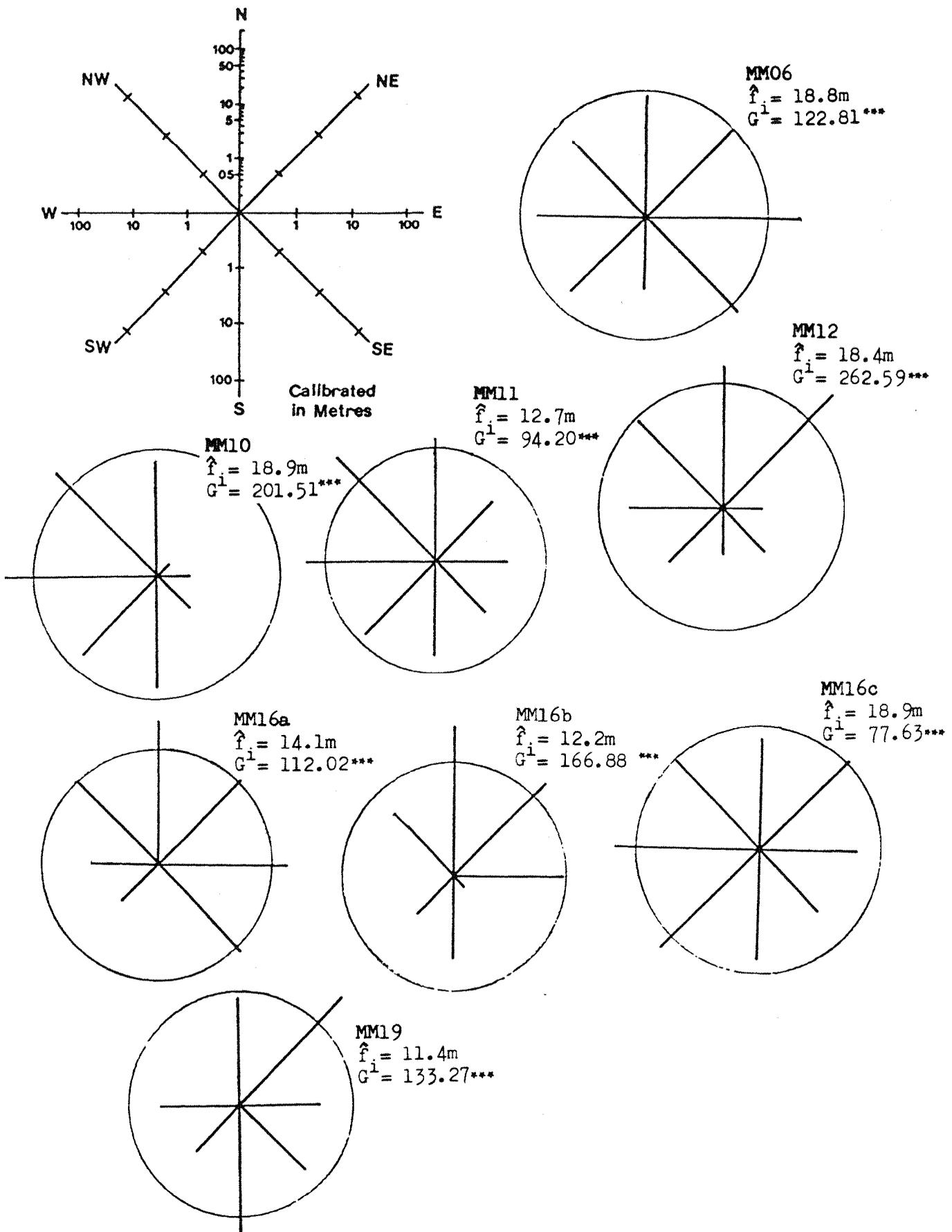


Fig. 4.10 B. : Males at Site One.

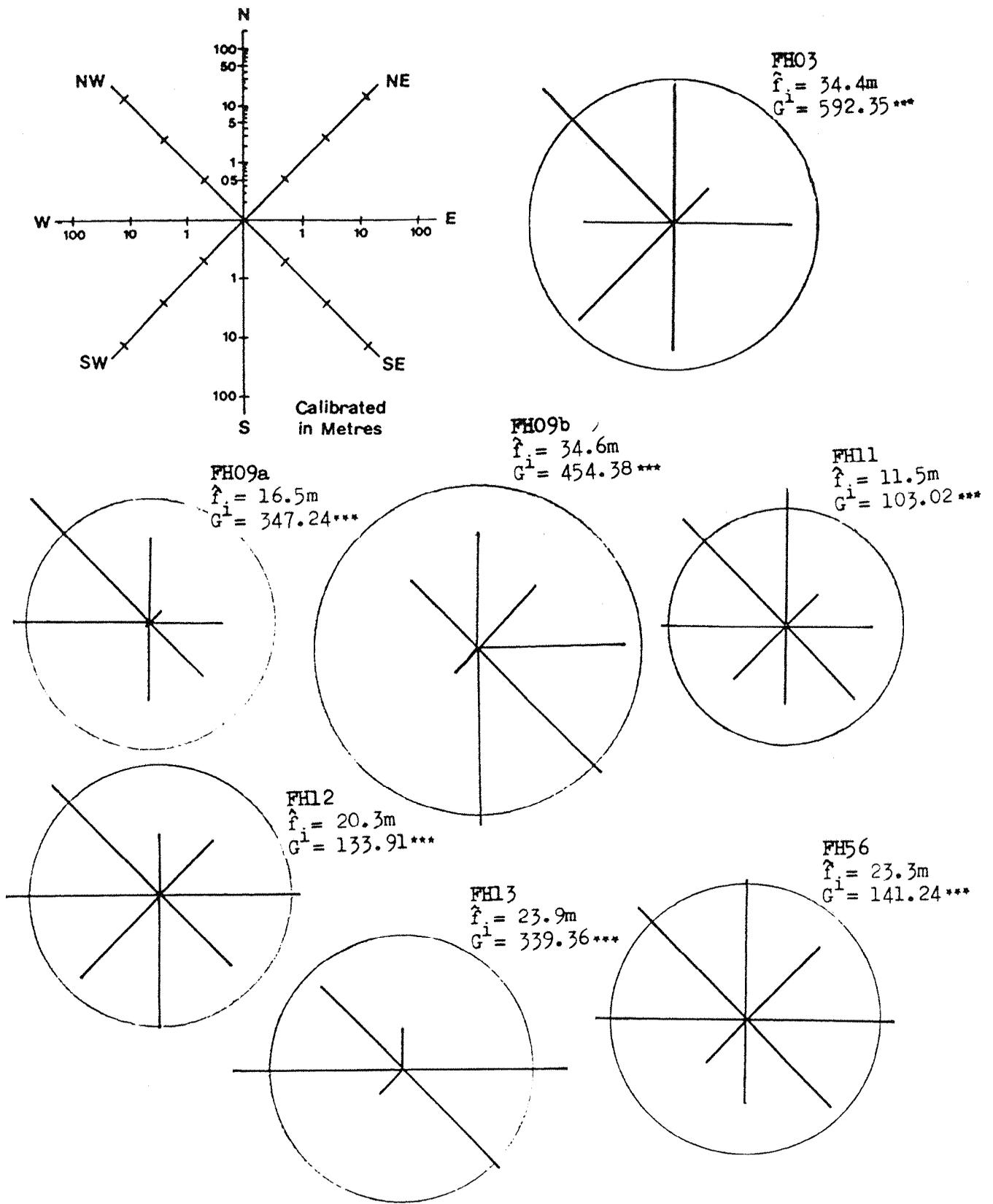
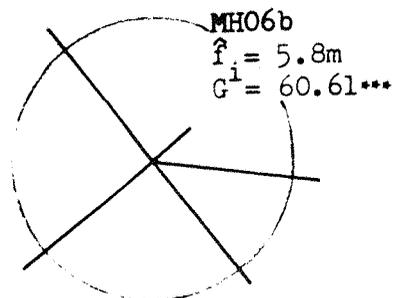
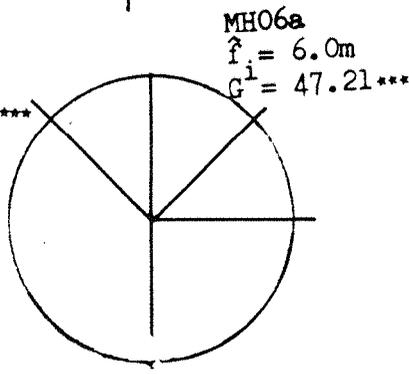
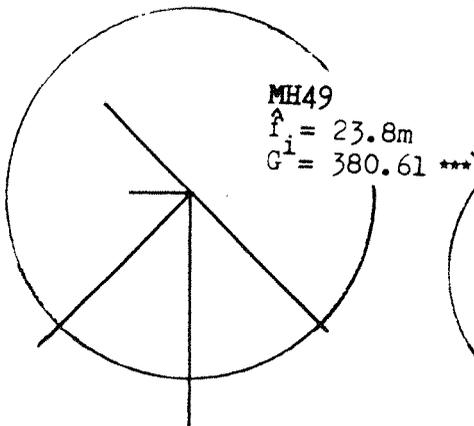
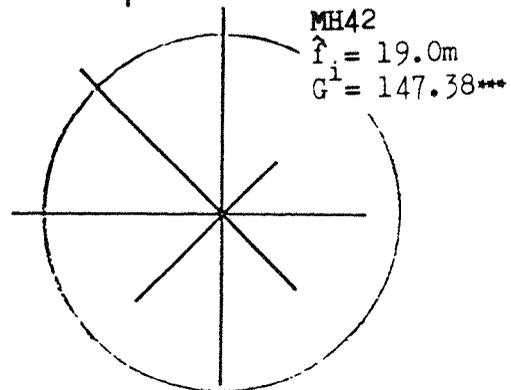
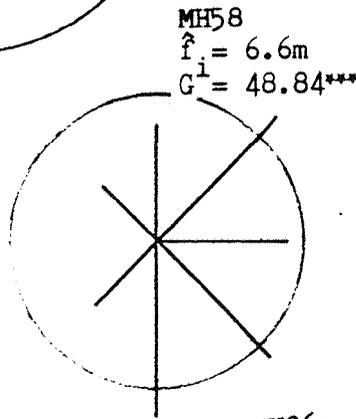
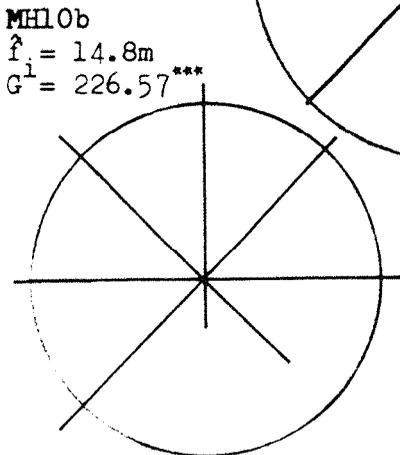
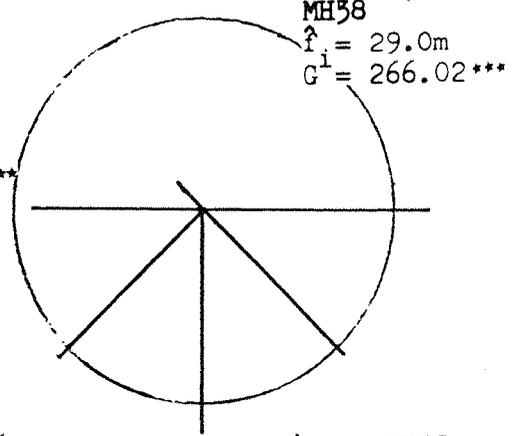
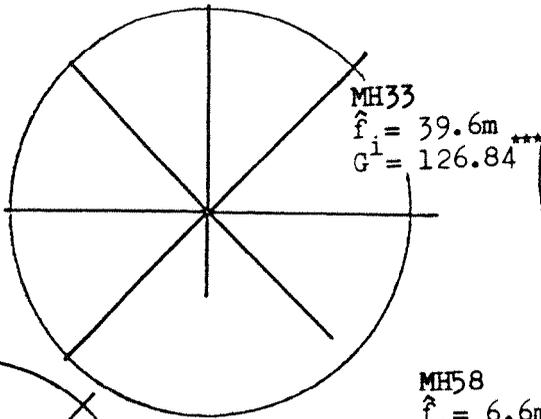
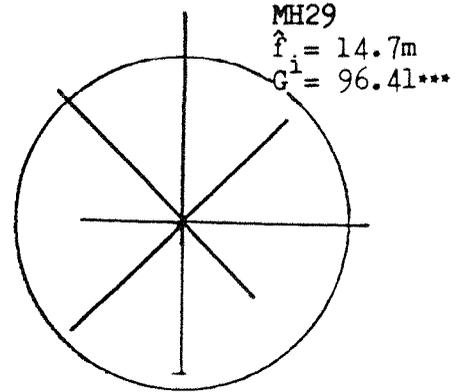
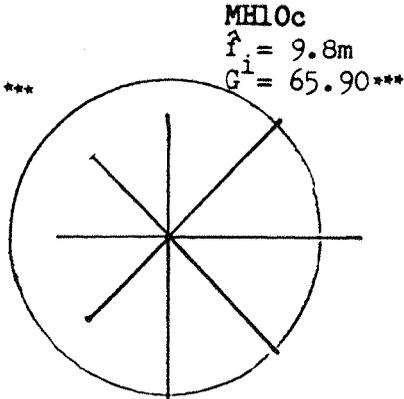
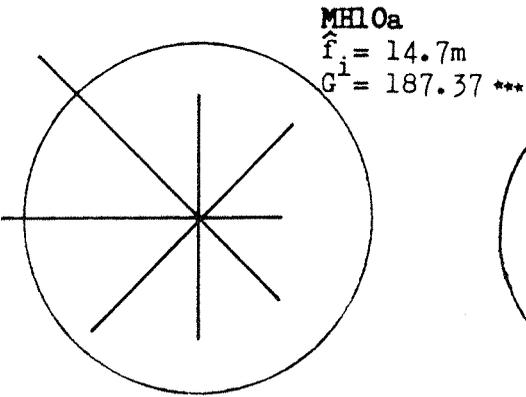
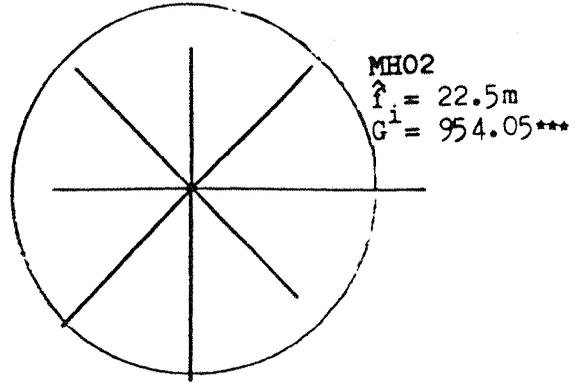
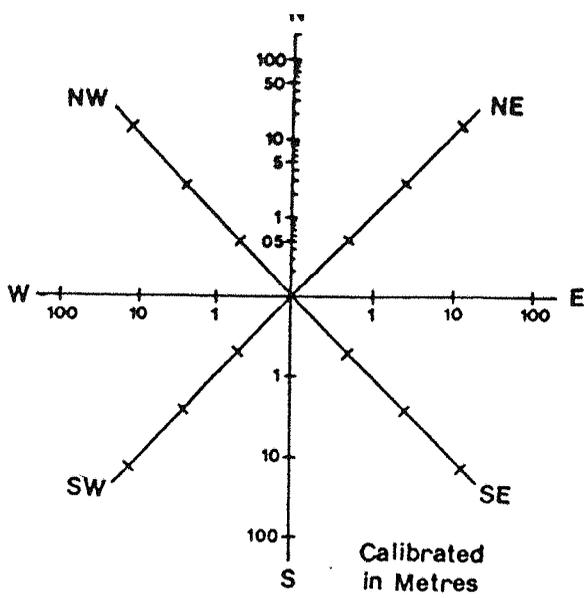


Fig. 4.10 C. : Females at Site Two.

Fig. 4.10 D. : Males at Site Two



were made in Tables 4.8 to 4.11 for the two sexes and two sites as above. A value of this ratio equal to or above 0.50 was arbitrarily considered as showing a large degree of dispersal, since 50% or more of the movement shown by that animal contributed to the net displacement. In cases where only few minimum monitored distances were collected this ratio will be greatly influenced by sample size as it is likely that the uneven movement would occur purely by chance. To reduce this possible bias, radio-tracking periods where less than a total of 20.0 m were travelled were arbitrarily chosen and excluded from further discussion. Movement of 20.0 m and over was likely to include data for the whole daily cycle and would reduce the possibility of any effects of diurnal changes in dispersal behaviour.

Values of this ratio ranged between 0.03 and 0.90. A total of 19 (47.5%) of the 40 suitable data sets (where 20.0 m or more had been travelled during the period) had a value equal to or in excess of 0.50. At Site One none of the six radio-tracking periods where females were used showed a Net/Total ratio of 0.50 or more, whereas eight (72.7%) of the 11 studies of males had values equal to or above 0.50. At Site Two both males and females showed similar dispersal patterns with half the cases having values for this ratio equal to or above, and the other half below, 0.50 for each sex. In males six (46.2%) of 13 and in females five (50.0%) of ten radio-tracking periods showed a value for the Net/Total ratio of 0.50 or over. No significant differences were detected between the values of these ratios between male and female snakes when data from both sites were pooled ($U= 266.5$, $n_1 = 16$, $n_2 = 24$, $p > 0.05$) or at Site Two ($U= 116.5$, $n_1 = 10$, $n_2 = 13$, $p > 0.05$), nor was a difference detected between the two sites when data for both sexes were pooled ($U= 321$, $n_1 = 17$, $n_2 = 23$, $p > 0.05$). Female snakes had lower values for these ratios than male snakes at Site One ($U= 27$, $n_1 = 6$, $n_2 = 11$, $p < 0.02$); this indicated that females tend to disperse less than males at this site.

4.3.9. Activity patterns in the field

a. Movement activity

Changes in signal strength associated with movement of the transmitter relative to the receiving equipment allow observation of the activity patterns of radio-tagged animals. Details of the method used during the present study are presented in Chapter 2 (section 2.2.3 c). Activity patterns observed from continuous monitoring of three specimens for short periods during the Summer of 1986 are presented in Fig. 4.11. Shade air temperatures recorded at hourly intervals (measured to the nearest 1°C) are presented graphically below the activity ethogram.

Activity, represented by vertical lines in Fig. 4.11, occurs mostly in a period from between one quarter of one hour and one and a half hours after sunrise, until one to two hours after sunset, with little or no activity being recorded during the night time. Data were recorded between 0000 hrs until after sunrise on four occasions and first recorded movement were observed at 0625 hrs (sunrise at 0448 hrs), 0609 hrs (sunrise at 0510 hrs), 0626 hrs (sunrise at 0515 hrs) and 0548 hrs (sunrise at 0520 hrs) although during the second of these periods slight movements were detected at 0004 and 0016 hrs. No movement records were observed in the hours immediately before sunrise. These first movements, post-sunrise, are associated with shade air temperatures of 17°, 9°, 11° and 15°C respectively.

Of particular interest to this method of study is the observation of nocturnal behaviour of the smooth snake which was not studied in the field by any other method. In all cases where a complete record of night time movement was recorded (four cases) a considerable period of non-movement was observed. Final detected movements prior to the onset of these periods of inactivity were at 2130 hrs (sunset at 2125 hrs), 0016 hrs (sunset at 2110 hrs), 2215

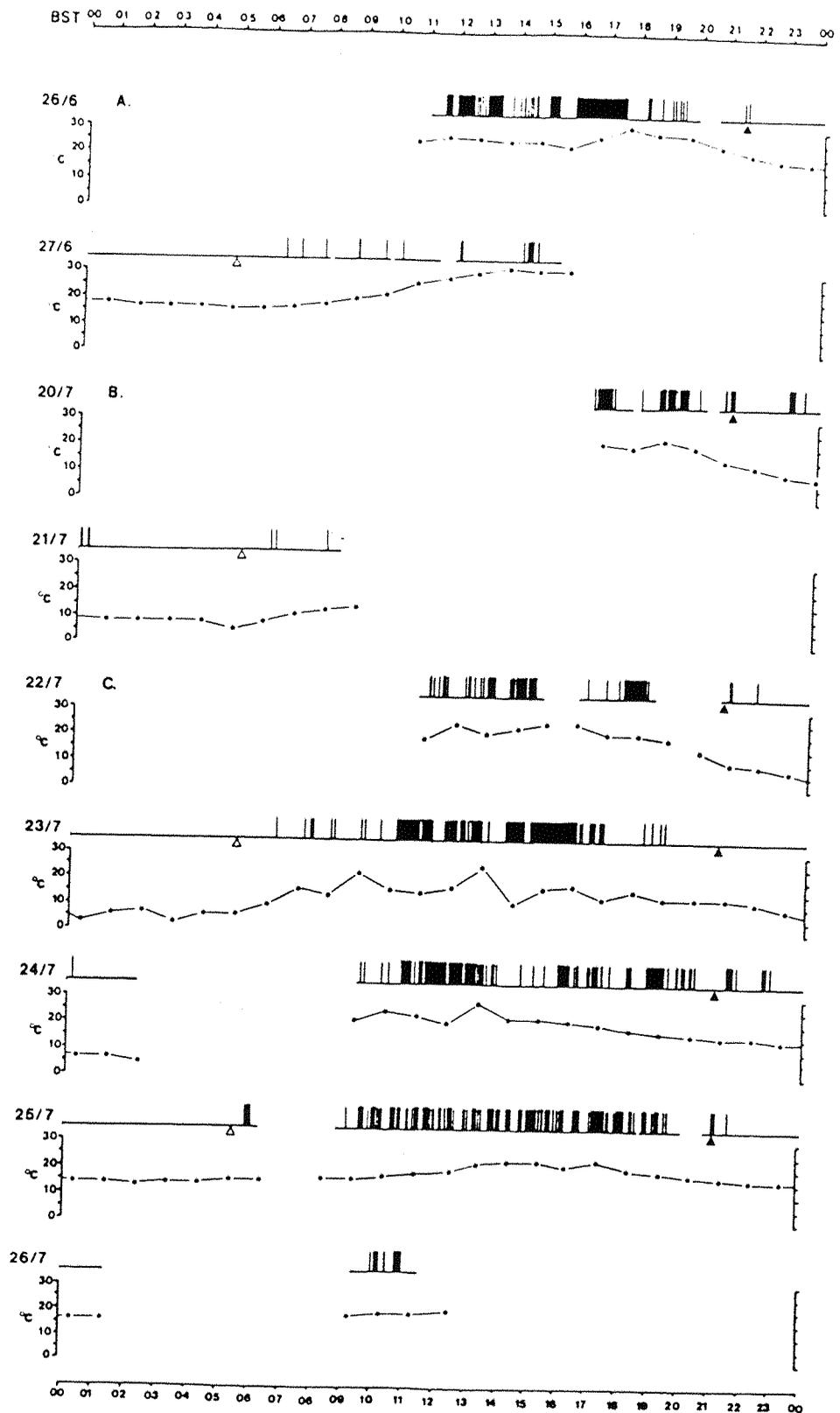


Fig. 4.11 : Movement activity of radio-tagged specimens of *C. austriaca* against time of day ('00 hrs BST) during Summer 1986 with corresponding shade air temperatures ($^{\circ}\text{C}$) below. Movement activity is indicated by a vertical line / block, non-movement by a horizontal line. Areas with no line indicate periods where no record was obtained. Data for three specimens are presented: A. Female M26 (26-27th June), B. Male H6 (20-21st July) and C. Female H56 (22-26th July). Sunrise and sunset are indicated by open (Δ) and closed (\blacktriangle) triangles respectively.

hrs (sunset at 2107 hrs) and 2252 hrs (sunset at 2105 hrs). These periods of inactivity lasted 8.92, 5.88, 8.18 and 6.93 hours respectively. Shade air temperatures at the onset of these periods of nocturnal inactivity were 20°, 9°, 9° and 16°C respectively.

Diel activity patterns were further investigated by arbitrarily dividing the day and night into forty-eight 30 minute periods, each beginning on the hour or at thirty minutes past the hour. All periods for which a unbroken record of activity was obtained were divided into either of two categories, namely: those in which some movement was observed and those in which no movement was observed. The number of records that indicated movement were totalled and expressed as a proportion of the total number of records for each thirty minute period. These proportions were then plotted for the relevant time period. These data are presented in Fig. 4.12.

Between two and six records of activity were available for each 30 minute time period (sample sizes for each case are presented in Fig. 4.12). During the early morning, between 0530 and 1030 hrs, a tendency for movement to occur in an increasing proportion of activity records was observed. In all cases between 1030 and 1930 hrs from 80 to 100% of activity records demonstrated some movement. This proportion tended to decrease progressively during the evening. No activity records that were obtained between 0030 and 0530 hrs demonstrated any movement at all.

Temperature data were divided into two categories, namely those values that were recorded when movement was detected within a one hourly period 'centred' on the time of the temperature record (i.e. 30 minutes on either side of the reading) and those where no movement occurred during that hourly period. Only data where a complete hourly period was available were used in this analysis. A total of 104 such temperature records were obtained, with 67 of these being associated with a period in which movement occurred and the remaining 37 temperatures were associated with hourly

periods where no movement was detected at all. These data are illustrated in Fig. 4.13. No heterogeneity of variances was detected between the time periods with movement and those where movement was not observed ($F_{max} = 1.042$, $p > 0.05$) and hence the two sets of data were compared via a Student's t-test. The mean shade air temperature associated with hours in which movement occurred was $19.3^{\circ}\text{C} \pm 5.72$ ($n = 67$) and was significantly higher than that obtained from those periods in which no movement was detected (mean = $12.6^{\circ}\text{C} \pm 5.84$ ($n = 37$)) ($t = 5.72$ with 102 d.f., $p < 0.001$).

b. Observed behaviour during the day

The behaviour of each smooth snake located was recorded and was assigned to one of nine behaviour categories as follows: locations where the snake could not be visually observed, or where more than 95% of the snake's body was concealed from view (e.g. by dense vegetation) were classified as being 'under cover', those that were basking were assigned to one of six bask posture categories with a larger number indicating a tighter coiled posture (see Chapter 2, section 2.2.2. and Fig. 2.1), animals that were moving above ground (for whatever reason) were assigned to 'Moving' and other activities (e.g. feeding, mating) were classified as 'Other'. No snakes were observed exhibiting any behaviour relevant to this latter category and hence the below analysis is limited to eight behaviour types.

Data from 1313 radio-locations were classified according to the above system. These were collated, separately for each sex, each study site and each of the three defined seasons (Spring = March to May, Summer = June to August, Autumn = September and October), and the total number of observations in each of the defined behaviour categories is presented in Table 4.12. When data were pooled the behaviours of snakes from the two study sites were shown not to be statistically different (using both the Spearman's rank test and G-test) ($r_s = 0.810$, $n = 8$, $p < 0.05$ (i.e. significant correlation); $G = 6.849$ with 7 d.f., $p > 0.05$), with the majority of records in each case being

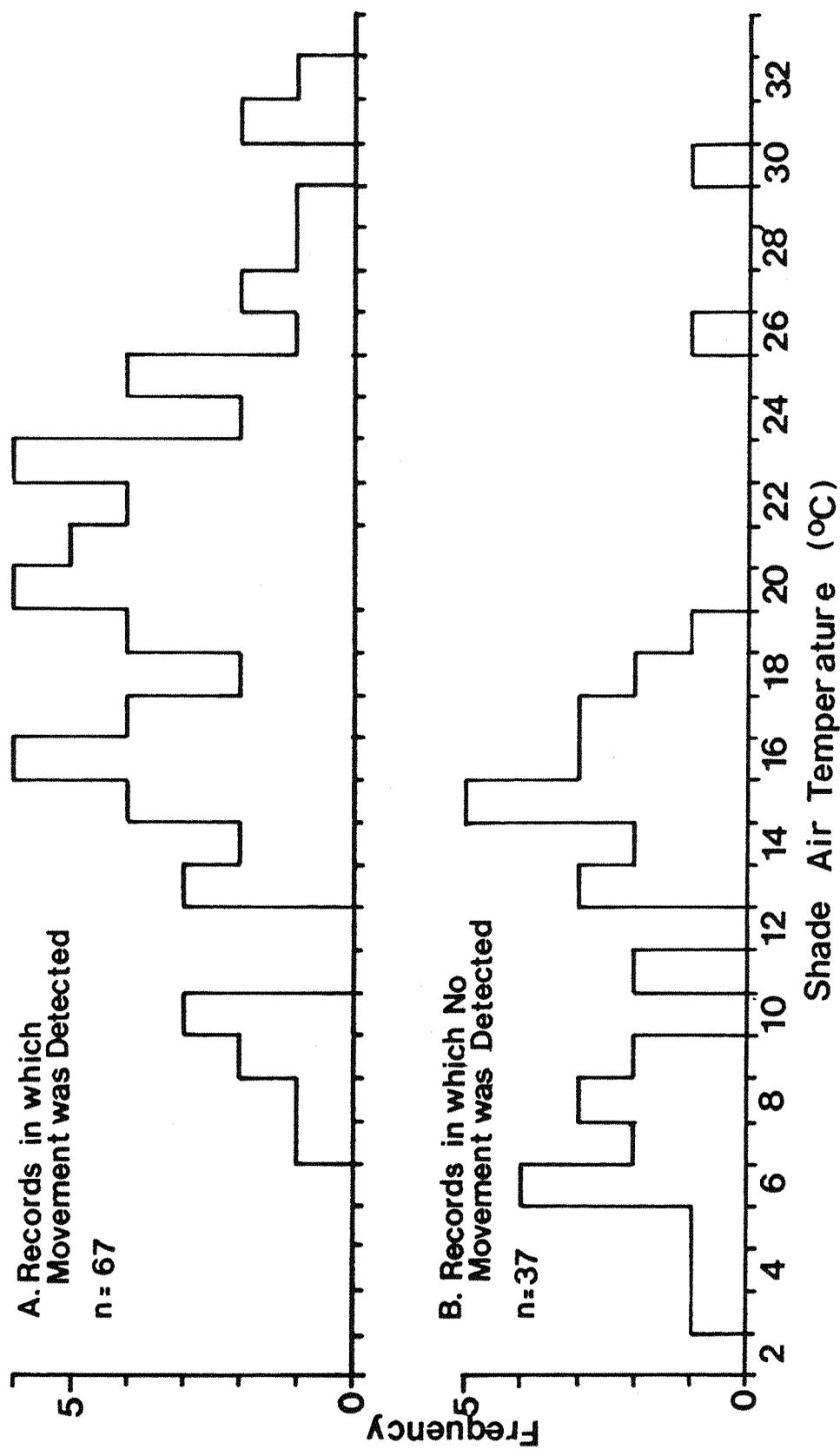


Fig. 4.13 : Shade air temperatures ($^{\circ}\text{C}$) associated with one-hour activity records for: A. those records in which movement was detected and B. those records in which no movement was detected as determined by continuous activity recording of three radio-tagged specimens of C. austriaca in June and July 1986. Sample sizes in each case are given (n).

	:Below:	Basking						:Moving:	n :
:cover:	1 :	2 :	3 :	4 :	5 :	6 :	:	:	
Males - Site One									
Spring	: 43	1	4	1	1	5	0	3 : 58:	
Summer	: 118	2	12	14	8	10	3	12 : 179:	
Autumn	: 115	1	6	3	15	8	7	8 : 163:	
Females - Site One									
Spring	: 8	0	5	1	1	0	0	0 : 15:	
Summer	: 76	0	9	15	13	9	11	3 : 136:	
Autumn	: 25	0	1	2	5	7	2	6 : 48:	
Males - Site Two									
Spring	: 57	0	0	1	1	4	2	4 : 69:	
Summer	: 173	2	8	10	15	18	8	21 : 255:	
Autumn	: 41	4	4	3	8	8	7	7 : 82:	
Females - Site Two									
Spring	: 0	0	0	0	0	0	0	0 : 0:	
Summer	: 109	1	12	8	17	17	5	14 : 183:	
Autumn	: 60	0	11	11	16	12	8	7 : 125:	
Both sites - all seasons									
Males	: 547	10	34	32	48	53	27	55 : 806:	
Females	: 278	1	38	37	52	45	26	30 : 507:	
Both sexes - all seasons									
Site One:	385	4	37	36	43	39	23	32 : 599:	
Site Two:	440	7	35	33	57	59	30	53 : 714:	
Total	: 825	11	72	69	100	98	53	85 : 1313:	

Table 4.12 : Number of observations of *C. austriaca* in each of the eight defined behaviour categories separated by sex and site for each of the three seasons and by sex and by site only for data from all three seasons together. Data collected by radio-tracking during 1984 and 1986 inclusive. Total numbers of observations in each category are given under the heading 'n'.

animals observed below cover, with fairly consistent intermediate number of observations of snakes basking in postures 2 to 5 inclusive and moving and lower numbers of tightly coiled snakes (posture 6) and outstretched snakes (posture 1). Data from both sites were therefore combined for further analysis.

Combined data from the two study sites showed a difference in the occurrence of each behaviour when compared between the sexes with regards to both the rank order ($r_s = 0.476$, $n = 8$, $p > 0.05$ (i.e. no correlation)) and the frequency of observations of each behaviour ($G = 38.031$ with 7 d.f., $p < 0.001$). A greater proportion of observations of male snakes were below cover and fewer observations of male snakes basking in postures 1, 2, 3 and 4 were observed than would have been expected for the given ratio of male to female snakes. Conversely, relatively fewer observations of females were below cover and relatively more females were observed basking in postures 1 to 4 inclusive ($G = 8.580$, $p < 0.01$; $G = 4.843$, $p < 0.05$; $G = 5.913$, $p < 0.05$; $G = 6.410$, $p < 0.01$; $G = 7.355$, $p < 0.01$ respectively, with 1 d.f. in all cases). There was no difference in the number of observations of males and females basking in postures 5 and 6 or moving ($G = 2.189$; $G = 2.347$; $G = 0.394$, with 1 d.f. and $p > 0.05$ in all cases).

The frequency of occurrences of each behaviour during each of the seasons is presented for each of the sexes for each site separately in Table 4.12 and for both sites combined in Table 4.13. Small sample sizes meant statistical comparisons of the occurrence of each behaviour between sexes for each season and between the seasons for each sex needed to be treated with some caution. Spearman's rank tests were performed on the data for both sites combined, and indicated a difference in the rank order between males and females in Spring ($r_s = 0.327$, $n = 8$, $p > 0.05$) and in Summer ($r_s = 0.691$, $n = 8$, $p > 0.05$). The rank order of behaviours for the two sexes was significantly correlated in Autumn ($r_s = 0.874$, $n = 8$, $p < 0.03$), which indicated similarity in behaviour between males and females

	:Below:	Basking						:Moving:	n :
	:cover:	1 :	2 :	3 :	4 :	5 :	6 :	:	:
Males - Site One and Site Two									
Spring	: 100	1	4	2	2	9	2	7	: 127:
Summer	: 291	4	20	24	23	28	11	33	: 434:
Autumn	: 156	5	10	6	23	16	14	15	: 245:
Total	: 547	10	34	32	48	53	27	55	: 806:
Females - Site One and Site Two									
Spring	: 8	0	5	1	1	0	0	0	: 15:
Summer	: 185	1	21	23	30	26	16	17	: 319:
Autumn	: 85	0	12	13	21	19	10	13	: 173:
Total	: 278	1	38	37	52	45	26	30	: 507:
Total	: 825	11	72	69	100	98	53	85	: 1313:

Table 4.13 : Number of observations of *C. austriaca* in each of the eight defined behaviour categories separated by sex for both sites combined, for each of the three seasons separately and together. Data was collected by radio-tracking during 1984 and 1986 inclusive. Total numbers of observations in each category are given under the heading 'n'.

during this latter season.

For male snakes, differences in behaviour between Spring and Autumn ($r_m = 0.708$, $n = 8$, $p > 0.05$) and between Summer and Autumn ($r_m = 0.691$, $n = 8$, $p > 0.05$) were indicated by rank correlation, although behaviour in Spring was correlated with that observed in Summer ($r_m = 0.854$, $n = 8$, $p < 0.03$). Thus, males showed a difference in behaviour in Autumn to that shown during the rest of the year. Females, however, demonstrated a difference in behaviour during the Spring to that shown during the rest of the year. Significant correlation was observed between the frequency of each behaviour during Summer and Autumn ($r_m = 0.958$, $n = 8$, $p < 0.02$) but not between Spring and Summer ($r_m = 0.664$, $n = 8$, $p > 0.05$) or Spring and Autumn ($r_m = 0.514$, $n = 8$, $p > 0.05$). It should be noted that only 15 radio-locations of female smooth snakes were made during Spring and included in this analysis.

Where data for both sites were combined (Table 4.13), the most frequently encountered behaviour category for both males and females in all seasons was where snakes were located below cover. In all three seasons a greater proportion of observations of male snakes were 'below cover' than female snakes (the percentage of observations of male snakes below cover was 78.7% in Spring, 67.1% in Summer and 63.7% in Autumn; for females 53.3%, 58.0% and 49.1% of observations were below cover in Spring, Summer and Autumn respectively). Rank orders indicated that movement was more important to males than females in all seasons (with movement being ranked third, second and fourth for males and sixth and a half, sixth and fourth and a half for females in Spring, Summer and Autumn respectively). The percentage of observations of snakes that indicated movement were, however, comparable between the sexes during the three seasons (for males 5.5%, 7.6% and 6.1% of observations were of moving snakes during Spring, Summer and Autumn; for females the respective percentages were 0.0%, 5.3% and 7.5%).

Females spent a greater proportion of time basking than males in all seasons. With the exception of bask posture 1, for which there were very few observations (and bask postures 5 and 6 in Spring for which no records of female snakes were made), the proportion of observations of snakes basking in each of the defined bask postures was greater for females than males during each season (the proportion of observations, in bask postures 1 to 6 respectively, were as follows: for females: i. Spring: 0.0%, 33.3%, 6.7%, 6.7%, 0.0%, 0.0%; ii. Summer: 0.3%, 6.6%, 7.2%, 9.4%, 8.2%, 5.0%; iii. Autumn: 0.0%, 6.9%, 7.5%, 12.1%, 11.0%, 5.8%; for males: i. Spring: 0.8%, 3.1%, 1.6%, 1.6%, 7.1%, 1.6%; ii. Summer: 0.9%, 4.6%, 5.5%, 5.3%, 6.5%, 2.5%; iii. Autumn: 2.0%, 4.1%, 2.4%, 9.4%, 6.5%, 5.7%).

Male snakes showed a decreasing relative occurrence of observations below cover during the progress of the seasons from Spring to Autumn. During the Autumn, the ranked value for movement decreased to fourth (having been third in Spring and second in Summer) this representing 6.1% of observations of male snakes (having been 5.5% in Spring and 7.6% in Summer). Male snakes spent a greater proportion of time basking during Autumn than during Spring or Summer, with the increase in both proportion and rank values of postures 4 and 6 being most notable. Females showed a fairly consistent use of cover during the three seasons although the greatest proportion of observations of this behaviour occurred in the Summer. Differences between behaviour in Spring and that recorded in the other seasons may in part be explained by the small sample size obtained for female snakes during that time. Nonetheless a large difference in the relative occurrence of bask posture 2 is notable with 33.3% of observations in Spring being this behaviour whereas only 6.6% and 6.9% of observations were of snakes in bask posture 2 in Summer and Autumn respectively.

Due to the small sample sizes encountered, data for males and females were combined for further analysis since this required further sub-division of the data set.

With the aim of investigating daily variation in behaviour, data were subdivided into observations made in each of eight two-hour time periods, between 0600 hrs and 2159 hrs (BST). The data were analysed separately for each season. The frequency of occurrences of each behaviour throughout the day are presented in Tables 4.14 A. to D. and the relative occurrence of each are shown in Fig. 4.14 A. to D. for Spring, Summer, Autumn and All seasons respectively.

A large proportion of the radio-locations found snakes below cover of some sort, with a minimum of 27.8% of observations being below cover during any one time period (during Autumn, 1200 to 1359 hrs). Throughout the study period 825 observations (62.8%) were of animals that were 'below cover'. During both the Summer and Autumn, the use of cover decreases during the morning to a minimum between 1200 and 1559 hrs. During Spring no clear trend of use of cover is detectable during the morning. During all three seasons, when analysed separately and together, an increase in the use of cover can be detected during the afternoon until the 2000 to 2159 hrs period. In this latter time period nearly all radio-locations showed the snake to be below cover in the Summer (and all seasons combined) with all observations of snakes being below cover by this time in Spring and Autumn. A greater proportion of snakes were observed out of cover during the 1800 to 1959 hrs category during the summer than during Autumn or Spring.

Basking behaviour (as shown by the total time spent on the six defined basking behaviours collectively) increased during the morning in all seasons. The greatest proportion of time assigned to basking was during 1200 to 1359 hrs in Spring and Autumn and 1400 to 1559 hrs in Summer; although only a slightly smaller proportion of time was spent basking between 0800 and 0959 hrs in the Spring. The occurrence of basking behaviour decreased during the afternoon with the latest periods of basking being observed during 1600 to 1759 hrs in the Spring and 1800 to 1959 hrs

A. Spring

	:Below:	Basking						:Moving:	n :
	:cover:	1 :	2 :	3 :	4 :	5 :	6 :	:	:
0600-0759	:	0	0	0	0	0	0	0	: 0
0800-0959	:	4	0	2	0	0	1	0	: 8:
1000-1159	:	23	0	2	0	1	1	0	: 29:
1200-1359	:	13	1	1	2	1	3	1	: 24:
1400-1559	:	22	0	2	0	1	1	1	: 28:
1600-1759	:	22	0	2	1	0	3	0	: 29:
1800-1959	:	22	0	0	0	0	0	0	: 22:
2000-2159	:	2	0	0	0	0	0	0	: 2:
Total	:	108	1	9	3	3	9	2	: 7 : 142:

B. Summer

	:Below:	Basking						:Moving:	n :
	:cover:	1 :	2 :	3 :	4 :	5 :	6 :	:	:
0600-0759	:	19	0	0	1	0	0	0	: 1 : 21:
0800-0959	:	71	3	9	8	3	3	1	: 5 : 103:
1000-1159	:	57	1	10	9	7	10	4	: 8 : 106:
1200-1359	:	62	0	8	9	14	9	5	: 9 : 116:
1400-1559	:	51	1	8	7	13	14	9	: 12 : 115:
1600-1759	:	60	0	2	7	10	13	5	: 13 : 110:
1800-1959	:	97	0	4	6	6	5	3	: 1 : 122:
2000-2159	:	59	0	0	0	0	0	0	: 1 : 60:
Total	:	476	5	41	47	53	54	27	: 50 : 753:

Tables 4.14 A and B: Title on following page.

C. Autumn

	:Below:		Basking						:Moving:	n
	:cover:	1	2	3	4	5	6	:		
0600-0759	:								:	0:
0800-0959	:	30	0	4	2	3	2	0	:	45:
1000-1159	:	36	2	4	4	15	6	3	:	73:
1200-1359	:	20	2	8	4	15	9	7	:	72:
1400-1559	:	18	0	4	6	8	11	9	:	63:
1600-1759	:	39	1	2	3	2	6	5	:	64:
1800-1959	:	93	0	0	0	1	1	0	:	96:
2000-2159	:	5	0	0	0	0	0	0	:	5:
Total	:	241	5	22	19	44	35	24	:	418:

D. All three seasons

	:Below:		Basking						:Moving:	n
	:cover:	1	2	3	4	5	6	:		
0600-0759	:	19	0	0	1	0	0	0	:	21:
0800-0959	:	105	3	15	10	6	6	1	:	156:
1000-1159	:	116	3	16	13	23	17	7	:	208:
1200-1359	:	95	3	17	15	30	21	13	:	212:
1400-1559	:	91	1	14	13	22	26	19	:	206:
1600-1759	:	121	1	6	11	12	22	10	:	203:
1800-1959	:	212	0	4	6	7	6	3	:	240:
2000-2159	:	66	0	0	0	0	0	0	:	67:
Total	:	825	11	72	69	100	98	53	:	1313:

Tables 4.14 C and D : see below for title

Tables 4.14 A. to D. : Number of observations of C. austriaca in each of the eight defined behaviour categories during two hour time intervals and for the whole day for A. Spring, B. Summer, C. Autumn and D. All three seasons combined. Data were collected by radio-tracking during 1984 and 1986 inclusive. Total numbers of observations in each time period are given under the heading 'n'.

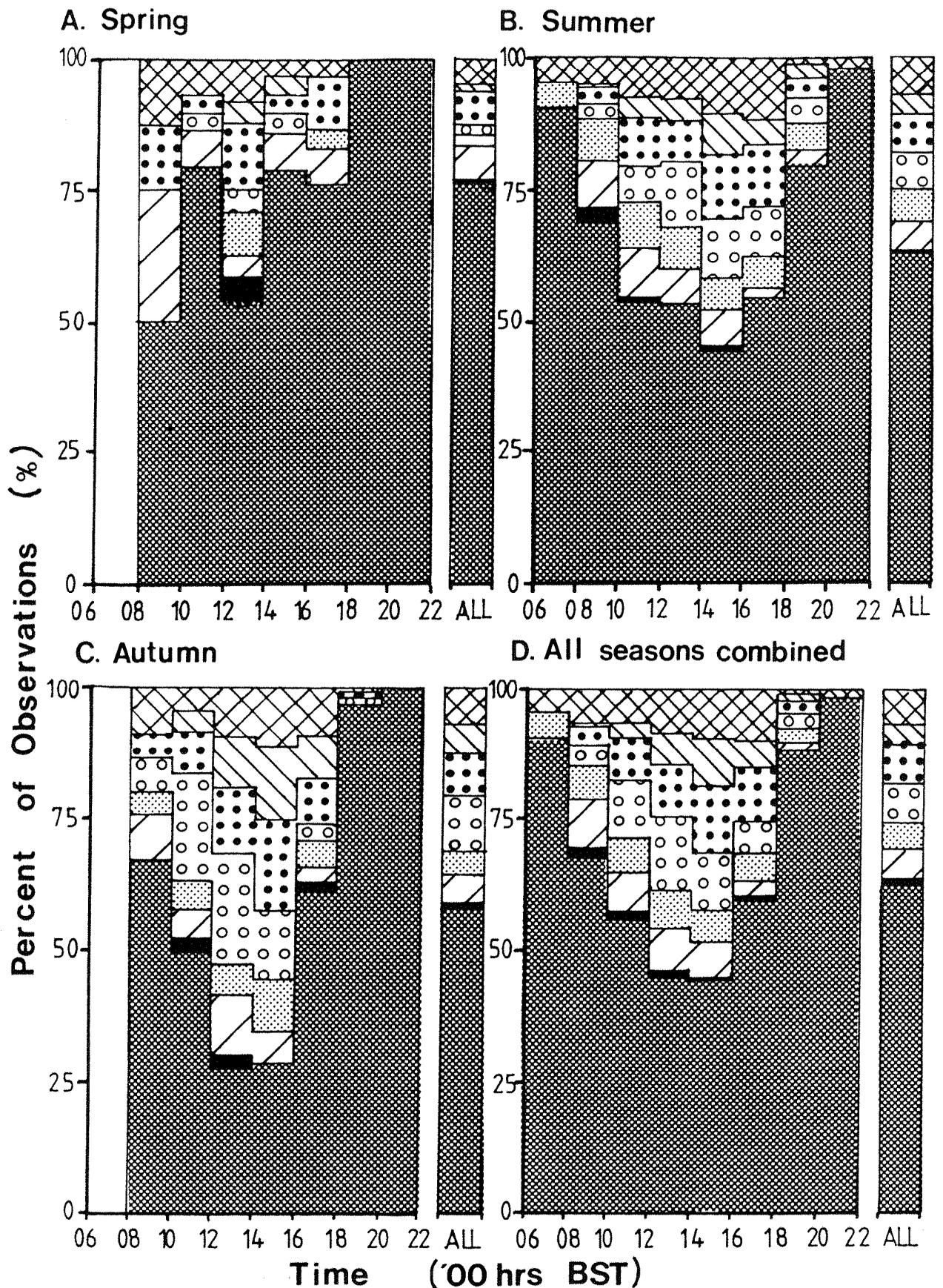


Fig. 4.14 A.to D. : Percent of observations of *C. austriaca* in each of the eight defined behaviour categories during two hour intervals and for the whole day for A. Spring, B. Summer, C. Autumn and D. All three seasons. Data are from radio-tracking observations in 1984 to 1986 inclusive of both male and female snakes at Sites One and Two.

Below cover.
 Basking:
 1,
 2,
 3,
 4,
 5,
 6.
 Moving.

during Summer and Autumn. The proportion of time spent basking increased from Spring, through Summer to a maximum in Autumn. During Autumn much larger proportions of time were spent basking during the afternoon than were observed in either Summer or Spring, although a smaller proportion of the 1800 to 1959 hrs category was dedicated to this activity in the former season than in the Summer.

The number of observations of a snake that was moving was small but remained fairly consistent between the seasons. Records of movement remained at a fairly consistent level through out the day. During Spring a slight decrease in the proportion of observations in which a moving animal was observed occurred during the morning and into the early afternoon from a maximum during the 0800-0959 hrs period. During Summer this pattern was reversed, with a maximum proportion of observations showing movement during the late afternoon (1600 to 1759 hrs). No clear pattern of change in the proportion of observations showing movement was detected during Autumn with a more or less consistent level being observed between 0800 to 0959 and 1600 to 1759 hrs. Only low levels of movement were observed after 1800 hrs in Summer and Autumn. Movement was observed in smooth snakes in all time periods between 0800 to 0959 hrs until 1600 to 1759 hrs in Spring, 0600 to 0759 hrs until 2000 to 2159 hrs in Summer and 0800 to 1800 to 1959 hrs in Autumn.

4.3.10 Laboratory analysis of movement behaviour

Captive animals were housed in a semi-natural arena and their behaviour was recorded using a time-lapse video recorder. Full details of the method are presented in Chapter 2, section 2.3.5. The main objective of this technique was to determine the effect of radio-transmitters upon the behaviour of the study animals. However similarities between radio-tagged and untagged specimens with regard to activity patterns, movement rates and 'vegetation' use (see section 2.3.5 c) indicated that the data could be usefully combined to provide further information on the behaviour of the species per se.

Information pertaining to the activity patterns and movement rates as determined by video analysis are presented below; observed 'vegetation' use determined by this technique is described in Chapter 5.

a. Activity patterns

A total of 20 hours observation was available for each hourly period studied except for 10-1059 hrs and 11-1159 hrs, where 18 hours data were obtained, and 12-1259 hrs, where 17 hours data were obtained. These data were obtained from four different animals. The activity of the study animal was assigned to one of five defined categories, two of which ('movement thermoregulating' and 'non-movement thermoregulating') could only occur during the period in which the heat lamp was illuminated (see Chapter 2, section 2.3.5) and the time assigned to each was summed for each hour. Observed proportions of time assigned to each category are presented diagrammatically for each individual hour of the day and, to permit consistency with the methodology used in the comparative study in Chapter 2 (section 2.3.5), also for six 4-hour time periods. The proportion of time spent on each of the five defined behaviours over the whole day is also illustrated.

The proportion of time assigned to each activity during each hour of the day is presented in Fig. 4.15. Between approximately 2100 and 0300 hrs almost no movement was detected, with the study animal being inactive in the open or below cover. Use of cover was at its greatest during this period. During the early morning activity increased, particularly after the overhead lighting was turned on. With the illumination of the heat lamps thermoregulatory behaviour was possible. During the morning (approximately 0800 to 1300 hrs) movement activity decreased and non-movement thermoregulation (basking) became the most frequent behaviour, reaching a maximum of 88% of the observed behaviours at just after 1300 hrs. Thermoregulation behaviours decreased slightly prior to the heat lamp being extinguished. A slight increase in activity

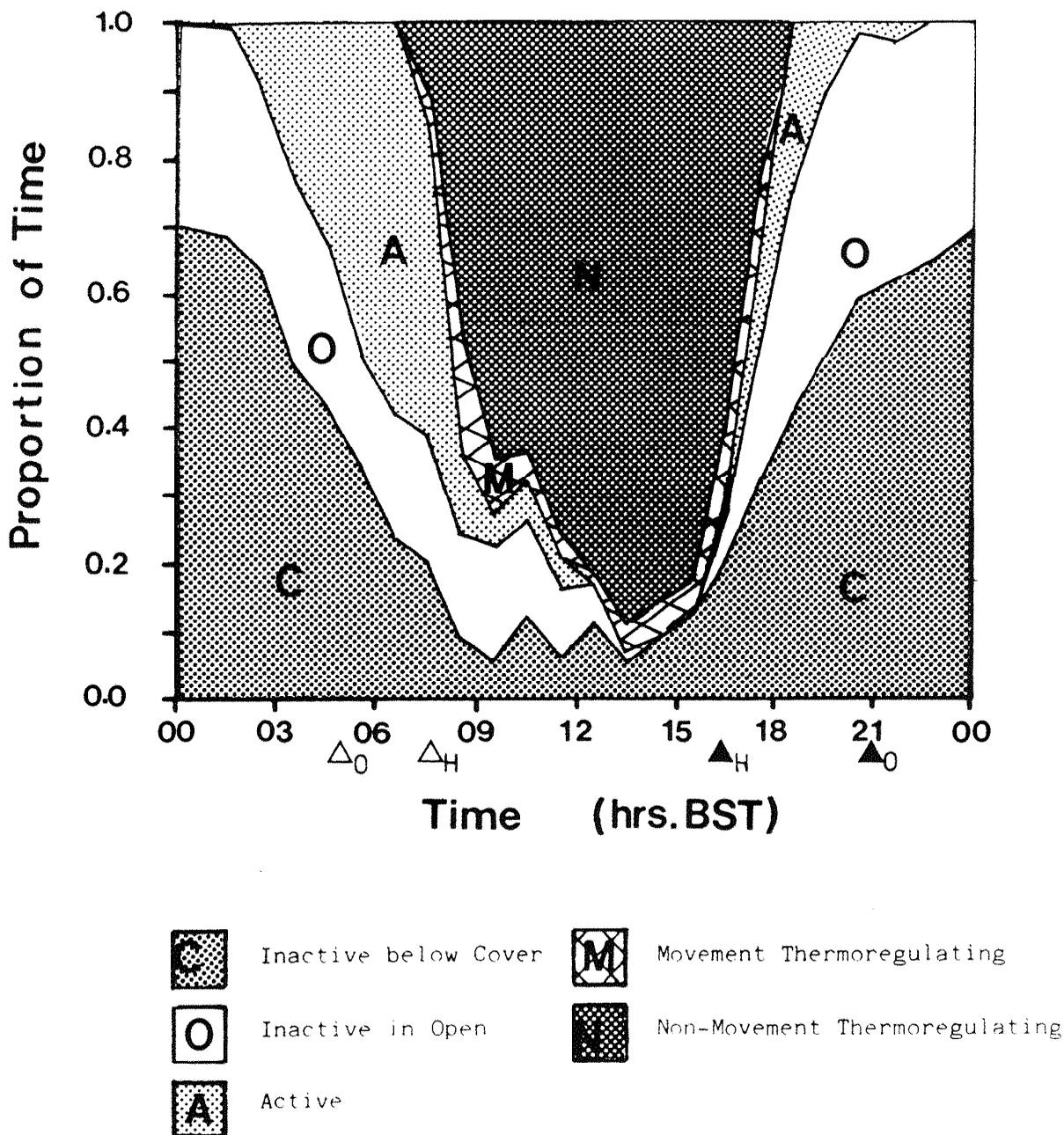


Fig. 4.15: Proportion of time assigned to each of five defined behaviours by four specimens of *C. austriaca* during each one hour period over the day as determined by video analysis of captured animals during 1986, (three male and one female specimens were used for between four and six days each). Open triangles indicate where lighting was turned on and closed triangles where the lighting was extinguished (O = overhead fluorescent lighting, H = heat lamps).

was observed in association with the end of the thermoregulation period. This was followed by an increased occurrence of inactivity and, particularly, an increased use of cover.

The trends described above were also apparent when the data were pooled in to six 4-hour time categories (see Fig. 4.16). Decreasing use of cover was observed during the time periods from 01-0500 hrs until 09-1300 hrs with this trend being reversed over the afternoon and into the night (i.e. between 13-1700 hrs until 21-0100 hrs). Periods of inactivity (not associated with basking) also showed a similar decrease, reaching a minimum during the middle of the day (13-1700 hrs) with maximum values during the night time. Movement activity was at its greatest during the early morning (05-0900 hrs) associated with the period following the provision of background illumination and prior to the illumination of the heat lamp and only small proportions of time were dedicated to movement over most of the remainder of the day. During the 09-1300 hrs and 13-1700 hrs periods non-movement thermoregulation was predominant; only small proportions of time were dedicated to this activity in the 05-0900 hrs and 17-2100 hrs periods (which in part reflects the time available for this activity since the heat lamp was not illuminated for the whole duration of these latter two periods). Movement thermoregulation occupied only a small proportion of the time during which the heat lamp was available.

The proportions of time assigned to each activity over the whole day are also presented in Fig. 4.16. Inactivity below cover occupied the largest proportion of time, with 35.7% of recorded time being dedicated to this activity. 27.7% of total observed time was assigned to non-movement thermoregulating (basking) and a further 20.8% was occupied by inactivity in the open which was not associated with thermoregulation. A total of 16% of recorded time was assigned to movement activity as follows; 12.9% was movement activity away from the heat lamp whilst 3.1% was movement deemed to be associated with thermoregulation.

b. Movement behaviour

A total of 474 hourly movement rates were obtained from the analysis of video recordings made of the behaviour of three male specimens and one female specimen of *C. austriaca* for a total of approximately 20 days (16 days and 4 days for the male and female specimens respectively). Movement rates were determined by tracing distances moved during hour long intervals from the video monitor on to acetate and these distances measured using a map measurer (see section 2.3.5 b). Hourly movement rates recorded throughout the day demonstrated a highly positively skewed distribution (Fig. 4.17) with rates varying between 0.00 and 14.97 m/ hr with a median of 0.05 m/ hr. Of the 474 records 219 (46.2%) had a movement rate of 0.00 m/ hr, 72 (15.2%) were between 0.01 and 0.10 m/ hr and 93 (19.6%) were between 0.10 and 0.49 m/ hr. Thus 81.0% of the hourly movement records (384 observations) were less than 0.50 m/ hr. A further 21 observations (4.4%) were between 0.50 and 0.99 m/ hr. Sixteen hourly movement records (3.4%) were in excess of 5.00 m/ hr with four of these (0.8% of the total) being greater than 10.00 m/ hr.

Daily movement rates were calculated for 12 complete 24 hour periods (from 0000 to 2359 hrs). Values recorded for the male snakes were 3.78, 2.96, 4.57, 3.14, 9.89, 5.31, 6.47, 1.88, 41.91 and 12.59 m/ day and for the female specimen were 13.90 and 12.53 m/ day. Daily movement rates thus varied between 1.88 m/ day to 41.91 m/ day with a median value of 5.89 m/ day.

Hourly movement rates were divided into data obtained from six 4-hourly periods and frequency distributions of movement rates in each time period are presented in Fig. 4.18. Eighty movement records were obtained in each time period except 0900-1259 hrs, where 74 records were obtained. In all time periods highly positively skewed distributions were observed with at least half the observations made in each being between 0.00 and 0.49 m/

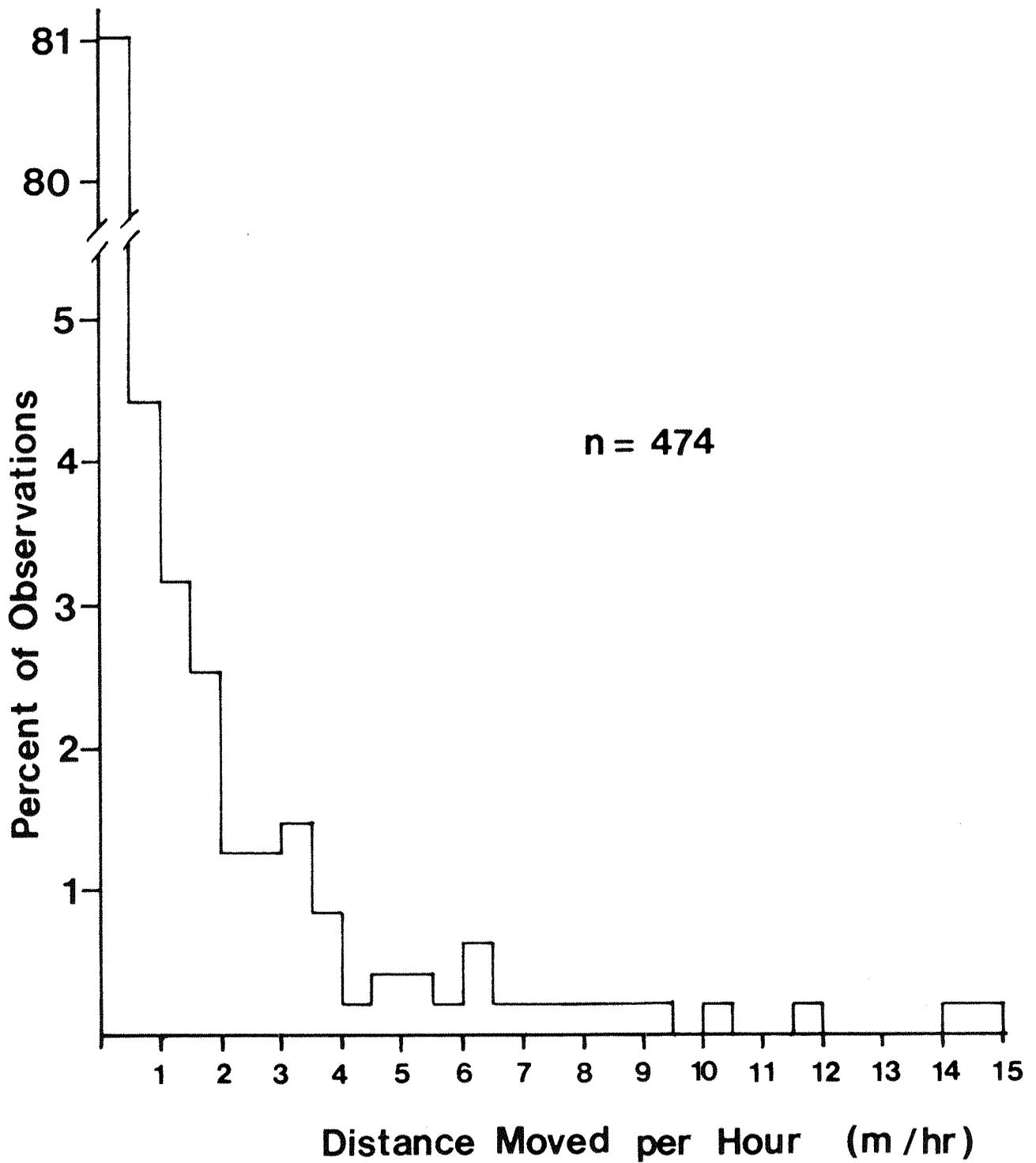


Fig. 4.17 : Percentage frequency distribution of hourly movement rates (m/ hr) of specimens of C. austriaca as determined by video analysis of captive animals (n = 474 one-hour time periods from four specimens (three male and one female)).

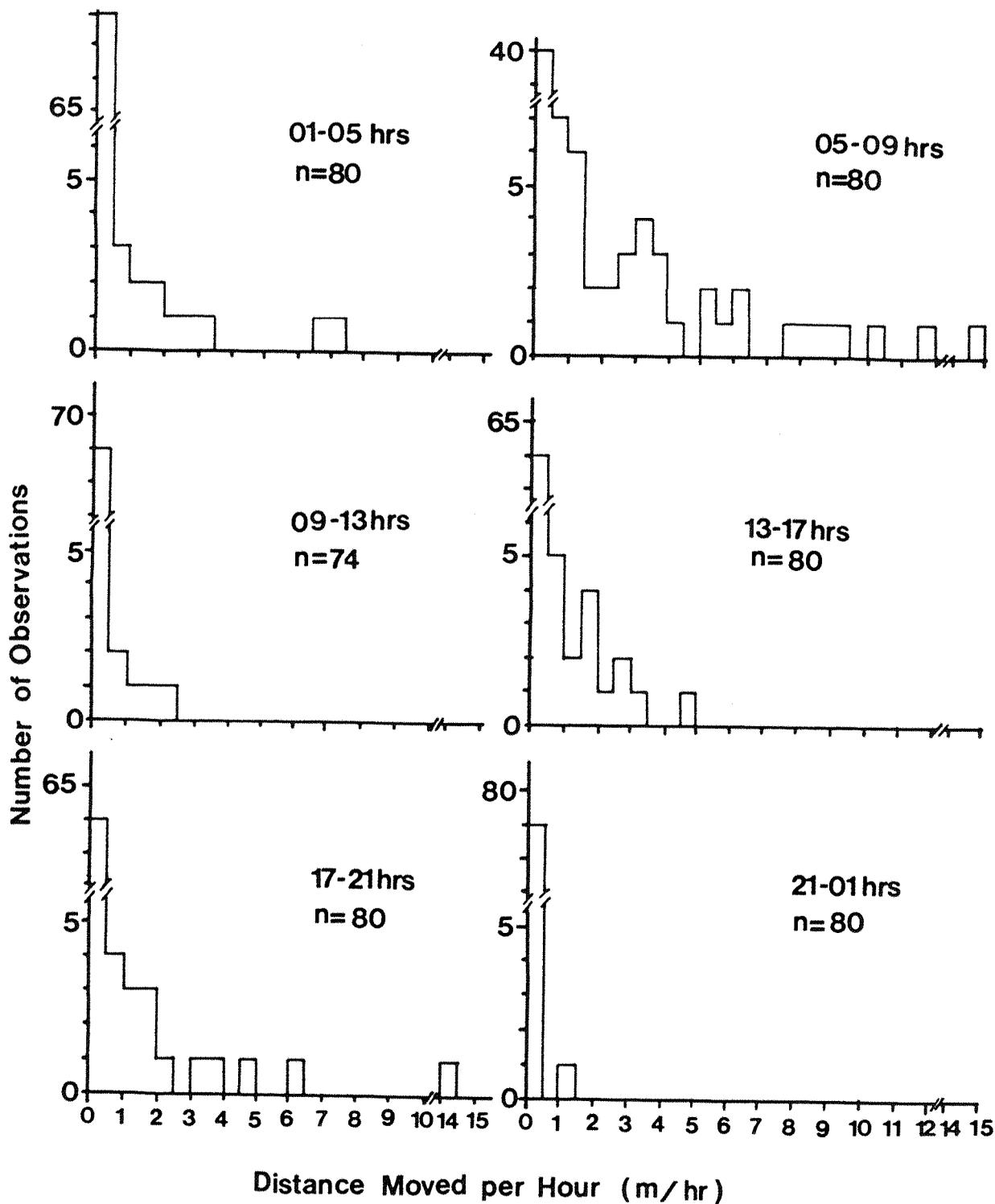


Fig. 4.18 : Percentage frequency distributions of hourly movement rates (m/ hr) of specimens of *C. austriaca* during six defined four-hourly periods i. 0100-0459 hrs, ii. 0500-0859 hrs, iii. 0900-1259 hrs, iv. 1300-1659 hrs, v. 1700-2059 hrs and vi. 2100-0059 hrs as determined by video analysis of captive animals (n = 80, 80, 74, 80, 80 and 80 one-hourly period respectively). Four specimens (three male and one female) were used.

hr. Movement in the 0100-0459 hr was mostly limited to movement rates less than 3.50 m/ hr although two observations between 6.50 and 7.49 m/ hr were made. Movement was at it greatest during the 0500 to 0849 hr period with 40 observations (50%) being in excess of 0.50 m/ hr and 12 records between 5.00 and 14.99 m/ hr. Only low levels of movement were recorded during the 09-1259 hr period, with all observations being less than 2.50 m/ hr. The occurrence of larger movement rates became more frequent throughout the afternoon (during the 1300-1659 hrs period) and into the evening (1700-2059 hrs) with two records between 6.00 and 14.49 m/ hr being recorded in this latter time interval. Only very low levels of movement were observed during the night (2100-0059 hrs) where all values but one were less than 0.49 m/ hr; this latter value was in the 1.00 to 1.49 category. Median values for the six time periods between 0100-0459 to 2100-0059 hrs were 0, 0.49, 0.41, 0.07, 0.05, 0.00 m/ hr respectively, reflecting the low levels of activity recorded during each time period.

4.4. Discussion

Movement can be associated with a variety of behaviour, and may be induced and influenced by a variety of intrinsic and extrinsic factors. In the following discussion the relationship between movement activity and some potentially important factors are considered.

4.4.1. Hourly and daily movement rates

Radio-tracking data from the present study support the thesis that C. austriaca is relatively sedentary compared to other snake species (Breeds 1973, Spellerberg and Phelps 1977, Goddard 1981, NCC 1983). No difference in either hourly or daily movement rates were detected between males and females (with median values of 0.57 m/ hr and 15.13 m/ day for males and 0.48 m/ hr and 10.18 m/ day for females respectively) (sections 4.3.1. and 4.3.3.) which suggests that both sexes have equal short and long term dispersal potential. Due to the similarity in movement behaviour of

the two sexes with regard to both movement rate and the number of observations made of radio-tagged snakes showing movement activity (section 4.3.9. b.), further discussion of movement rate shall be restricted to data from both sexes together.

Frequency distribution of hourly (see section 4.3.1., Fig. 4.1) and daily movement rates (see section 4.3.3., Fig. 4.2) show that the majority of movements observed were small. Of 1074 hourly movement rates, 62.6% were less than 1.00 m/ hr and 48.3% were below 0.50 m/ hr with 18.7% showing no movement at all (0.00 m/ hr). The median value obtained was 0.54 m/ hr. Similarly, low values for daily movement rates were predominant with 17.4% of observations less than 5.00 m/ day, 38.4% less than 10.00 m/ day and 54.3% less than 15.00 m/ day from 138 days of radio-tracking data. The median daily movement rate was 13.30 m/ day.

Although the results show that the smooth snake has generally a small movement rate, it is useful to look at the upper extremes of movement rate to assess the dispersal potential of the species. Of the hourly movement rates, 3.8% were greater than 10.00 m/ hr and of these four (0.004%) were in excess of 30.00 m/ hr. Hourly movement rates were calculated from data recorded as a minimum monitored distance over approximately two hourly periods and consequently a straight line distance between observations of over 20.00 m (approximately) would be required to yield a calculated movement rate in excess of 10.00 m per hour. The four highest hourly movement rates recorded were 32.99, 35.72, 44.07 and 44.26 m/ hr, these being calculated from minimum monitored distances of 62.67, 81.55, 94.02 and 98.11 m respectively. It is likely that greater estimates of hourly movement rate would have been obtained if shorter intervals between locations had been used.

Only 12.3% (18 values) of daily movements exceeded 50.00 m/ day and 2.9% (five values) were greater than 100.00 m/ day.

The five highest daily movement rates were 101.12, 108.60, 117.47, 123.25 and 166.81 m/ day. These data were obtained from both male (three values) and female (two values) specimens and thus the ability to demonstrate long movements is not restricted to either of the sexes. A further observation, in which a snake (a female) moved 170.92 m/ day was discarded from the above analysis as this was based upon the summation of only four minimum monitored distances (see section 4.3.2.). This observation is, however, relevant when considering dispersal potential as this individual would have been likely to have yielded an even greater daily movement rate had the recording of more minimum monitored distances been possible.

Laboratory studies (section 4.3.10. b.) supported the above observations. Although the use of small, artificial arenas during the laboratory experiments will preclude direct comparison with the field observations, the analysis of video recordings showed generally low hourly (median= 0.05 m/ hr, range 0.00 to 14.97 m/ hr) and daily (median= 5.98 m/ hr, range= 1.88 to 41.91 m/ day) vagilities. Much of this low level of activity can be explained by the prolonged periods of thermoregulatory activity during the day and only limited activity during the night.

Breeds (1973) cited several instances of large movements, following capture of C. austriaca, that occurred in one day. Rates of 20, 36 and 46 m/ hr were recorded for two individuals in intervals between 1.75 and 5.0 hours. A further movement of 180 m was detected between two successive afternoons. Breeds (1973) and Spellerberg and Phelps (1977) give data on distances moved between captures, over varying lengths of time, yet, with the exception of above stated cases, no estimates of vagility were calculated. Breeds reports a maximum between capture movement of 400 m and in an analysis of eleven individuals in the same area calculated a mean movement of 66.6 m (range= 4 to 251 m). The latter study showed a range of movements between 2 and 130 m, mostly in the range of 70 to 80 m. Goddard (1981) also presented data for mean movement

distance between captures, these being 65.0 m (range= 1 to 385 m) and 55.4 m (range= 1 to 300 m) for his Sites One and Two respectively.

Additionally Goddard calculated vagilities for both sexes on both sites. For his Site One no significant differences in vagilities were observed between males and females with mean values of 8.98 m/ day and 7.02 m/ day respectively. However, he observed that females on Site Two exhibited a higher vagility than males, 8.90 m/ day as opposed to 3.14 m/ day. He attributed this difference between the sexes to the more frequent locations of female snakes, thereby reducing the between capture time interval and hence increasing vagility estimates. Such sampling problems were avoided in this present study through the use of radio-tracking.

The observations of movement behaviour from the present study yield comparable results to those from previous studies. Regular and frequent sampling, permitted by radio-telemetry, meant more accurate estimates of movement rate could be obtained; the general conclusions reached, however, were consistent with those proposed by earlier workers. Movement rates of C. austriaca indicate that the species is, habitually, fairly immobile. However, long movements (both hourly and daily movement rates) were observed on a small number of occasions which suggest that the dispersal potential of the species may in fact be reasonably large. That this dispersal potential is only infrequently used is shown by the observations that the median movement rate represents only 1.2% of the maximum hourly movement rate and the median daily movement rate is equivalent to 7.9% of the maximum daily movement rate (166.81 m/ day).

It is worth speculating upon the adaptive advantages of such movement behaviour. In an ectotherm, such as C. austriaca, movement will greatly increase the metabolic rate, typically up to ten fold (Bennett 1982). In addition, rapid movement in reptiles usually requires anaerobiosis

which will result in the production of lactic acid, and hence the reduction in blood pH, as a bi-product of this type of respiration (see Chapter 7). Thus, where possible, it will be beneficial for animals to minimise movement. Many aspects of the biology of the smooth snake suggest that the species is, indeed, adapted to minimising movement. Resting metabolism at typical field body temperatures is fairly low and consequently only low food intake will be required (see Chapters 6 and 7). Thus the need for active foraging will be decreased. In addition, smooth snakes frequently use a 'sit and wait' hunting strategy (see section 4.4.5.) thereby further reducing the need for locomotion.

Thermoregulation is mostly achieved through basking and habitat selection, which need require only small movements in a thermally heterogeneous environment (this aspect is investigated further in Chapter 6). Smooth snakes are non-venomous and their primary defence against predation is crypsis; this behaviour will also favour a low vagility. The use of a structurally heterogeneous habitat will facilitate both thermoregulatory and cryptic behaviours whilst exhibiting only a small movement rate.

Occasionally longer movements may be required, for example for migration to or from over-wintering sites or for searching for mates. Short bursts of rapid movement may provide the optimum strategy in that these will minimise the period during which the snake is active and hence reduce the time in which it is more vulnerable to predation. Such periods of activity would be followed short spells of inactivity in which the bi-products of anaerobiosis, synthesised during the period of movement, are excreted or reconverted to glycogen.

Data for vagilities of the other British snakes are sparse, however the data that is available suggest that C. austriaca has the lowest movement rate and dispersal potential of the three British species. Prestt (1971), using recapture techniques, reported long movements in

Vipera berus with a maximum recapture distance of 1.9 km. No attempt was made to calculate vagility. Madsen (1984) presented daily movement rates for radio-tagged Natrix natrix in Sweden. Although snakes were usually radio-located only once per day (and hence lower movement estimates were obtained than would have been calculated from more frequent sampling), Madsen demonstrated that the grass snake is a highly mobile animal. He also indicated a strong seasonal influence. Male grass snakes moved most during May, with a mean rate of 54.8 m/ day \pm 16.8 and showed a minimum movement rate of 13.0 m/ day \pm 8.6 in July. Peak movement in female N. natrix occurred in July, in the weeks prior to and immediately after oviposition, when the mean movement rate was 114.4 m/ day \pm 74.5.

Many studies on the movement behaviour of snakes have been published (e.g. Stickel and Cope 1947, Carpenter 1952, Freedman and Catling 1977) and an increasing number using telemetry (e.g. Fitch and Shirer 1971, Brown and Parker 1976, Henderson et al 1976, Shine 1979, Reinhert et al 1984, Madsen 1984, Shine and Lambeck 1985, Tiebout and Cary 1987). Few of these, however, describe detailed short term movement studies and of those that do, differences in methodology often preclude direct comparisons with other published work (Tiebout and Cary 1987). Studies employing only visual observation are prone to sampling biases (Cook 1983 in Tiebout and Cary 1987). Comparisons between telemetric and non-telemetric studies may therefore be difficult. Two telemetric studies, where different time intervals between successive locations or different methods of transmitter attachment (e.g. force feeding, surgical implantation, external attachment), may also be incomparable. Indeed, equipping snakes with transmitters may itself affect behaviour (MacDonald 1978, Shine 1985). Results obtained from radio-tracking during the present study seem comparable with observations made from snakes not provided with transmitters in both the field and the laboratory (see Chapter 2, section 2.3.5.). Consequently, it is believed that these data were, on the whole, representative of the true behaviour of the species.

Carpenter (1952) gave some estimates of maximum movement rates of Thamnophis sirtalis sirtalis. Blanchard and Finister (1933) recorded an individual T. s. sirtalis that moved 1800 feet in one hour (540 m/ hr) and rates of 60 and 62.4 m/ hr were calculated for the species from Carpenter's own data. Henderson et al (1976) presented movement data from several radio-locations per day on three species of tropical snake. These were based on samples of only one individual per species over very short periods. Vagilities of 0.4 m/ hr (9.6 m/ day), 0.15 m/ hr (3.6 m/ day) and 0.5 m/ hr (11.3 m/ day) were calculated for Chironius carinatus (L.), Helicops angulatus (L.) and Bothrops atrox (L.) respectively. These low vagilities were attributed to these species being arboreal and hence using the vertical plane, as well as the horizontal one, which was not included in the calculation of movement distance. Low vagilities have also been associated with low metabolic rates; this relationship does not always hold true. Shine (1986) showed that Acrochordus arafurae, a nocturnal and aquatic snake species, showed large movements (Mean displacement at night= 141 m and during the day= 19 m) despite having a metabolic rate less than one half as high as most other reptiles.

Watersnakes of the genus Nerodia (previously included within the genus Natrix), particularly N. sipedon, have been extensively studied. Reported movement rates of N. sipedon vary greatly with values of 33.5 m/ hr (Blanchard and Finster 1933), less than 0.136 m/ hr (Brown 1940), 0.007 m/ hr (Stickel and Cope 1947), less than 0.042 m/ hr (Fitch 1958), 0.26 to 2.66 m/ hr (Fraker 1970), 0.15 m/ hr (Fitch and Shirer 1971) and 5.2 m/ hr (Tiebout and Cary 1987). Such variation in results largely reflects the different methodology employed in collecting the data.

4.4.2. Movement rates and 'weather' variables

Hourly movement rates showed a positive correlation with

both shade air and bask site temperature (section 4.3.4.) such that movement increased as temperatures increased. Weather variables may be expected to effect the behaviour of ectotherms, such as the smooth snake, in that the body temperature of these animals are determined by environmental temperatures; increased temperatures typically yield raised body temperatures (see Chapter 6). Body temperature, in turn, affects both the aerobic and anaerobic metabolism in reptiles (Bennett 1982). Increased temperature increases the resting metabolic rate and the aerobic scope and the combination of these greatly increases the potential for sustained activity. Similarly, although to a lesser degree than aerobic metabolism, the anaerobic metabolic rate (scope and capacity) increases at higher body temperatures. Anaerobic metabolism is important for short bursts of activity in reptiles. Consequently increased temperatures permit greater activity. (Further discussion of the relationship between temperature and metabolism is presented in Chapter 7).

Further analysis of the relationship between environmental temperatures and movement rate (section 4.3.4.) shows that greatest (median and maximum) movement rates were associated with intermediate temperatures ($T_a = 18$ to 24°C , $T_{\text{BS}} = 18$ to 26°C) and not the upper extremes as indicated by regression and correlation analysis. This apparent anomaly was due to the much greater sample sizes observed at the low and intermediate temperatures than at the higher temperatures. These smaller sample sizes meant that the reduced movement rates, recorded at higher temperatures, made only a small contribution to the correlation analysis. Highest median and maximum movement rates were associated with shade air temperatures of 18.0 to 19.9°C (median = 0.75 m/ hr and maximum = 44.26 m/ hr) and bask site temperatures of 18.0 to 19.9°C (median = 0.72 m/ hr) and 20.0 to 21.9°C (maximum = 44.26 m/ hr). These environmental temperatures are equivalent to body temperatures of 22.9 to 24.6°C , 20.7 to 22.1°C and 22.2 to 23.7°C respectively (based on regression equations in Chapter 6, section 6.3.2.).

Continuous activity monitoring (section 4.3.9. a.) showed that, while movement behaviour was observed at shade air temperatures of between 6 and 32°C, the majority of movement was associated with shade air temperatures of between 13 and 25°C, with a mean value of 19.3°C ± 5.72. These observations are directly comparable with the results obtained from radio-tracking.

The occurrence of the greatest movements at intermediate temperatures was not unexpected. At low environmental temperatures (e.g. between 10°C and 15°C) snakes would have only a low body temperature through contact with the substrate and air and would have to bask for longer periods than they would at higher environmental temperatures to achieve suitably high body temperatures. Snakes that moved whilst cool would be less mobile through having a low body temperature (Bennett 1982). At even lower temperatures (e.g. below 10°C) snakes would seek or remain in refuges and hence little or no movement would be observed. Temperatures that are too warm are also avoided by ectotherms. Such conditions (e.g. with temperatures of above 30°C) would induce inefficiently high metabolic rates and, at higher temperatures, may cause heat coma.

It appears, therefore, that environmental temperatures that yield a body temperature of between 20 and 25°C are favoured for longer movements and may be optimal for foraging and migration activities. Movements associated with micro-habitat selection, particularly bask site selection following emergence from overnight refuges, would be expected to be much shorter.

Spellerberg and Phelps (1977) related daily activity of the smooth snake to changes in environmental temperatures and, subsequently, Bont et al (1986) have studied the thermal biology of the species in the field using radio-telemetry. The former authors described an increase in capture rate, associated with an increase in basking behaviour, during the morning between 0900 and 1100 hrs. This was attributed to the emergence of animals from their nocturnal retreats

being followed by a period of basking. Emergence was associated with fairly low environmental temperatures, which related to body temperatures between 13 and 19°C. The latter authors suggested that emergence behaviour was initiated by the warming of the overnight shelter and showed an increase in both body temperatures and substrate temperatures associated with emergence during each of the three months the snakes were studied in Spring; mean body temperatures of 10.7 ± 1.0 , 13.6 ± 4.4 and $15.5^\circ\text{C} \pm 3.3$ and the associated mean substrate surface temperatures 13.9 ± 2.1 , 16.1 ± 3.2 and $17.7^\circ\text{C} \pm 3.2$ were recorded at the time of emergence for snakes in April, May and June respectively. Typical environmental temperatures associated with emergence during the present study were in the range 10 to 14°C (shade air) and 8 to 14°C (bask site) based on radio-tracking observations and between 9 and 17°C (shade air) based on four records using continuous recording of radio-telemetry signals (section 4.3.9. a.).

The body temperature of a basking smooth snake can increase very quickly if favourable environmental conditions prevail (Bont et al 1986). Throughout the morning, as the body temperature of the snake increases, the likelihood of movement increases. Data from the present study indicated that movement is greatest when the snake has achieved a body temperature of between 20 and 25°C. Once this temperature has been reached snakes are likely to move away from their basking sites. This would explain the decreasing number of captures of basking snakes during the morning after about 1100 hrs reported by Spellerberg and Phelps.

Cloud cover will affect the amount of sunlight reaching the ground and will therefore influence the body temperatures of basking snakes (Gibson and Falls 1979, Goddard 1981, Bont et al 1986). Cloud cover is also likely affect the relative humidity (although no measurements of humidity were made during the present study). Insofar as temperatures and cloud cover are likely to be related, an effect of cloud cover upon movement rates may have been expected. During the present study, no correlation between

movement rate and cloud cover was observed. The apparent absence of any relationship between these two variables may be a result of the crude level at which the test was applied, with other factors and possible relationships being overlooked in the analysis. Nonetheless, from the results of the fieldwork, it can be concluded that there was no simple relationship between movement rate and the degree of cloud cover.

Heckrotte (1962) proposed that temperature and relative humidity both affect inherent activity patterns in snakes. Increasing either of these parameters tended to yield an increased activity period in the plains garter snake Thamnophis radix radix. In general, relative humidity and temperature vary inversely with each other; thus as temperature rises so relative humidity falls and vice versa. As a consequence, this system tends to provide a compensatory mechanism. Increased humidity will partially offset the reduced activity resulting from a drop in temperature and, conversely, any increase in activity following an increase in temperature will be moderated by a fall in the relative humidity. Such a 'buffering effect' may be observed with changing levels of cloud cover, with low relative humidities and comparatively high temperatures being associated with cloudless days and relatively cool and humid conditions being associated with cloudy days.

4.4.3. Movement rates, behaviour and activity and time of day

Coronella austriaca is reported as being a diurnal species (Spellerberg and Phelps 1977, Arnold and Burton 1978). Results from the present study support this view. Activity monitoring in the field, using continuous recording of radio-telemetry signals (as used in studies of other terrestrial vertebrates, e.g. hares Lepus timidus and roe deer Capreolus capreolus (Cederlund and Lemnell 1980) and woodcock Scolopax rusticola (Hirons and Owen 1982)), showed movement activity to occur almost exclusively in the period between one quarter to one and a half hours after sunrise

and one to two hours after sunset (section 4.3.9. a.). Only very small, and occasional, amounts of movement were observed between this latter time and 0016 hrs with no movement being observed between 0017 and 0548 hours. Although these conclusions are advanced somewhat tentatively, since they are drawn from only a small number of observation periods, a diurnal pattern of activity is clearly illustrated by the data collected using this method.

Video recording of behaviour of captive animals in the laboratory, under simulated natural day lengths, (section 4.3.10.) also showed behaviour consistent with a diurnal species. Snakes used cover at all times during the day, but the greatest proportion of time spent on this behaviour was during the night. Where the animal was not below cover during the night time, it was nearly always inactive (no movement activity was observed between 2230 and 0130 hrs and very little was detected between 2000 and 0200 hrs). The greatest proportion of time spent moving corresponded to the period around first light until the heat lamp came on (approx. 0500 to 0800 hrs). Although long periods during the day time were associated with non-movement, most of the behaviours observed during these periods were associated with thermoregulatory behaviour and, hence, a form of activity. Movement rates from the laboratory studies also showed variation during the day consistent with that expected for a diurnal species. Greatest movement rates were observed during the day time with median movement rates of 0.00 m/ hr being observed for the two four-hour periods between 2100 and 0459 hrs.

Spellerberg and Phelps (1977) also observed the activity of C. austriaca in the laboratory and found diurnal behaviour, relating to the prevailing light:dark cycle, when the temperature was maintained at a constant 25°C. However, activity became more erratic, with movement being recorded during the day and night, when a temperature of 30°C was maintained. Changes in activity relating to temperature regimes have been reported elsewhere. Some snake species

show a transition from being diurnal in Spring to becoming crepuscular or nocturnal during the Summer (Heckrotte 1962); this phenomenon has been explained as being due to the seeking out of that period of the day with the most favourable temperatures. Klauber (1939), for example, reported that nocturnalism in desert snakes was associated with high day time temperatures. Heckrotte (1962, 1975), however, proposed that temperature selection alone does not fully explain the change in behaviour. From his work on Thamnophis radix radix, Heckrotte concluded that changing temperatures caused changes in the periodicity of inherent activity patterns. It is therefore possible that C. austriaca may become increasingly crepuscular, and even partially nocturnal, in the south of its range during the Summer.

The southern smooth snake Coronella girondica, which has a more southerly distribution than C. austriaca (and where the ranges overlap tends to inhabit lower ground), is described as being mostly active in the evening (Arnold and Burton 1978). The similar false smooth snake Macroprotodon cucullatus is found even further south than C. girondica and is active at dusk and at night (Arnold and Burton 1978). The increasing ambient temperatures associated with decreasing latitudes may in part explain this tendency towards nocturnalism in the more southerly species. This apparent trend, however, is less clear in other European snake taxa, e.g. Elaphe spp., Vipera spp. Whether intra-specific variation in the periodicity of behaviour occurs throughout the geographic range of C. austriaca remains a matter for conjecture.

As smooth snakes showed only diurnal activity, further discussion of movement rate and behaviour and their relationship with time of day shall be restricted to data collected from observations of behaviour made during the day-time.

Throughout the day the majority of observations were of snakes below cover, although the proportion of observations

in this category decreased during the middle of the day (section 4.3.9., Fig. 4.14 D.). This category included all sightings where snakes could not be seen and may therefore have included many cases where the snake was moving (e.g. in small mammal burrows) or thermoregulating, either through avoidance of high temperatures or through basking, since some vegetation allows the penetration of reasonable amounts of sunlight (Bont et al 1986). Observations of basking increased towards the middle of the day, being greatest when environmental temperatures were at their highest. These data are contrary to the commonly reported observation that two peaks in basking behaviour are found during the day, these occurring in the morning and the evening (Spellerberg and Phelps 1977, Bont et al 1986). Similar patterns of behaviour were recorded in the laboratory studies (section 4.3.10.) with a maximum period of basking being observed during the middle of the day. Although the patterns of behaviour observed in the laboratory and field were similar, the timing of the onset and cessation of the behaviours were not directly comparable. This is probably due to differences in the temperatures and photoperiods between the two situations.

Movement rates determined by radio-tracking in the field showed a significant variation with time of day when all animals were considered together. Such a relationship, however, was not apparent in all cases when the data were subdivided by sex and season (section 4.3.6.).

When data for all seasons were pooled, median hourly movement rates showed a greatest value in the late afternoon, between 1600 and 1659 hrs, with a smaller peak of activity at 1200 to 1259 hrs. The maximum hourly movement rates were not, however, during these periods, with the three largest values (35.72, 44.07 and 44.26 m/hr) being observed at 1700 to 1759, 1000 to 1059 and 1500 to 1559 hrs respectively. Diurnal movement behaviour can also be considered by looking at the relative number of observations of snakes that were moving during each time period (section 4.3.9. b., Fig. 4.14 D.). The proportion of

snakes observed moving in the 1600 to 1759 hr period was greater than that in any other time period (total for all seasons). However, during all time periods between 0900 until 1759 hrs, the proportion of observations of snakes that were moving was fairly consistent.

The consideration of the results from the continuous activity recording experiments and laboratory observation of movement behaviour would be instructive here. Because these experiments were only undertaken in Summer (June and July 1986), some caution needs to be exercised when relating these observations to results from radio-tracking experiments conducted over all three seasons. Continuous activity monitoring in the field (section 4.3.9. a., Fig. 4.11) showed that during the day-time and the first part of the night movement occurred in all time periods (from 0530 to 0030 hrs) except 2030 to 2059 hrs. Less frequent movements were observed, and generally a lower proportion of time periods showed movement, before 0900 and after 2030 hrs. The observation of many short periods of movement interspersed with periods of inactivity, shown by this method, is consistent with the recording of movement behaviour in all time periods from radio-tracking.

Movement activity in the laboratory studies was greatest during the early morning, an observation not consistent with the findings in the field. The onset of this morning activity in the laboratory was just prior to the overhead lighting being switched on and the level of movement decreased with the illumination of the heat lamp. A slight increase in activity was observed in the late afternoon, relating to a period just after the heat lamp had been turned off. The movement activity of smooth snakes in the laboratory, therefore, seem related to the timing of the artificial lighting.

Significant variation in median movement rate was observed in male smooth snakes with peaks in movement activity being observed at 1100 to 1259 hrs and 1500 to 1659 hrs and minima at 0700 to 0859 and 1900 to 2059 hrs (Table 4.5).

The minima relate to the periods prior to the onset of activity in the morning and the end of activity during the evening. No such variation was observed in female specimens indicating that this sex showed a constant rate of movement between 0700 hrs and 2059 hrs. The lowest median values were, however, recorded during the first and last radio-tracking periods and therefore suggests a similar reduction in movement at either end of the day-time as that shown by males. No difference in movement rates were detected between the sexes during any of the time periods. This latter observation suggests that any apparent difference in movement behaviour indicated for the two sexes should, at best, be regarded with some caution.

Movement activity, therefore, showed no clear time-related activity peaks when data for all seasons were pooled as above. The fairly consistent (median) movement rates between 0900 and 1759 hrs and the similarly consistent proportion of observations of moving snakes between these periods, together with the inconsistency between the timing of activity periods in the laboratory and field studies, suggested that time of day itself did not primarily determine movement behaviour. That the largest movement rates did not occur in the time periods in which the greatest median movement rates were observed is an indication that the factor(s) that influences movement rate can in fact occur at various times during the day. Continuous activity monitoring also shows movement throughout the day. The timing of fluctuations in movement rate suggest that this factor, or factors, was nevertheless related to time of day since marked decreases in the movement rates, and decreased proportions of observations of movement, were observed at the beginning and end of the day. The most likely factors, which show such diurnal variation were temperature and light (intensity and photoperiod). Both these factors increase during the morning and decrease again towards the evening. The period at which they would exert maximum influence on behaviour (which need not necessarily be when they themselves are at their greatest value) would, however, vary with season and

with the prevailing weather conditions on any particular day.

Much discussion of activity patterns in animals have considered the observation of rhythmic patterns of activity which relate to the daily cycle (Carthy and Howse 1979, Manning 1979). The nature of the regulation of these circadian rhythms and the degree to which they are governed by an autonomous 'clock mechanism' (endogenous rhythms) or by external factors, such as temperature and light, (exogenous rhythms) varies greatly between different taxa. In terrestrial reptiles circadian activity will be greatly influenced by environmental factors; activity behaviours in lizard species, e.g. Lacerta agilis and L. vivipara, (House et al 1980), crocodiles, e.g. Crocodilus niloticus (Cloudsley-Thompson 1964) and snakes e.g. Thamnophis radix (Heckrotte 1975) are related to temperature, for example, and other studies have shown the importance of light in controlling behaviour e.g. the Agamid lizard species Sitana ponticeriana (Subba Rao and Rajabai 1973). Enright (1970) suggested, however, that daily activity patterns in reptiles are not solely the result of stimulus response behaviour. Rather, these patterns are a result of the interaction between endogenous circadian rhythms and direct responses to the environment.

The laboratory studies suggested that the onset of activity was related to light where as the end of activity, corresponding to the turning off of the heat lamp, (but prior to the cessation of the overhead lighting), appeared to be governed by temperature. The pattern of movement behaviour, a series of movements interspersed by periods of basking, together with the relationship between environmental temperatures and movement rate (see section 4.4.2. above) indicated that temperature was the major factor controlling daily activity patterns in this species.

To fully understand the possible role of endogenous rhythms laboratory studies using constant light and temperature would be needed. There would, however, appear to be little

adaptive advantage for the development of endogenous circadian activity rhythms in this species. The smooth snake is ectothermic and consequently can only achieve efficient metabolism or movement rates when the environmental temperatures are suitably high. Foraging behaviour of some animals is related to the activity of their prey species or availability of prey, for example the feeding behaviour of the dunlin Calidris alpina, a wading bird, is related to tide times (Worral 1984). This would not favour the development of circadian activity patterns in C. austriaca. The activity of reptilian prey is largely related to weather (House et al 1980). Small mammals, such as shrews Sorex spp., may be active during the day or night and nestling mammals, which are taken in their nests, are available to C. austriaca at all times of the day.

Variations in daily activity patterns may occur with season, particularly through changes in photoperiod and mean temperatures (Cloudsley-Thompson 1971, Heckrotte 1975). Such variation may affect movement and activity during the activity season and provide the cues for the onset of hibernation. Seasonal behaviour may be controlled by inherent activity patterns. The consistency, and apparent independence from weather conditions, of emergence from and submergence into hibernation of the lizards Lacerta agilis and L. vivipara suggest that these behaviours are controlled by endogenous rhythms (Nuland and Strijbosch 1981). Seasonal affects on movement and activity are discussed in the next section (section 4.4.4.).

4.4.4. Movement rates and behaviour and season

The absence of any variation in either the hourly or daily movement rates between the three seasons suggests that smooth snakes have a uniform pattern of movement throughout the activity period. No variation in either measure of movement rate was observed between seasons for either sex when the data for males and females were analysed separately (sections 4.3.5. a. and b.); this indicates that movement behaviour is consistent within and between the

sexes.

Movement is associated with a variety of behaviour including foraging, site selection, thermoregulation and migration, however the degree to which movement is shown differs between species. Certain behaviour is seasonal, notably migration and mating. Feeding behaviour and the need to move in relation to thermoregulation may also show seasonal changes. As such, where a particular species shows significant movement in association with these behaviours, seasonal variation in movement rate would be expected.

Migration between overwintering sites and summer ranges has been reported in a number of temperate species of snake, including three species of Thamnophis (Carpenter 1952), Vipera berus (Prestt 1971), Coluber constrictor (Brown and Parker 1976), Crotalis viridis (Duvall et al 1985) and Nerodia sipedon (Tiebout and Cary 1987). Such behaviour has not been reported for C. austriaca (Goddard 1981). Although certain areas within the study areas appeared to be used by some specimens of C. austriaca for hibernation, the absence of large movement rates during the Spring suggested that no such migratory behaviour was shown by smooth snakes. The short periods for which radio-transmitters were attached to any individual meant it was possible that migratory behaviour could simply have been missed. However observations in the Autumn period, in which snakes would have been expected to return to hibernation sites, indicated that no migration took place in this season either.

No observations of mating, or behaviour that indicated searching for mates, were made during the present study. Mating takes place in Spring (Spellerberg and Phelps 1977, Goddard 1981, Bont et al 1986) and male snakes locate and trail female snakes by odour. The effect of such activity on movement rate of male snakes will therefore depend upon the proximity of a receptive female and may therefore serve to increase or decrease movement. Madsen (1984) observed the greatest movement rate in male Natrix natrix during the

mating season and attributed this to their search for mates. Smooth snakes alter their feeding behaviour during the activity period; there being a period after emergence from hibernation in Spring and a second period prior to submergence in Autumn during which they do not feed (Duguay 1961). This seasonal change in feeding behaviour, however, would appear to be unlikely to cause a change in seasonal movement rate as little difference in movement rate seems to be attributable to feeding condition (see 4.4.5 b. below).

Prior to further discussion of seasonal variation in behaviour, it is useful to mention seasonal changes in environmental conditions. These are likely to strongly influence seasonal behaviour. Mean daily air temperatures at sea level (England and Wales) during 1984 to 1986 inclusive were 7.9°, 15.4° and 12.6°C for Spring (March to May), Summer (June to August) and Autumn (September and October) respectively (HMSO 1987). Similarly the day lengths and amount of sunlight increased. Sunrise and sunset times (BST) at mid-season were as follows: Spring 0605 hr and 1957 hr (16th April), Summer 0500 hr to 2111 hr (16th July) and Autumn 0724 hr to 1807 hr (16th October) using 1987 figures for London (Whitaker's Almanack 1987). Times in the New Forest were approximately 6 minutes later than London. With changes in day length, there are associated changes in the number of hours of sunshine recorded. Mean daily sunshine hours for England and Wales during 1984 to 1986 are as follows: 4.85 hours in Spring, 6.17 hours in Summer and 4.06 hours in Autumn (HMSO 1987).

The most noticeable change in the observed behaviour was the increasing proportion of time spent on basking behaviours during the middle of the day as the activity period progressed from Spring, through Summer to Autumn (section 4.3.9. b., Fig. 4.14 A. to C.). These behavioural changes probably related to the changes in temperature and day length summarised above. The low overall level of basking behaviour during Spring was exaggerated by the shorter period of daily activity, with snakes submerging

into cover before 1800 hr. However the proportion of observations of basking snakes throughout the day was also generally low during this season. This was perhaps somewhat unexpected as previous accounts of smooth snake behaviour have reported Spring basking. This behaviour has been attributed to the establishment of hormone levels and the development of reproductive organs (Duguy 1961, Bont et al 1986). The proportion of time spent basking in the early morning (0800 to 0959 hrs) was higher in Spring than in the other seasons. This may have provided enough sunlight for the reproductive organs to develop. Avoidance of protracted basking during the later part of the day, when it is warmer, could possibly serve to reduce the rate at which food reserves are used up during this period where they apparently do not feed.

During the Summer basking behaviour was observed during all two-hour time periods between 0600 hr and 1959 hr, but most basking behaviour was noted during the middle of the day (1000 hr to 1759 hr). During Autumn nearly all basking behaviour had ceased by 1800 hr but a much larger proportion of time was spent basking during the middle of the day than was observed in the other two seasons. This was probably due to the shorter day lengths and reduced air temperatures making attainment of the high body temperatures more difficult than in the Summer combined with the need to maintain higher body temperatures for the development of ova, in pregnant female snakes, and for the assimilation of food as fat reserves, in all specimens, prior to the onset of hibernation. No comparisons between the basking behaviour in the early morning was possible as no data were collected in the 0600 to 0759 hrs period during Spring and Autumn.

Combined data for all three seasons indicated a difference in behaviour between the two sexes. Male snakes were recorded below cover more than females whilst females showed a greater tendency to bask. Analysis for each of the seasons separately, suggested that this difference occurred only during the Spring and Summer and that the behaviour of

male and female snakes was similar during the Autumn. The similarity of behaviour during this latter season appears to be the result of a change in behaviour by male snakes.

During the Spring and Summer, breeding females will need to bask to achieve the raised body temperatures (and hence raised metabolic rates) required for ovogenesis and the subsequent development of the embryos. Spermiogenesis in male C. austriaca occurs at several times during the year, particularly during early Spring and during July through to September (Duguy 1966). Males, however, appear to maintain sufficient quantities of spermatozoa to allow them to mate at any time during the year (Goddard 1981). Male snakes, therefore, will not need such raised metabolic rates during the Spring and Summer. Since basking in the open increases the risk of predation, individuals are likely to use cover in preference to basking, where possible. Non-breeding females, may be expected to show similar behaviour to males. However females that bred in previous years may need to become more active in order to replenish reserves lost during pregnancy; this may require these specimens increasing the time spent basking. Consequently, non-breeding females may show either increased or decreased amounts of time basking.

During the Autumn males (and non-breeding females) will need to increase the time spent basking to ensure assimilation of fat reserves prior to hibernation; consequently less time will be able to be spent below cover. Thus, during this latter season the behaviours shown by males and females will become increasingly similar. The increased period of basking during the Autumn may additionally explain the increase in spermiogenesis in C. austriaca during the latter months of the activity season reported by Duguy (1966).

The analysis of diurnal variation in movement rate (section 4.3.6. c.) showed that there was a constant movement rate throughout the day during Spring and Summer but during Autumn significant differences in hourly movement rate were

observed. In this latter season the highest median movement rates were recorded during the 1100 to 1259 hrs and 1500 to 1659 hrs periods. Although no significant differences were observed in movement rate during the first two seasons the greatest median movement rate occurred at 1100 to 1259 hrs whilst in Summer two peaks in median movement rate were observed. In this season these peaks were at 0900 to 1059 hrs and 1700 to 1859 hrs. This apparent shift in the timing of these larger movements, with the first peak occurring earlier in Spring and Autumn than in the Summer and the second peak being later in the Summer than the Autumn, relates to the change in photoperiod and the time at which the seemingly optimum temperature for movement was reached (see section 4.4.2. above).

Further subdivision of diurnal variation in movement rate in each season such that data were analysed separately for each sex, showed that no difference in movement behaviour is found throughout the day for female snakes in any season or for males in Spring or Summer. Male snakes in Autumn showed greatest movement in the 1100 to 1259 hrs period and a progressive reduction in movement thereafter. The apparent consistency of movement rate data produced by this analysis was probably partially a consequence of decreasing the sample size with each subdivision of the data. Where sample sizes are reduced in each time category the relationship between time of day and temperature becomes less well defined. Thus, this data supports the earlier hypothesis that movement rate is primarily governed by exogenous factors and not by time of day itself.

4.4.5. Movement rates and individual condition

a. Slough condition

Smooth snakes showed a lower movement rate prior to sloughing than they did after they had shed their skins. Movement was at its lowest just prior to sloughing and increased thereafter throughout then following stages of the sloughing cycle. The observations made during the

present study were in agreement with those made by Madsen (1984) in his study of Natrix natrix. Reduced movement during the period before shedding probably served to reduce the snakes vulnerability to predators. At this time the eyesight will be poor as a result of the sloughing process (prior to shedding the eye becomes 'milky' in appearance due to the secretion of a fluid between the stratum corneum and the epidermis). The sloughing cycle may be accelerated through longer periods spent basking. This activity may also have served to reduce the observed movement rate.

b. Feeding condition

Significant variation was observed between the daily movement rates of smooth snakes in different feeding states, with the greatest median movement rate being associated with recently fed snakes. However the observation of hourly movement rates indicated no difference between snakes in different feeding conditions. These anomolous observations may be caused by a different number of minimum monitored distances being summed to calculate daily movement rates between the different feeding conditions. Although there is no reason to expect such a difference, the apparent variation in daily movement behaviour may be the result of the methodology. Thus hourly movement rates may provide the better measure of movement activity here.

Two extreme types of foraging behaviour have been recognised in reptiles, namely 'sit and wait' and 'actively foraging' (Pianka 1977). The former of these behaviours is where the predator remains in one place and ambushes prey as it comes close, whereas the latter involves actively searching for prey. These two strategies will mean that foraging snakes may show different levels of movement activity. The smooth snake is believed to demonstrate both types of activity, in that it actively seeks immobile prey, such as nestling mammals, but will also take mobile prey, such as lizards. Consequently a recently fed snake may show either increased or decreased movement depending upon which

foraging strategy had been employed previously.

Regal (1966) reported a thermophilic response following feeding in Constrictor constrictor, such that a recently fed snake sought warmer conditions which facilitated digestion. Any change in movement behaviour may be related to a change in activity associated with thermoregulation. Because of the different movement rates associated with the different foraging behaviours an increase in thermoregulatory behaviour need not affect the observed movement rate.

c. Female breeding condition

Decreased movement has been reported during pregnancy in Elapid and Colubrid snakes (Shine 1979, Madsen 1984). This change in behaviour was considered to reduce vulnerability to predation but may also be attributed to the reduction in feeding associated with the latter stages of pregnancy (Shine 1980, Reinert et al 1984). Pregnant snakes are often believed to spend greater proportions of the day basking than non-pregnant individuals (Goddard 1981). The similarity in both hourly and daily movement rates in pregnant and non-pregnant specimens showed that movement rates were not affected by breeding condition. This also suggested that there was no difference in the basking behaviour between snakes that were pregnant and those that were not.

These data were collected over the whole activity period. Thus it is possible that behavioural differences existed towards the end of the season between different breeding states but these were overlooked due to the way in which the data were separated.

4.4.6. Direction of movement

The area occupied by a snake will result from the distance travelled and the direction of travel. Long dispersal movements, such as migration, would involve a fairly

uniform direction of travel, whereas animals occupying a small and defined range would show many changes in direction of movement. During the present study the short term dispersal behaviour of C. austriaca was investigated. In all of the 31 radio-tracking periods (for which such analysis was possible) the movement behaviour differed significantly from that which would be expected if snakes moved equally in all directions. Such equi-directional dispersal behaviour may be expected from an animal occupying a 'home site' from which it travels each day where each direction is equally suitable for movement.

The above analysis however does not necessarily imply dispersal. Snakes may occupy and travel to and from a 'home site' yet not demonstrate equi-directional movement. This could be due to the nature of the terrain, for example snakes often show movement along banks and ditches and hence a disproportionately large amount of movement could occur along the lengths of such structures. Random movement, which may or may not result in a net dispersion may also occur. Such behaviour would also be likely to show a deviation from a hypothesis of equal movement (to address this possibility comparison against a Poisson distribution could be undertaken, this was not done during the present study).

An index to express dispersal, relative to total movement, was devised to investigate the tendency to move away from a given point and allowed the animals during each radio-tracking period to be arbitrarily classified as dispersers (where the index was equal to or above 50%) and non-dispersers (where the index value was below 50%). No consistent pattern was observed with C. austriaca with approximately half the observations falling into each category. These observations suggested that smooth snakes did not occupy a small, well defined range but rather moved between areas where they stop for a while prior to moving on again. Movement of this nature may relate to foraging behaviour but could also serve to reduce predation. Movement between sites would decrease the likelihood of a

predator finding and exploiting a population of snakes as a food source. Data from Site One suggested that females may disperse less than males, however this was not substantiated at Site Two or with the data from both sites together.

4.5. Summary

- i. Hourly and daily movement rates and activity behaviour were studied in the field using radio-tracking and continuous activity monitoring (radio-telemetry) and in the laboratory using video-recording.
- ii. Smooth snakes habitually showed low hourly and daily movement rates (median values of 0.54 m/ hr and 13.30 m/ day). Greater movement rates of up to 44.26 m/ hr and 166.81 m/ day suggested a reasonable dispersal potential for this species.
- iii. No difference in hourly and daily movement rate was shown by the two sexes.
- iv. Data indicated that C. austriaca is almost exclusively diurnal.
- v. Hourly movement rate was related to temperature with maximum movement being associated with intermediate environmental temperatures ($T_a = 18.0$ to 19.9°C , $T_{es} = 18.0$ to 21.9°C) which were equivalent to body temperatures in the range 20.0 to 25.0°C . No relationship between movement rate and cloud cover was observed.
- vi. Movement behaviour related to time of day but this was apparently a consequence of diurnal changes in environmental conditions, particularly temperature. Any circadian rhythms in this species are primarily exogenous in nature.
- vii. Smooth snakes were below cover throughout much of the day with this behaviour being predominant in the early morning and evening. Basking behaviour increased in

frequency during the morning, reached a peak during the middle of the day and decreased throughout the afternoon.

viii. The activity period was protracted in the Summer compared with the other two seasons probably through changes in temperature and photoperiod. Hourly and daily movement rates remained constant between all seasons.

ix. Female snakes basked more than male snakes during the Spring and Summer, during which time males used cover to a greater degree. In Autumn both sexes showed similar behaviour, through a change in behaviour by males. The greater requirement for females to bask probably related to the development of ova and embryos. The increase in basking shown by males in Autumn related to the need to assimilate fat reserves prior to hibernation and correlated with a time of high spermiogenesis reported in the literature.

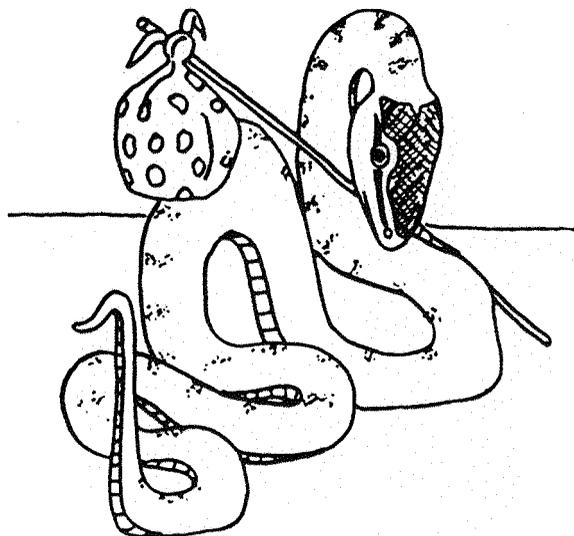
x. Smooth snakes were less active prior to molting than after they had shed their skins. This related to thermoregulatory and predator avoidance behaviours.

xi. No clear change in movement rate was associated with feeding condition. This was probably a consequence of the different foraging behaviours shown by C. austriaca.

xii. Similar movement rates were shown by pregnant and non-pregnant smooth snakes.

xiii. Dispersal behaviour suggested that smooth snakes did not stay within small, well defined ranges. These snakes apparently wandered between sites which were occupied for only a relatively short while.

V. Movement Biology II:
Range Use



CHAPTER FIVE

MOVEMENT BIOLOGY II

RANGE USE

5.1. Introduction

5.1.1. Home range size and shape

An understanding of the range use and ranging behaviour of a species is of fundamental importance for the management and conservation of that species. In this chapter, aspects of the ranging behaviour of C. austriaca are investigated and the use of the biotic habitat studied. Movement behaviour and activity of C. austriaca is discussed in the previous chapter (Chapter 4).

The size and shape of areas occupied by terrestrial vertebrates, and in particular mammals, has been the subject of many studies. Much of the earlier work has been reviewed by Jewell (1966) and Sanderson (1966). The concept of 'home range' is, itself, the subject of controversy (O'Farrell 1978) and numerous definitions have been proposed. Burt (1943) distinguished between the terms 'territory' and 'home range'. 'Territory' represents a defended or exclusively occupied area whereas Burt defined 'home range' as 'the area traversed by the individual in its normal activities of food gathering, mating and caring for young'; the definition of the latter term was limited in application to animals that had established themselves and excluded occasional movements away from this area. Other definitions of home range describe 'core areas', i.e. parts of the animal's range that are used most frequently (e.g. Kaufmann 1962).

In this study 'home range' shall be defined as the entire area in which an animal moves (Rose 1982). This definition, which is similar to Carpenter's (1952) 'activity range' and Jewell's (1966) 'lifetime range', makes no assumptions

about restricted movement or repeated use of favoured areas, nest sites or hibernacula that are inherent in some other definitions (e.g. Barbour et al 1969). Goddard (1981) used the term 'limited movement area' (LMA) when describing the ranging behaviour of C. austriaca. Implicit in this term is the assumption that ranging behaviour is, in some way, restricted. Goddard, however, does qualify the use of the term LMA by stating that movement could be regarded as 'limited' as 'snakes did not move everywhere in the habitat but remained in certain areas'.

Estimation of home range area is dependent upon many factors, not least the method that is employed for its calculation (Jennrich and Turner 1969, Rose 1982). Many different methods have been used for calculating range areas, some relying on mathematical assumptions that may be applicable to some species but not to others (Jennrich and Turner 1969), and, indeed, some that are often biologically unrealistic. The simplest methods, both in design and concept, are the outline techniques in which the outer sightings are joined to form a convex polygon. Range area estimates so produced, however, yield no information on the intensity of use of different parts of the range and are particularly influenced by peripheral sightings. Since individuals are likely to make excursions well outside their 'normal' activity area, convex polygons are likely to include large areas that are never visited by the animals. Several techniques have been proposed for reducing the unvisited areas. The range outlines can be made concave (minimum polygons) or unused areas of habitat simply excluded. As these methods are rather arbitrary and lack standardisation they are somewhat unsatisfactory (Kenward 1987).

Recapture radii are based upon the calculation of the average distance between each sighting and the geometric centre (i.e. the arithmetic mean) of all sightings. This average distance is taken as the radius of an individual's home range. Areas based upon recapture radii (r^2) and recapture radii (r) have been used in studies of Anolis

limifrons (Andrews and Rand 1983). Although this method is independent of sample size, recapture radii estimates for home range are based upon the assumption of independence of successive sightings and that a normal distribution underlies the distribution of sightings. Recapture radii also suffer large biases when ranges are not circular (Jennrich and Turner 1969), although estimates of true home range area can be calculated by multiplying areas (r^2) by constants (Schoener 1981) for different shapes of home range.

The determinant method or covariance matrix method (Jennrich and Turner 1969) is a variant of the recapture radius methods which allows range areas to be assessed for elliptically shaped home ranges. However the model assumes that locations conform to a bivariate normal distribution and that successive locations are independent of each other. Jennrich and Turner (1969) also proposed formulae for making home range estimates obtained by convex polygon, minimum polygon and the determinant method comparable. A table of 'biases' were also presented by these authors such that areas of convex polygons obtained from different numbers of observations (for sample sizes between 3 and 25) could be standardised to allow comparisons between them. The formula for the standardised area estimate takes the form:

$$\text{Area estimate} = \text{Convex polygon area} / C_n$$

where C_n = the bias for a sample size of 'n' (presented in Table 2 of Jennrich and Turner 1969). This correction formula has been used in previous home range studies (e.g. Goddard 1981).

Various parametric methods have been devised to calculate 'core areas' of home ranges, i.e. estimating areas that represent a certain proportion of the sightings (often 95% (e.g. Jennrich and Turner 1969) or 99%). Thus range areas could be defined as a series of probabilistic circles or ellipses about an activity centre. In a further development,

Don and Rennolls (1983) developed a model which allowed for clumping in the data. This method allowed a more accurate assessment of range areas where observations are based around several activity centres, by creating probability contours around each. More complex (non-parametric) estimates of home range area are based upon the calculation of a 'harmonic mean' as an estimate of the activity centre (e.g. Dixon and Chapman 1980). This harmonic mean is regarded as being more representative of the true centre of activity than the arithmetic means calculated in other models. Range areas are calculated as probability isopleths around this harmonic mean.

The topic of home range area estimation, and its application to lizards, has been reviewed by Rose (1982) who recommended the use of convex polygon analysis. She cautioned the use of area correction factors (e.g. Jennrich and Turner 1969) because of their inherent mathematical assumptions (i.e. locations following a bivariate normal distribution) and the requirement for independence of successive sightings, both features that are unlikely to apply to free ranging animals. Further, Rose suggested that if a large enough number of observations are used (she recommended a minimum of 18 locations for each range) accurate estimations of home range areas can be obtained using polygon methods.

The methodology employed may be dependent upon the nature and quantity of the data collected and upon the objective behind the estimation of home range areas. In the present study, range area estimates were required for comparisons between sites and between sexes and consequently any standardised technique would prove adequate. In addition estimates of the area typically occupied by smooth snakes are of interest for species management. In a species that appears not to maintain rigid home range boundaries (see Chapter 4) or where data are collected over varying lengths of time (and with varying numbers of observations) statistically determined range areas (e.g. based on recapture radii or probability contours) are probably

unnecessarily complex and no more representative of 'actual' range areas than simple polygon estimates. Estimates of home range area have been produced for C. austriaca and other species of British and non-British reptile species in previous studies (e.g. Goddard 1981, Madsen 1984, Dent 1986). The most frequently used method of home range area estimation has been the convex polygon. Thus to permit comparison between the present and previous studies, whilst achieving the primary objectives of the present study, the convex polygon method seemed the most applicable form of home range estimation during this present study. As this method is sensitive to variations in the number of observations made and the period of observation associated with each home range estimate (Rose 1982), the relationships between range area and the number of observations and the observation period were also investigated.

5.1.2. Vegetation use and habitat selection

In Britain, C. austriaca is primarily regarded as a lowland heathland species, typically being found in dry heath dominated by Calluna vulgaris and Erica cinerea (e.g. Arnold and Burton 1978, Corbett 1980), although references to the use of bog and woodland and various intermediate habitats have been made (Smith 1973, Breeds 1973, Spellerberg and Phelps 1977, NCC 1983). However, a greater variety of habitats are reportedly frequented by C. austriaca throughout its range in continental Europe, Scandinavia and Russia, e.g. woodland, scrub and bog (e.g. Andren and Nilson 1976, Arnold and Burton 1978). Spellerberg and Phelps (1977) described three factors common to all habitats used by C. austriaca, namely a substratum in which the snakes can burrow, a dense ground cover (e.g. grass, heathland or deciduous leaf litter) and an upper vegetation layer (such as open woodland, sparse shrubs or gorse (Ulex spp.)). These habitat characteristics were regarded of importance as they offer cool and moist conditions.

Goddard (1981) described the microhabitat use of C. austriaca by assigning each of his observations of snakes to one of eight habitat types (with a ninth category for animals located below tin sheeting or similar). Calluna vulgaris dominated heathland, bare ground and Calluna vulgaris / Erica cinerea heathland were the most commonly used vegetation types. Goddard, however, did remark on the very catholic nature of microhabitats used within the heathland.

Corbett (1980) expressed concern over the reliance on short term research for establishing habitat preferences of rare amphibians and reptiles, since these studies often did not consider the past distribution of these species and the changes that may have occurred to the vegetation at the sites during recent history. He blamed these oversights as the cause of misinterpretations of observations on habitat use and, consequently, the fundamental differences between primary (or optimum) habitat and secondary refuges of the species were being overlooked. Corbett suggested that species, such as C. austriaca and Lacerta agilis, were primarily heathland species that may utilise adjacent habitat types or persist only temporarily in successional habitats (such as forests). Indeed, Corbett believed that the observation of animals in these marginal habitats may lead to the wrong targetting of conservation efforts and that consideration of these areas as suitable habitat may even imperil these species in the long term.

Goddard (1981) was critical of the insistence that mature dry heath is the 'optimal' habitat of C. austriaca. He suggested that this conclusion appeared to rest simply on the observation of most snakes of this species have been recorded in this type of habitat. Aswell as seasonal, diurnal and physiological, etc., variations being likely to affect the probability of capturing snakes in any particular locality, Goddard also queried the amount of search effort expended in sites that were not preconceived as being of optimal (or near optimal) habitat types. As such, Goddard felt the significance of survey work was

difficult to assess and that, in consequence, all C. austriaca localities should be regarded as being important as each other.

The decline and fragmentation of heathland throughout lowland Britain has been well documented (e.g. Moore 1962, Webb and Haskins 1980, Hazel 1983, NCC 1983, see also Chapter 1) and hence the habitat most frequently associated with the smooth snake in Britain is threatened. During the present study, the vegetation types occupied by C. austriaca were described so that the nature of the habitats used by the species in the study areas could be determined.

Although the identification of the most frequently used vegetation types is of interest for the conservation and management of C. austriaca, an understanding of the use of 'marginal' habitat types is also necessary as these are likely to become increasingly important with the reduction in the area of 'prime' habitat. With increased urbanisation, forestry and agriculture and other pressures on land use, it is becoming increasingly necessary to determine what features (natural or unnatural) represent barriers to dispersal and which serve as corridors through which animals can move. For example, the use of forestry plantations by C. austriaca needs to be determined since sensitive management of these may not only reduce the effect of habitat fragmentation upon heathland species (e.g. by preventing them becoming barriers to dispersion) but may even allow these areas to serve as permanent refuges for the species.

Habitat use is not necessarily equivalent to habitat selection, since certain movements, e.g. migration, may take an animal through less desirable habitats (Heatwole 1977). During this present study habitat usage was investigated and no experimental attempts were made to determine the mechanisms by which C. austriaca recognise and select favoured habitats. Vegetation species and communities and the heights of the vegetation were assessed in small (0.25 m²) quadrats; these small units were studied

as they were deemed to be representative of the habitat immediately affecting a small, ground-living vertebrate. Surrounding vegetation may influence particular sites, for example through shading, although this was not studied directly during the present investigation. There are many facets to an animal's habitat, including biotic and abiotic factors. This chapter is primarily concerned with biotic aspects (namely vegetational and faunal components). Temperature variables associated with habitat selection in the field are investigated further in Chapter 6.

For any species food abundance and distribution may affect range size and range use. Smooth snakes prey upon reptiles and small mammals (Goddard 1981, NCC 1983) and consequently the distribution of prey species may be an important factor in determining the dispersion of C. austriaca within the habitat. In addition, other species may influence habitat selection through competition or agonistic interactions (Heatwole 1977). The possibility of competition between C. austriaca and V. berus has been suggested (Spellerberg and Phelps 1977). As small mammal and other reptile species were deemed likely to affect habitat use by C. austriaca the relationship between the distribution of these species was investigated.

5.2. Methods and materials

5.2.1. Home range analysis

Estimates of home range were calculated using the convex polygon method (sensu Rose 1982) for each animal for which three or more observations were made during all three study seasons. For each observation, the position of each animal was described relative to markers in the field and a grid reference later assigned to it (as described in Chapter 2, section 2.2.1.). The data were analysed using a computer package on the BBC micro-computer, termed the 'Ranges suite' (Kenward 1987), and range areas and the grid references that described the corners of the convex polygon were recorded. Grid references used in this analysis

described the location of the snake to the nearest 1 metre.

5.2.2. Quantification of biotic components of habitat

The vegetation species composition and height class composition within a 0.25 m² quadrat centred upon the location of each snake was described using the method detailed in Chapter 2, section 2.2.4. a. Each quadrat so described was subsequently assigned to one of 33 vegetation categories according to the relative abundance of the plant species within it. The criteria used for this classification are presented in Appendix I. At each of Site One and Site Two a further 100 quadrats were placed within the study area at pre-determined, randomly selected grid co-ordinates and the species composition, height class structure and vegetation category determined for each, as above. Thus, an indication of the relative abundance of each of the vegetation characteristics studied could be estimated at each site.

The relative use by C. austriaca and other reptile species of different vegetation types was also assessed using a standardised sampling technique. This involved the placing of a fixed number of small squares of tin sheeting along transects in different vegetation types and counting the numbers of each species observed along each transect. The methodology for this experiment is described in Chapter 2, section 2.2.5.

The abundance and distribution of other reptiles and mammalian and avian components of the fauna likely to be predatory upon or prey items for C. austriaca were recorded. The location of all reptiles observed on Sites One and Two were described using the grid reference system used for C. austriaca. The general location of observations of mammalian and avian species was described. In addition, small mammal populations were assessed on three defined habitat types by trapping (see Chapter 2, section 2.2.4. b. for details of methodology).

5.2.3. Analysis

Significance values obtained from statistical analysis are presented with the value of each test statistic in the relevant results section. A summary of the analyses undertaken, and the statistical tests used in each case, are presented below:

a. Home range areas and shape

Convex polygon area and the outer grid co-ordinates were calculated for the home range of each animal in which three or more observations were obtained, using the 'Ranges suite' (Kenward 1987) BBC micro-computer programs. Home ranges were plotted individually to show range size and shape and on a common set of axes to show spatial overlap.

b. Intra-specific comparison of range area

i. Effect of methodology

A frequency distribution of range area was produced. Range areas calculated from data collected from 'visual location only', 'radio-tracking only' and 'Visual location and radio-tracking' were compared to see if methodology yielded apparent differences in estimates of home range using the Kruskal-Wallis test. Range area estimates were tested between the different methods pairwise using the Wilcoxon/ Mann-Whitney pairs test.

ii. Comparisons between study sites

Home range area estimates were tested for differences between the two major study sites using the Wilcoxon/ Mann-Whitney pairs test.

iii. Comparisons between sexes

Home range area estimates were tested for differences between the two sexes using the Wilcoxon/ Mann-Whitney

pairs test.

iv. Relationship between range area and number of observations

The relationship between range area and the number of observations was plotted and correlation between the two variables assessed via the Spearman's rank correlation coefficient. Where significant correlations were detected, regression equations were calculated and regression lines drawn.

v. Relationship between range area and the period of observation

The relationship between range area and the period of observation (expressed as 'activity days', i.e. the total time between first and last observation less the number of these days that occurred during a defined winter period) was plotted and correlation between the two variables assessed via the Spearman's rank correlation coefficient. Where significant correlations were detected, regression equations were calculated and regression lines drawn.

c. Vegetation use

i. Vegetation categories used in the field

Each 0.25 m² quadrat assessed for vegetation cover was assigned to one of 33 vegetation categories depending upon the relative abundance of each plant species found within it (see Appendix I for details). Frequencies and relative frequencies of use of each vegetation category were tabulated (including observations where quadrats were dominated by tile/ tin sheeting placed in the field) for each sex, each site and each method of location separately. Pie charts were drawn to illustrate the relative usage of each vegetation category (excluding cases where tile/ tin sheeting dominated any quadrat) collectively for the two sexes but separately for each site and each method.

These 32 vegetation categories (i.e. excluding tile/ tin sheeting category which was omitted from this further analysis) were amalgamated to yield ten habitat categories to allow statistical analysis. The frequencies and relative frequencies of observation of smooth snakes in each of these habitat categories was tabulated. Habitat use was compared between the two methods of observation via a G-test for both sexes and both sites separately. Habitat use was compared between the sexes, using radio-location data only, with a G-test separately for each site. Observed habitat use by radio-tagged snakes was compared against the relative abundance of each habitat category at each site (based upon random quadrat sampling) via a G-test, keeping data for males and females separate in each case.

Seasonal variation in habitat use (using ten vegetation categories) was investigated for radio-tagged males and females at each site by pairwise comparisons between the three seasons using Spearman's rank correlation coefficients. Differences in habitat use during the day and during the night were investigated by pairwise comparisons of vegetation category use between the last radio-locations during each day (where the animal was assumed to be in its over-night refuge) and radio-locations throughout the remainder of the day, for males and females separately at each site, using Spearman's rank correlation coefficient (G-tests were not employed in these latter cases as sample sizes were such that they yielded 'expected' values less than five in many cases).

ii. Vegetation species composition used in the field

The total percentage cover of each plant species, bare ground and tile/ tin sheeting, etc., was described and tabulated separately for each sex, site and method of location for all quadrats assessed in the field. In addition, the percentage cover of each species in random quadrats was described to ascertain the relative abundance of different types of vegetation at each site. The relative

abundance of each plant species was assessed to give an indication of their importance as components of the habitat of C. austriaca. No statistical comparisons were undertaken on these data.

iii. Height of vegetation used in the field

At every observation of a smooth snake, the relative proportion of the vegetation in each of 16 defined height categories (see Chapter 2, section 2.2.4 a) was assessed within a 0.25 m² quadrat centred on the location of the snake. The ground cover in the different height categories was described as a percentage of the total area for all quadrats for each sex, site and method of location separately as well as for randomly positioned quadrats at each site. Bar charts showing the percentage frequency with which each height class was observed were produced for each category of 'snake quadrats' and for the random quadrats at each site. Thus a representation of the overall height structure used by smooth snakes, and that available at each site, could be obtained.

Median vegetation heights were calculated for each quadrat and each of these assigned to one of 16 height categories (as above) (i.e. these represented the height category that contained the 50th percentile). The frequency distributions of median heights within these categories (for each sex, site and method of location) were plotted on bar charts. The frequency of occurrence of each vegetation height category was compared between the methods of location, separately for each sex at each site via the G-test. Vegetation height category use was compared between sexes for radio-tagged snakes at each of the two sites using the G-test. The G-test was employed to compare the observed frequency of use of each median height category against the relative abundance of each height category at each site (based on randomly positioned quadrats).

Seasonal variation in median height category use was investigated for radio-tagged males and females at each

site by pairwise comparisons between the three seasons using Spearman's rank correlation coefficients. Diurnal variation in median vegetation height use was undertaken by pairwise comparisons of the number of observations in each median height category between the final locations during each day (where the animal was assumed to have entered its over-night refuge) and height category use during the remainder of the day by radio-tagged male and female snakes at each site using Spearman's rank correlation coefficient (G-tests were not employed in these latter cases as sample sizes were such that they yielded 'expected' values less than five in many cases).

iv. Abundance of smooth snakes in different vegetation communities

Vegetation species composition and heights were described for each transect. The number of *C. austriaca* and other species of reptile observed on each transect were totalled and tabulated. Due to the small sample sizes encountered, no statistical analyses were undertaken on these data.

v. Vegetation use demonstrated by selection of 'vegetation type' in laboratory video recording experiment

The proportion of time spent in each of the two defined vegetation types ('open' and 'vegetation') were analysed for differences in each of the six 4-hour periods and over the whole day, using the Wilcoxon/ Mann-Whitney pairs test. Variation in the use of each of the two vegetation types and the use of cover between the 4-hour period was assessed using the Kruskal-Wallis test.

d. Distribution of potential prey, predator and competitor species

i. Reptilian and amphibian species

The reptilian and amphibian fauna was qualitatively described at each site. The reptilian species present

within all 10 x 10 m grid squares in the study areas (defined by the outer most sightings of C. austriaca at each site) were recorded. Tests for association of C. austriaca with each of the other reptile species observed at each site were undertaken using 2 x 2 contingency tables (recording the number of squares in which both species, the first species but not the second species, the second species but not the first species and neither species were present). Expected frequencies for each cell of each contingency table were calculated and these compared with the observed frequencies via a G-test. Tests of association were performed on the data in two ways, firstly using the total number of squares at each study site as the sample size and, secondly, using only the maximum number of squares that could have been occupied by the species in each pair (i.e. the sum of the number of squares that were occupied by each of the species individually). These two approaches tested for association between the species over the whole study site and for association between the species based on the observed relative distribution of the sightings of the two species.

ii. Mammalian and avian species

The mammalian and avian fauna was qualitatively described at each site. Small mammal trapping was undertaken on three habitat types at Site One. The number of animals of each species captured were tabulated although, due to small sample sizes, no further statistical analysis was performed.

5.3. Results

5.3.1. Home range size and shape

a. Home range areas and shape

Home range areas were calculated, using the convex polygon method (sensu Rose 1982), for all specimens of C. austriaca for which three or more observations were made during the

present study (April 1984 to October 1986). The resulting polygon was drawn in each case to show its shape and the relationship between it and the ranges of other snakes at each site. A total of 55 home ranges were described; 14 for male specimens at Site One, 12 for female specimens at Site One, 15 for male specimens at Site Two and 14 for female specimens at Site Two.

Home range areas, the mean body (snout to vent) length, the number of observations made, the observation period and the method(s) of observation employed for each snake are presented in Tables 5.1 to 5.4 inclusive, as follows: males at Site One (Table 5.1), females at Site One (Table 5.2), males at Site Two (Table 5.3) and females at Site Two (Table 5.4). The minimum home range area recorded was 34 m² (0.003 ha) and the maximum area observed was 17215 m² (1.722 ha). A median range area of 688 m² (0.069 ha) (n=55) was calculated for C. austriaca from the combined observations of the two sexes at the two sites that were used for intensive fieldwork.

Convex polygons describing the shape of the home ranges of each snake are presented in Figs. 5.1a, 5.1b, 5.2a and 5.2b as follows: males at Site One (Fig 5.1a), females at Site One (Fig. 5.1b), males at Site Two (Fig. 5.2a) and females at Site Two (Fig. 5.2b). Home range shape was not consistent between individuals, sexes or study sites and varied from being greatly elongated to being fairly regular. The degree of overlap of the home ranges of C. austriaca at each of the two study sites was illustrated by plotting each home range upon a grid representing point co-ordinates at each study site. These patterns of range use are illustrated in Figs. 5.3 and 5.4 for males and females respectively at Site One and Figs. 5.5 and 5.6 for males and females respectively at Site Two. At both study sites considerable overlap was observed in the ranges of snakes both within and between the sexes.

Snake	Range Size (m ²)	SVL (mm)	Number of Sightings	Period of Observation	Methods
MM01	1519	367	4	11/04/84 to 21/10/85	V
MM03	68	430	18	11/04/84 to 08/05/84	V & R
MM04	1343	307	6	11/04/84 to 07/09/85	V
MM06	2136	427	43	20/04/84 to 12/09/84	V & R
MM07	143	417	63	05/05/84 to 20/06/85	V & R
MM09	829	394	14	17/05/84 to 08/08/84	V & R
MM10	2008	418	38	20/05/84 to 08/08/84	V & R
MM11	499	405	42	04/07/84 to 10/07/84	R
MM12	4504	370	36	07/07/84 to 28/06/85	V & R
MM14	2009	408	15	08/08/84 to 08/09/85	V & R
MM16	13709	442	149	13/08/84 to 12/09/85	V & R
MM19	448	396	36	15/09/84 to 21/09/84	R
MM76	177	434	5	13/08/85 to 19/07/86	V
MM77	187	410	3	15/08/85 to 19/07/86	V

Table 5.1 : Home range size (m²) of male C. austriaca at Site One and the mean body length (snout to vent (SVL)) (mm), the associated number of observations and the period over which each animal was observed. The method(s) of observation (V= visual location and R=radio-tracking) are also given.

Snake	Range Size (m ²)	SVL (mm)	Number of Sightings	Period of Observation	Methods
FM02	4613	380	50	11/04/84 to 24/04/86	V & R
FM08	3257	395	31	05/05/84 to 06/06/84	V & R
FM13	2136	453	106	11/07/84 to 09/05/86	V & R
FM17	3139	394	64	15/08/84 to 10/06/85	V & R
FM26	468	448	42	10/06/85 to 27/06/86	V & R
FM71	59	400	4	16/07/85 to 04/09/85	V
FM72	208	442	10	17/07/85 to 11/09/85	V
FM73	34	451	6	17/07/85 to 11/09/85	V
FM74	93	490	8	17/07/85 to 11/09/85	V
FM77	187	408	3	15/08/85 to 19/07/86	V
FM80	2053	564	5	22/06/86 to 24/07/86	V
FM82	91	451	3	23/07/86 to 04/09/86	V

Table 5.2 : Home range size (m²) of female C. austriaca at Site One and the mean body length (snout to vent (SVL)) (mm), the associated number of observations and the period over which each animal was observed. The method(s) of observation (V= visual location and R= radio-tracking) are also given.

Snake	Range Size (m ²)	SVL (mm)	Number of Sightings	Period of Observation	Methods
MH02	11035	362	58	18/06/84 to 15/05/86	V & R
MH04	662	380	30	28/06/84 to 15/05/85	V & R
MH05	72	395	5	12/07/84 to 19/09/85	V
MH06	10650	433	34	12/07/84 to 21/07/86	V & R
MH10	5513	440	102	01/08/84 to 24/05/85	V & R
MH17	960	420	8	03/09/84 to 27/08/85	V & R
MH22	688	374	28	26/09/84 to 18/09/85	V & R
MH27	120	411	5	10/05/85 to 24/04/86	V
MH29	682	430	60	14/06/85 to 11/07/85	V & R
MH33	5261	412	56	02/07/85 to 10/07/85	R
MH36	56	363	10	09/07/85 to 27/07/86	V
MH38	6968	402	30	05/08/85 to 09/08/85	R
MH42	1195	435	24	19/08/85 to 28/04/86	V & R
MH49	3390	415	16	17/09/85 to 20/09/85	R
MH58	269	386	25	22/07/86 to 26/07/86	R

Table 5.3 : Home range size (m²) of male *C. austriaca* at site Two and the mean body length (snout to vent (SVL)) (mm), the associated number of observations and the period over which each animal was observed. The method(s) of observation (V= visual observation and R= radio-tracking) are also given.

Snake	Range Size (m ²)	SVL (mm)	Number of Sightings	Period of Observation	Methods
FH01	150	422	19	05/06/84 to 22/06/84	V & R
FH03	2667	427	48	25/06/84 to 19/07/86	V & R
FH09	17215	489	66	31/07/84 to 16/10/85	V & R
FH11	2240	497	32	01/08/84 to 29/09/84	V & R
FH12	1611	425	70	29/08/84 to 25/09/85	V & R
FH13	277	413	58	30/08/84 to 08/09/84	V & R
FH21	10479	392	6	24/09/84 to 19/09/85	V
FH28	586	426	10	07/06/85 to 17/09/85	V
FH30	39	473	16	16/06/85 to 23/09/85	V
FH37	53	425	31	10/07/85 to 16/09/85	V & R
FH39	183	467	21	05/08/85 to 19/09/85	V & R
FH43	351	451	3	23/08/85 to 10/09/85	V
FH44	500	377	19	24/08/85 to 18/09/85	V & R
FH56	1056	383	35	20/07/86 to 26/07/86	R

Table 5.4 : Home range size (m²) of female C. austriaca at site Two and the mean body length (snout to vent (SVL)) (mm), the associated number of observations and the period over which animal was observed. The method(s) of observation (V= visual observation and R= radio-tracking) are also given.

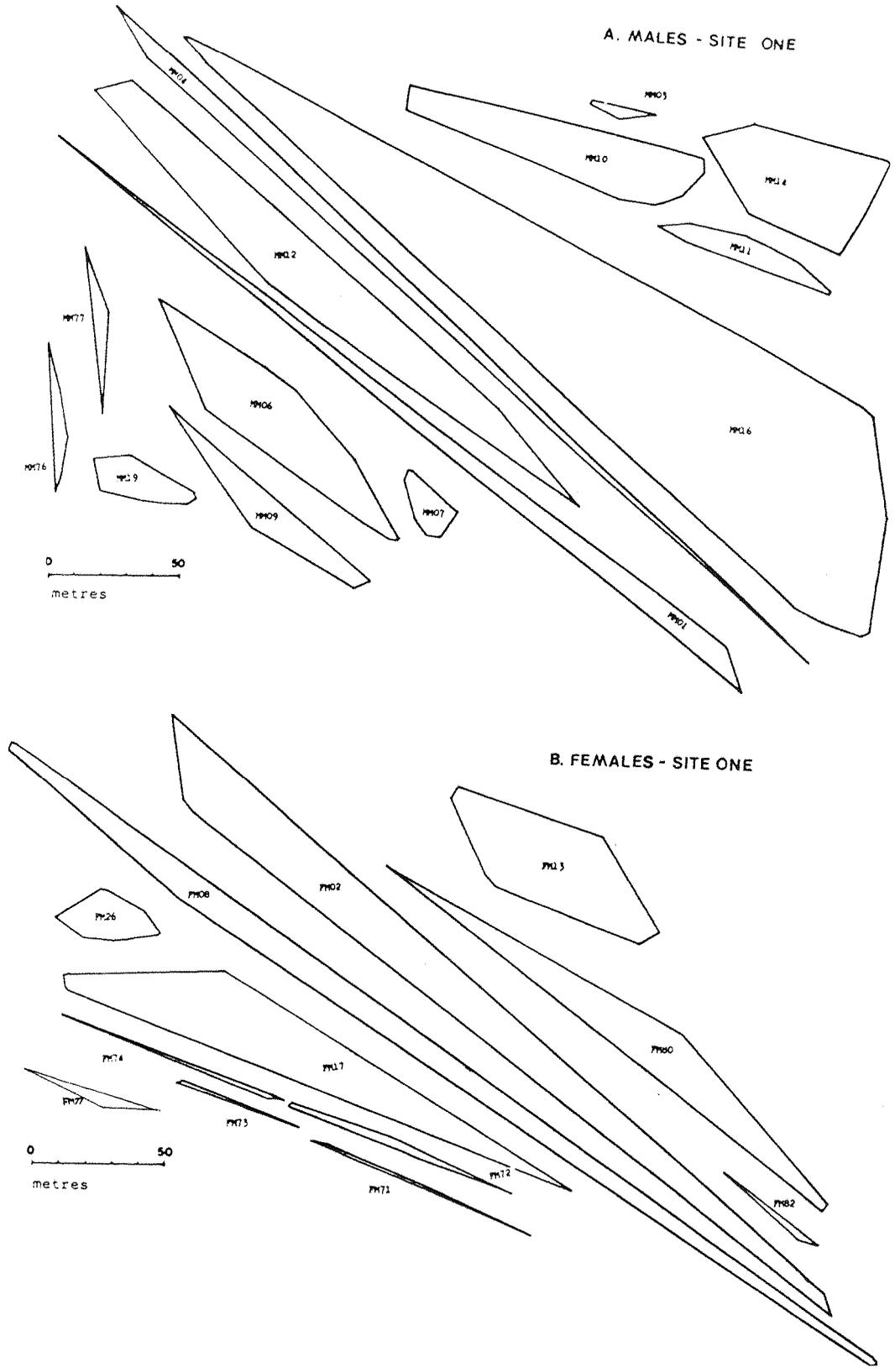


Fig. 5.1 : Convex polygons describing home ranges of *C. austriaca* at Site One for A. Male specimens and B. Female specimens. Numbers associated with each polygon are snake identification codes (a scale in metres is included).

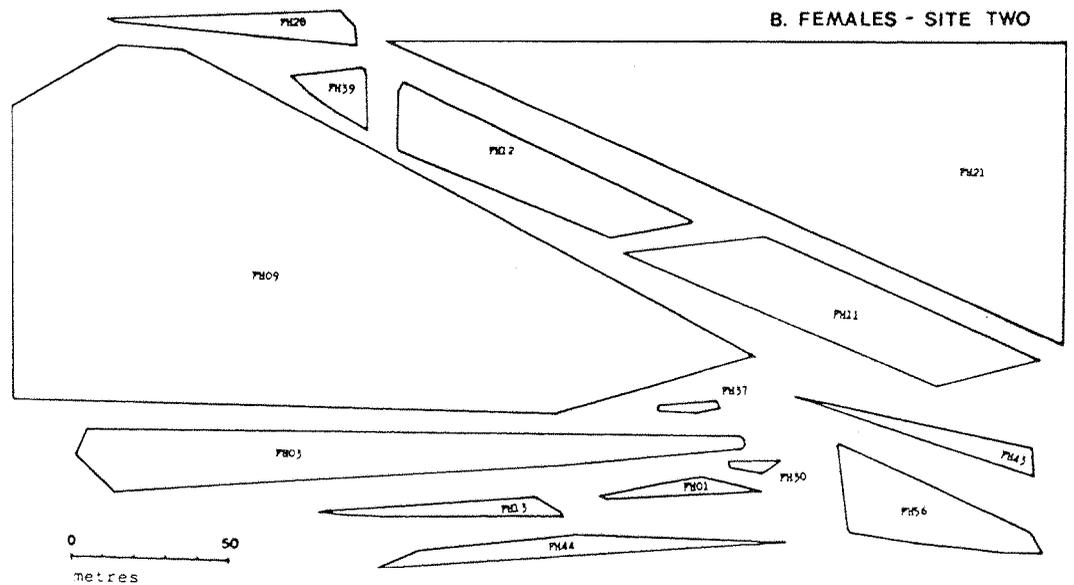
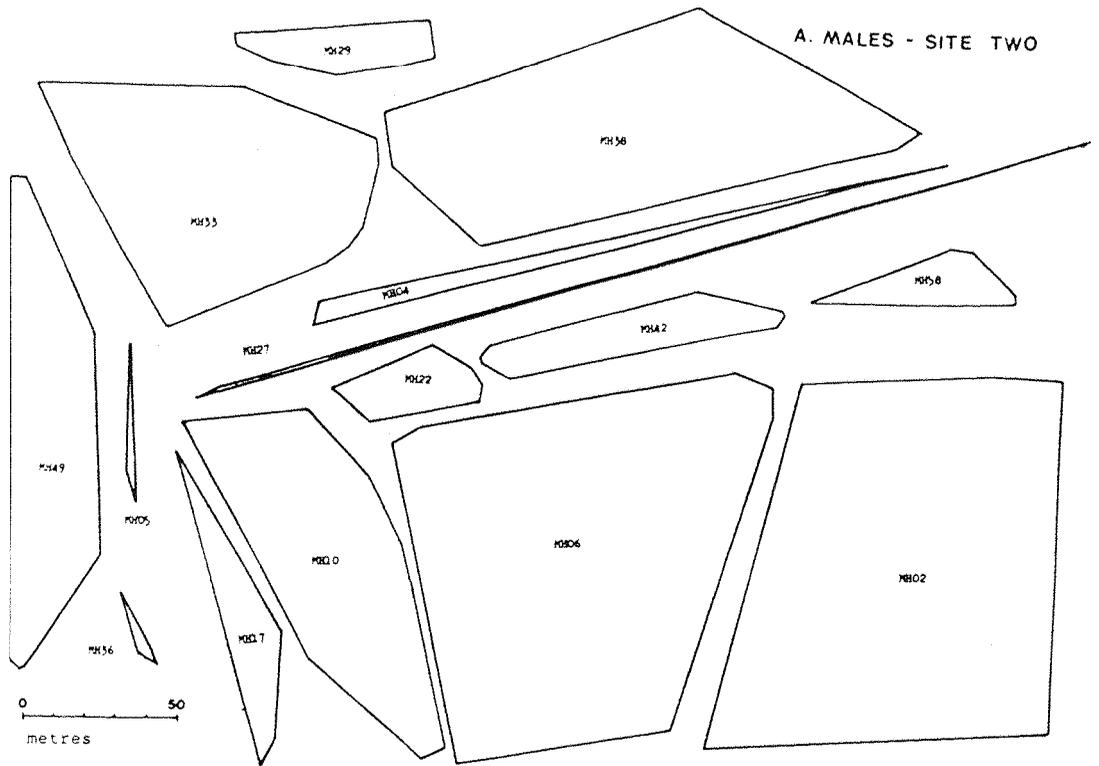


Fig. 5.2 : Convex polygons describing home ranges of C. austriaca at Site Two for A. Male specimens and B. Female specimens. Numbers associated with each polygon are snake identification codes (a scale in metres is included).

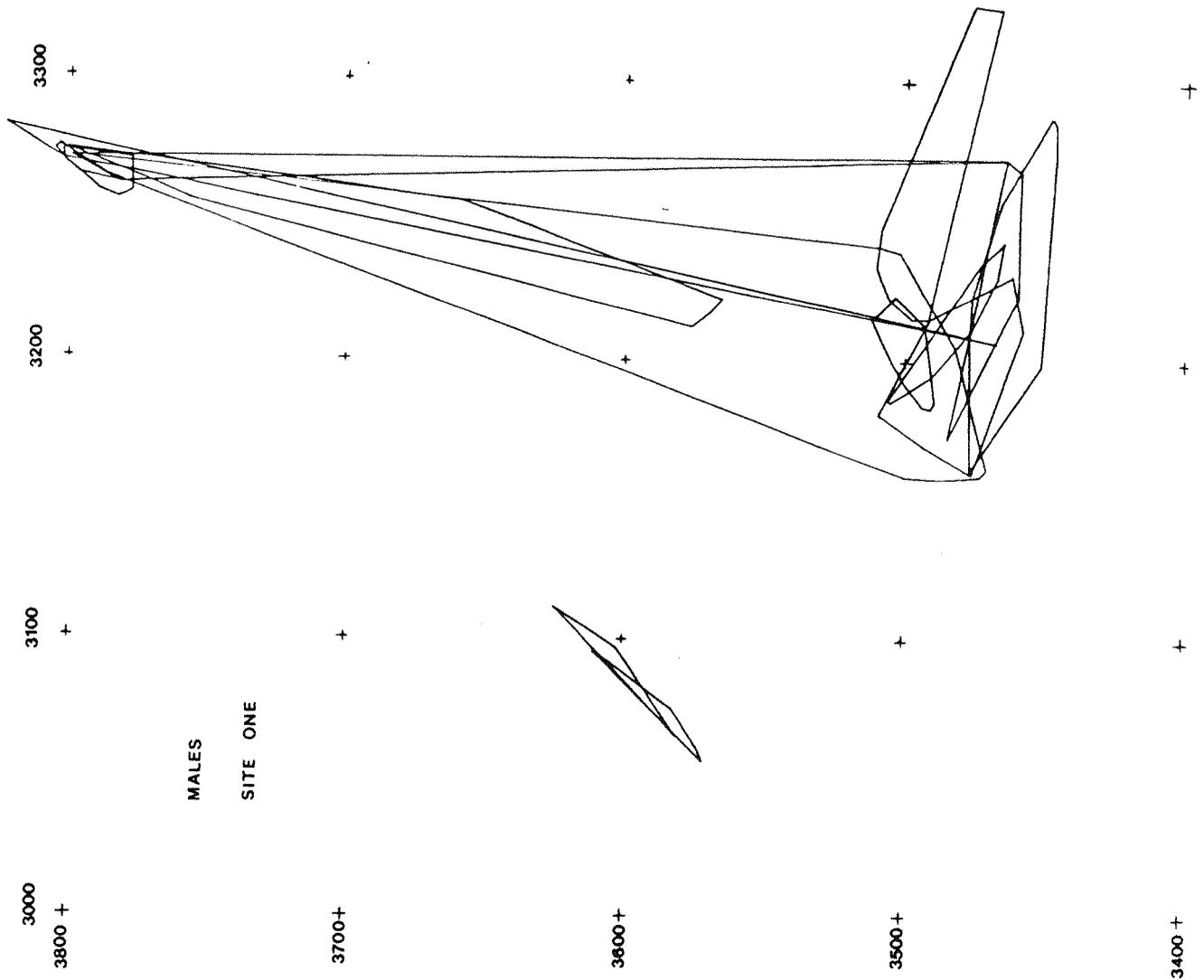


Fig. 5.3 : Convex polygons showing spatial overlap of home ranges of male *C. austriaca* at Site One. Major grid co-ordinates (100 metre intervals) are included; the crosses represent points of intersect of these major grid lines.

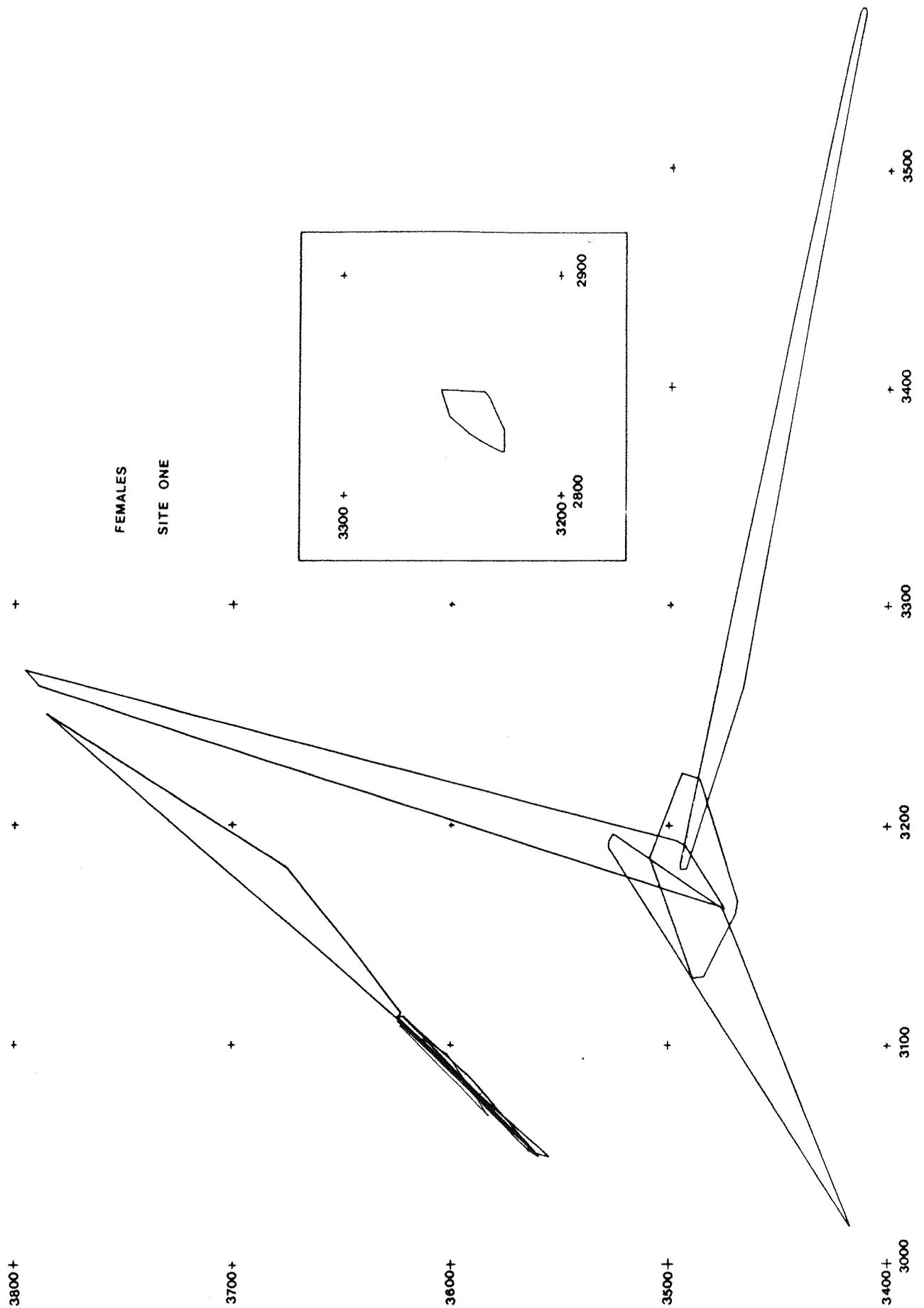


Fig. 5.4 : Convex polygons showing spatial overlap of home ranges of female C. austriaca at Site One. Major grid lines (100 metre intervals) are included; the crosses represent points of intersect of the grid lines.

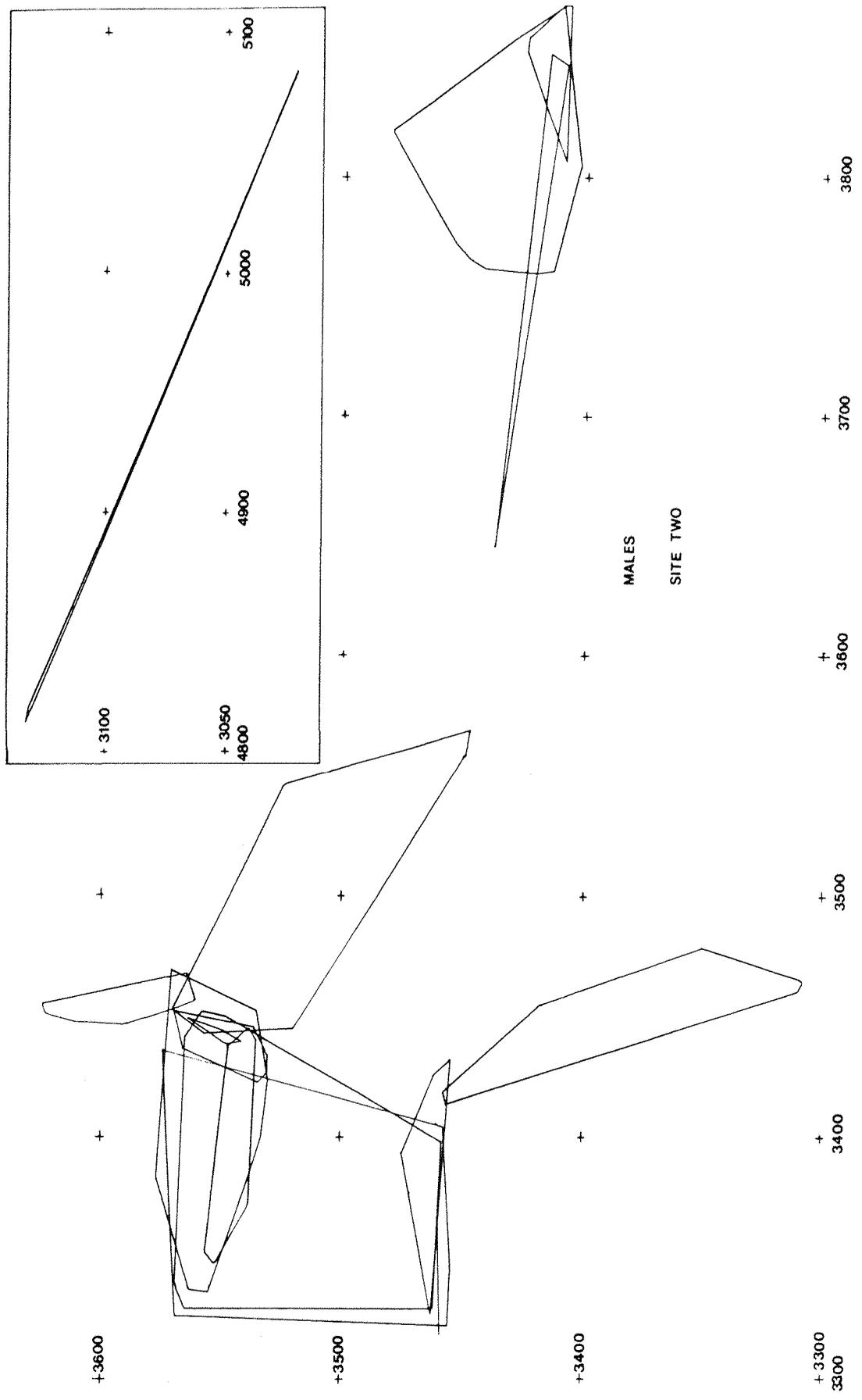


Fig. 5.5 : Convex polygons showing spatial overlap of home ranges of male C. austriaca at Site Two. Major grid lines (100 metre intervals) are included; the crosses represent points of intersect of the grid lines.

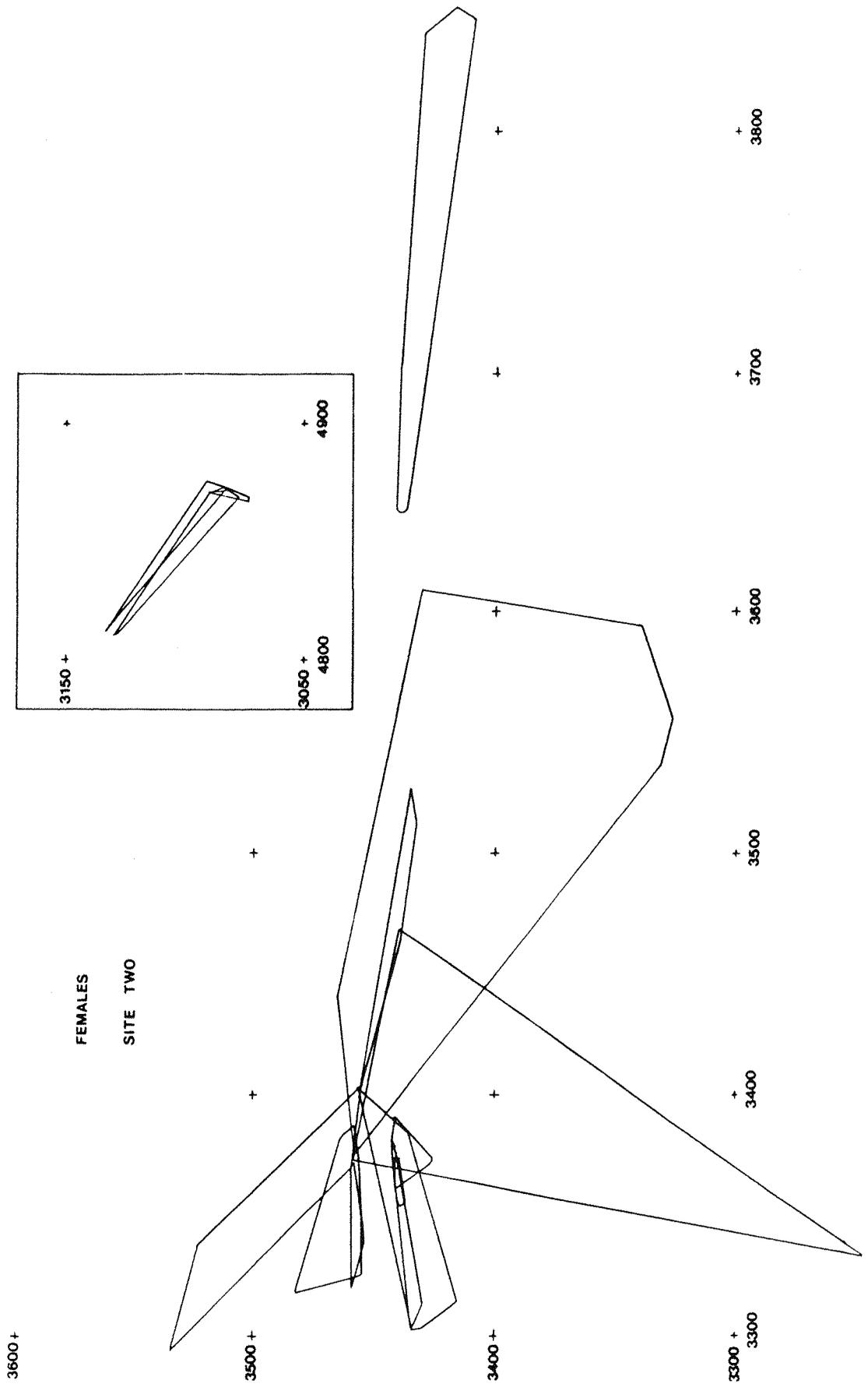


Fig. 5.6 : Convex polygons showing spatial overlap of home ranges of female C. austriaca at Site Two. Major grid lines (100 metre intervals) are included; the crosses represent points of intersect of the grid lines.

b. Intraspecific comparisons of range area

i. Effect of methodology

The distribution of range areas observed during the present study was highly positively skewed, with more than half of the home range areas calculated being less than 1000 m² (0.1 ha) (see Fig. 5.7). Two methods of observation were employed during the study period, namely radio-tracking and visual location, and the manner in which the observations were collected was deemed likely to influence the calculation of range area. As such, one of three 'method categories' was assigned to each home range depending upon which method, or combination of methods, were used to collect the data from which it was calculated. These categories were: 'Visual location only', 'Visual location and radio-tracking' and 'Radio-tracking only'.

The frequency of range sizes obtained from each of these 'method categories' is indicated by shading in the frequency distribution of range areas shown in Fig. 5.7. The largest estimates of range area were calculated from data collected from 'Visual location and radio-tracking' data for both sexes and both sites. Median range area estimates for the three methods were: 'Visual location and radio-tracking' 1809.5 m² (0.181 ha) (range= 53 to 17215 m² (0.005 to 1.722 ha), n= 30), 'Visual location only' 182 m² (0.018 ha) (range= 34 to 10479 m² (0.003 to 1.048 ha), n= 18) and 'Radio-tracking only' 1056 m² (0.106 ha) (range= 269 to 6968 m² (0.027 to 0.697 ha), n= 7).

Significant variation was detected between estimates of home range area calculated using the three method categories (Kruskal-Wallis chi-square= 12.367, n= 55, p<0.003). Pairwise testing, using the Wilcoxon/Mann-Whitney pairs test, showed significant variation in estimates of range areas between 'Visual location only' and 'Radio-tracking only' data (z= 2.391, n₁= 18, n₂= 7, p<0.02) and between 'Visual location only' and 'Visual location and

radio-tracking' data ($z = 3.312$, $n_1 = 30$, $n_2 = 18$, $p < 0.001$). No difference was observed, however, between home range areas estimated from 'Radio-tracking only' and 'Visual location and radio-tracking' data ($z = 0.000$, $n_1 = 30$, $n_2 = 7$, $p > 0.05$). For further analyses, therefore, data were separated into two method categories, namely 'Visual location only' and a category formed from the combination of 'Visual location and radio-tracking' and 'Radio-tracking only' data. The median range area estimated from this latter category was 1611 m^2 (0.161 ha) (range = 53 to 17215 m^2 (0.005 to 1.722 ha), $n = 37$).

ii. Comparisons between study sites

The median home range areas at Site One and Site Two were 664 m^2 (0.066 ha) (range = 34 to 13709 m^2 (0.003 to 1.371 ha), $n = 26$) and 688 m^2 (0.069 ha) (range = 39 to 17215 m^2 (0.004 to 1.722 ha), $n = 29$) respectively, using data from all methods combined. These data were not significantly heterogeneous ($z = -0.683$, $n_1 = 29$, $n_2 = 26$, $p > 0.05$).

No significant differences were detected between home range area estimates at the two sites when the data were separated into either of the two method categories. The median home range areas calculated using 'Visual location only' data were 187 m^2 (0.019 ha) (range = 34 to 2053 m^2 (0.003 to 0.205 ha), $n = 11$) and 120 m^2 (0.012 ha) (range = 39 to 10479 m^2 (0.004 to 1.048 ha), $n = 7$) for Site One and Two respectively ($z = 0.272$, $n_1 = 11$, $n_2 = 7$, $p > 0.05$). The combined 'Radio-tracking only' and 'Visual location and radio-tracking' category yielded median home range estimates of 2009 m^2 (0.201 ha) (range = 68 to 13709 m^2 (0.007 to 1.371 ha), $n = 15$) and 1125.5 m^2 (0.113 ha) (range = 53 to 17215 m^2 (0.005 to 1.722 ha), $n = 22$) for Sites One and Two respectively ($z = -0.108$, $n_1 = 22$, $n_2 = 15$, $p > 0.05$).

The similarity between estimates of home range areas for C. austriaca from the two study sites permitted data from Sites One and Two to be pooled for further analysis.

iii. Comparisons between sexes

No significant difference was detected between home range estimates for male and female C. austriaca when analysing combined data from all methods ($z = 1.087$, $n_1 = 29$, $n_2 = 26$, $p > 0.05$). Median home range areas were 484 m^2 (0.048 ha) (range = 34 to 17215 m^2 (0.003 to 1.722 ha), $n = 26$) for female snakes and 960 m^2 (0.096 ha) (range = 56 to 13709 m^2 (0.006 to 1.371 ha), $n = 29$) for male snakes.

The median home range areas for the two sexes calculated from 'Visual location only' data were 187 m^2 (0.019 ha) (range = 34 to 10479 m^2 (0.003 to 1.048 ha), $n = 11$) and 177 m^2 (0.018 ha) (range = 56 to 1519 m^2 (0.006 to 0.152 ha), $n = 7$) for female and male specimens respectively. These estimates were not significantly different ($z = 0.000$, $n_1 = 11$, $n_2 = 7$, $p > 0.05$). Home range area estimates calculated from the combination of 'Visual location and radio-tracking' and 'Radio-tracking only' data were also homogeneous between the sexes ($z = 0.619$, $n_1 = 22$, $n_2 = 15$, $p > 0.05$). The median area estimates were 1611 m^2 (0.161 ha) (range = 53 to 17215 m^2 (0.005 to 1.722 ha), $n = 15$) for female snakes and 1601.5 m^2 (0.160 ha) (range = 68 to 13709 m^2 (0.007 to 1.371 ha), $n = 22$) for male snakes.

Homogeneity of range area estimates between the two sexes means that these two data sets could be combined during further analysis.

iv. Relationship between range area and number of observations

The relationship between the estimated home range area and the number of observations made is presented in Fig. 5.8. A significant increase in home range area was detected with an increase in the number of observations when data for both sexes and both method categories were pooled ($r_s = 0.528$, $n = 55$, $p < 0.0001$). This relationship was described by the regression equation:

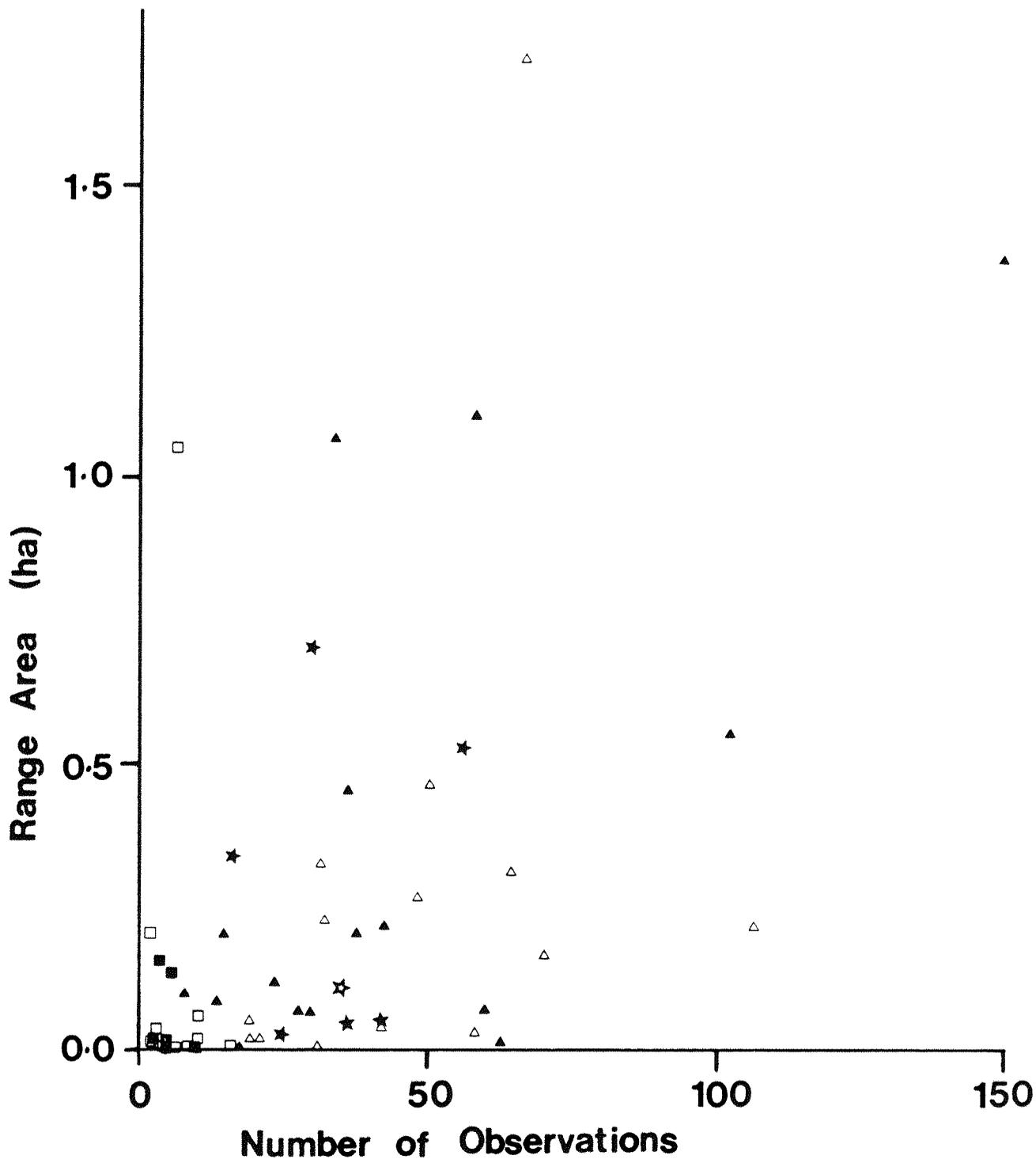


Fig. 5.8 : Estimated home range area (ha) against number of observations of *C. austriaca* at Sites One and Two. Closed symbols represent male snakes, open symbols represent female snakes:

★☆ Radio-tracking only, ■□ Visual location only, ▲△ Visual location and radio-tracking

$$\text{Area} = (64.08 \times \text{No. Obs.}) + 364.56$$

where Area is the home range estimate (m^2) and No. Obs. is the number of observations made.

Significant effects of the number of observations upon home range area estimates were detected when the data were subdivided by sex, with increasing sample sizes yielding larger home range estimates for both male and female snakes ($r_m = 0.482$, $n = 29$, $p < 0.02$ and $r_m = 0.523$, $n = 26$, $p < 0.01$, respectively). These relationships were described by the regression equations:

$$\text{Males: Area} = (75.71 \times \text{No. Obs.}) + 144.50$$

$$\text{Females: Area} = (44.54 \times \text{No. Obs.}) + 754.68$$

where Area is given in m^2 and No. Obs. is the number of observations. The regression lines described by these equations are illustrated in Fig. 5.9 A.

No significant effect of number of observations on estimated home range area was detected for range areas calculated from 'Visual location only' data for male snakes ($r_m = -0.519$, $n = 7$, $p > 0.05$), female snakes ($r_m = -0.055$, $n = 11$, $p > 0.05$) or for both sexes combined ($r_m = -0.161$, $n = 18$, $p > 0.05$). A significant positive correlation was observed between home range area and the number of observations made for areas calculated from 'Visual location and radio-tracking' and 'Radio-tracking only' data combined for pooled data from male and female snakes ($r_m = 0.383$, $n = 37$, $p < 0.03$), a relationship described by the following regression equation:

$$\text{Area} = (69.75 \times \text{No. Obs.}) + 10.79$$

where Area is estimated home range area in m^2 and No. Obs. is the number of observations made. The regression line for this relationship is illustrated in Fig. 5.9 B. No significant relationships were detected for 'Visual

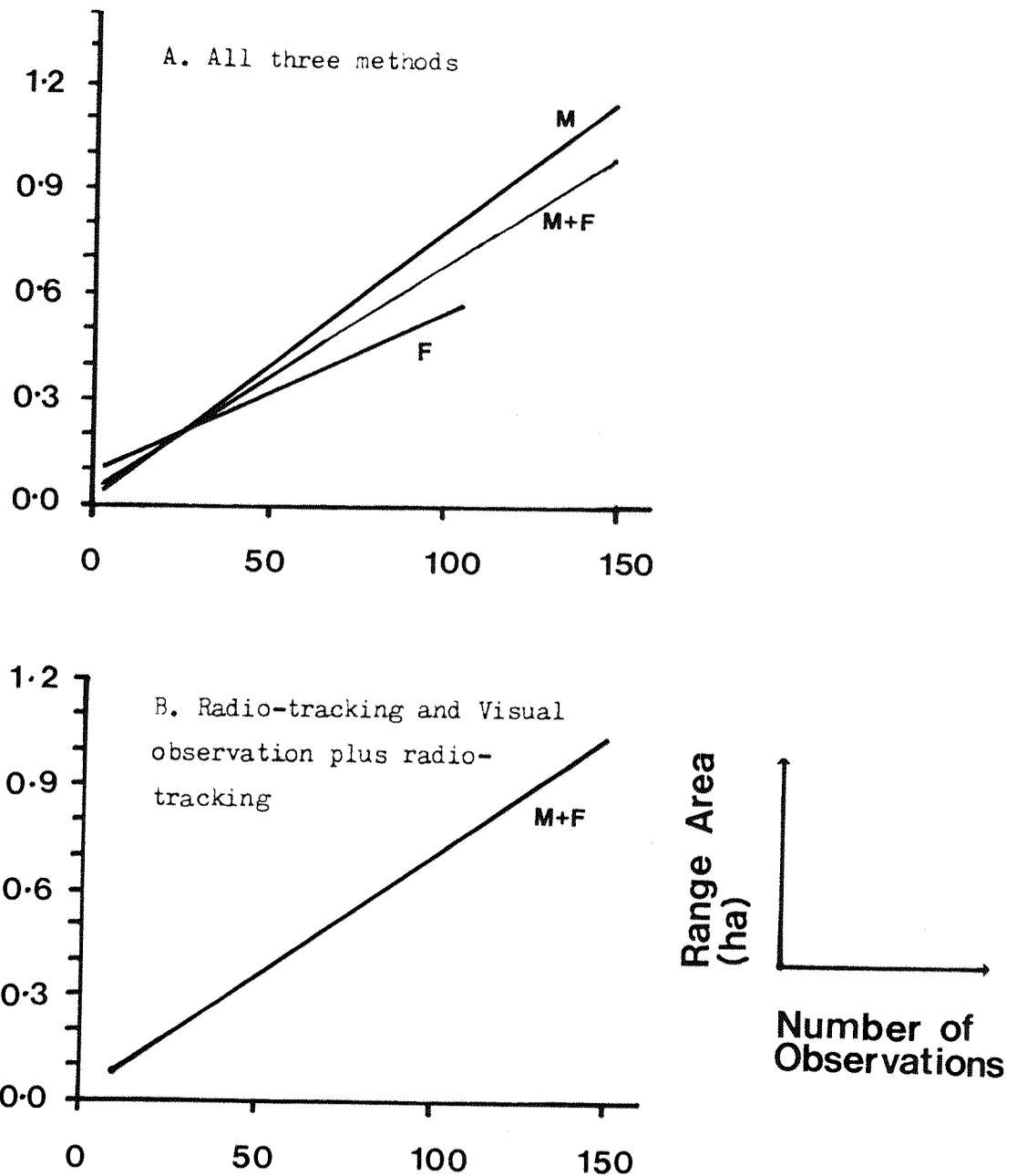


Fig. 5.9 A. and B. : Regression lines for the relationship between Home range area (ha) and the Number of observations for *C. austriaca* as determined by A. All three methods and B. Radio-tracking and Visual observation plus Radio-tracking. M+F represents male and female specimens, M represents male specimens only and F represents female specimens only.

location and radio-tracking' and 'Radio-tracking only' data combined when analysed for each sex separately (females: $r_{\text{m}} = 0.508$, $n = 15$, $p > 0.05$; males: $r_{\text{m}} = 0.283$, $n = 22$, $p > 0.05$).

v. Relationship between range area and the period of observation

Observation periods were calculated as an estimate of the number of days that a snake was active between the first and the last location of that snake; thus the effect of the potential time for dispersal upon estimates of home range area could be considered. The number of 'activity days' was therefore the difference in time between the first and last observation excluding the winter period (defined as being between 25th October (the latest date a smooth snake was observed during the present study) and 31st March (the earliest record of a smooth snake during the present study); a period of 157 days).

The relationship between range area and the observation period (number of 'activity days') is illustrated in Fig. 5.10. In general, larger home range areas were associated with longer periods of observation when all methods of observation were considered together. These data were significantly correlated ($r_{\text{m}} = 0.272$, $n = 55$, $p < 0.05$) and the relationship was described by the regression equation:

$$\text{Area} = (10.52 \times \text{No. Days}) + 821.55$$

where Area is home range area estimate in m^2 and No. Days is the number of 'activity days'. The regression line of this equation is illustrated in Fig. 5.11 A.

Analysis of the data for all three methods combined, but separated for each sex, showed that no significant correlation existed between range area and observation period for male snakes ($r_{\text{m}} = 0.116$, $n = 29$, $p > 0.05$) but that the two variables were correlated when using data collected from female specimens ($r_{\text{m}} = 0.400$, $n = 26$, $p < 0.05$). The latter relationship was described by the regression

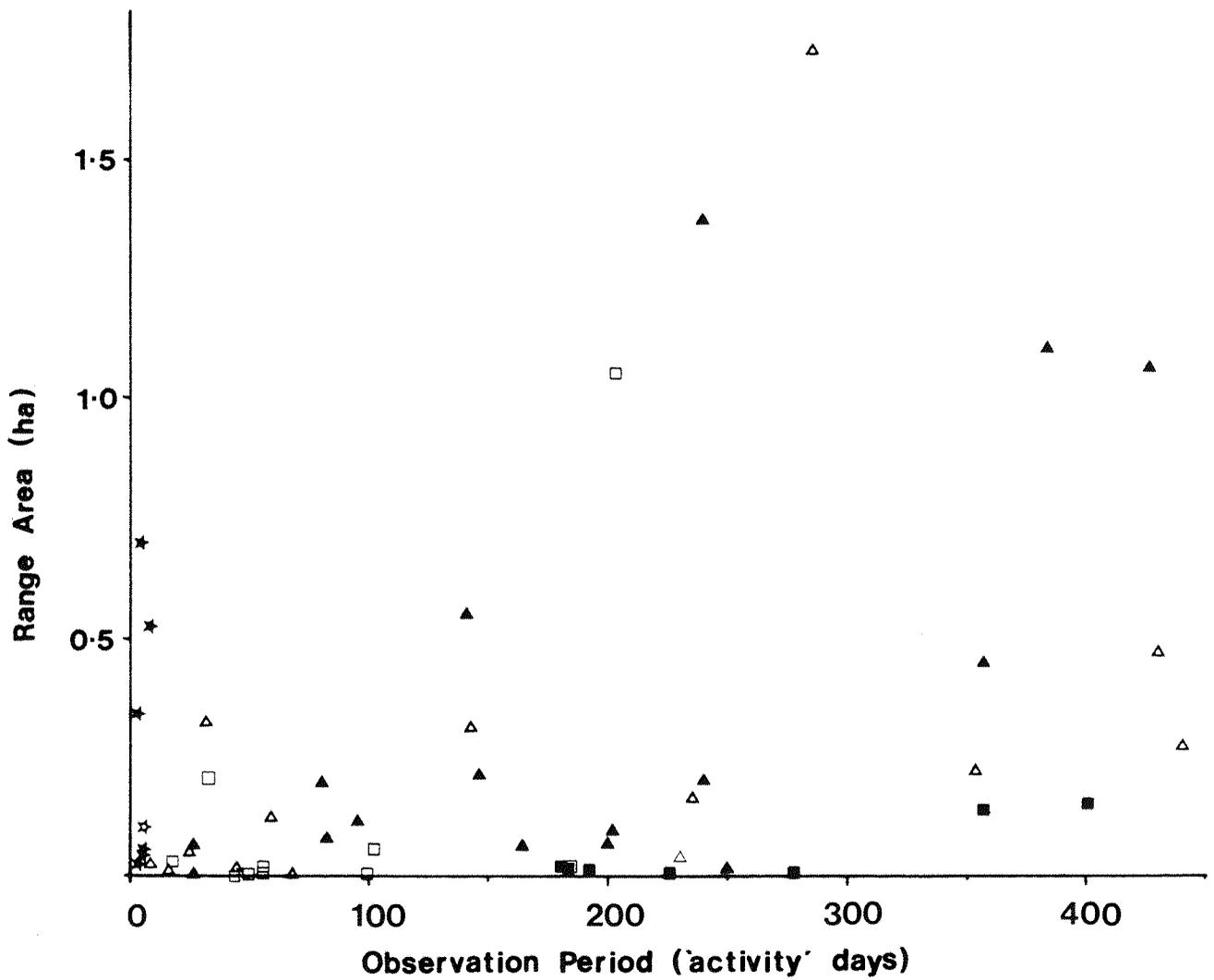


Fig. 5.10 : Estimated home range area (ha) against observation period ('Activity days') of *C. austriaca* at Sites One and Two. Closed symbols represent male snakes, open symbols represent female snakes: ★☆ Radio-tracking only, ■□ Visual location only, ▲△ Visual location and radio-tracking.

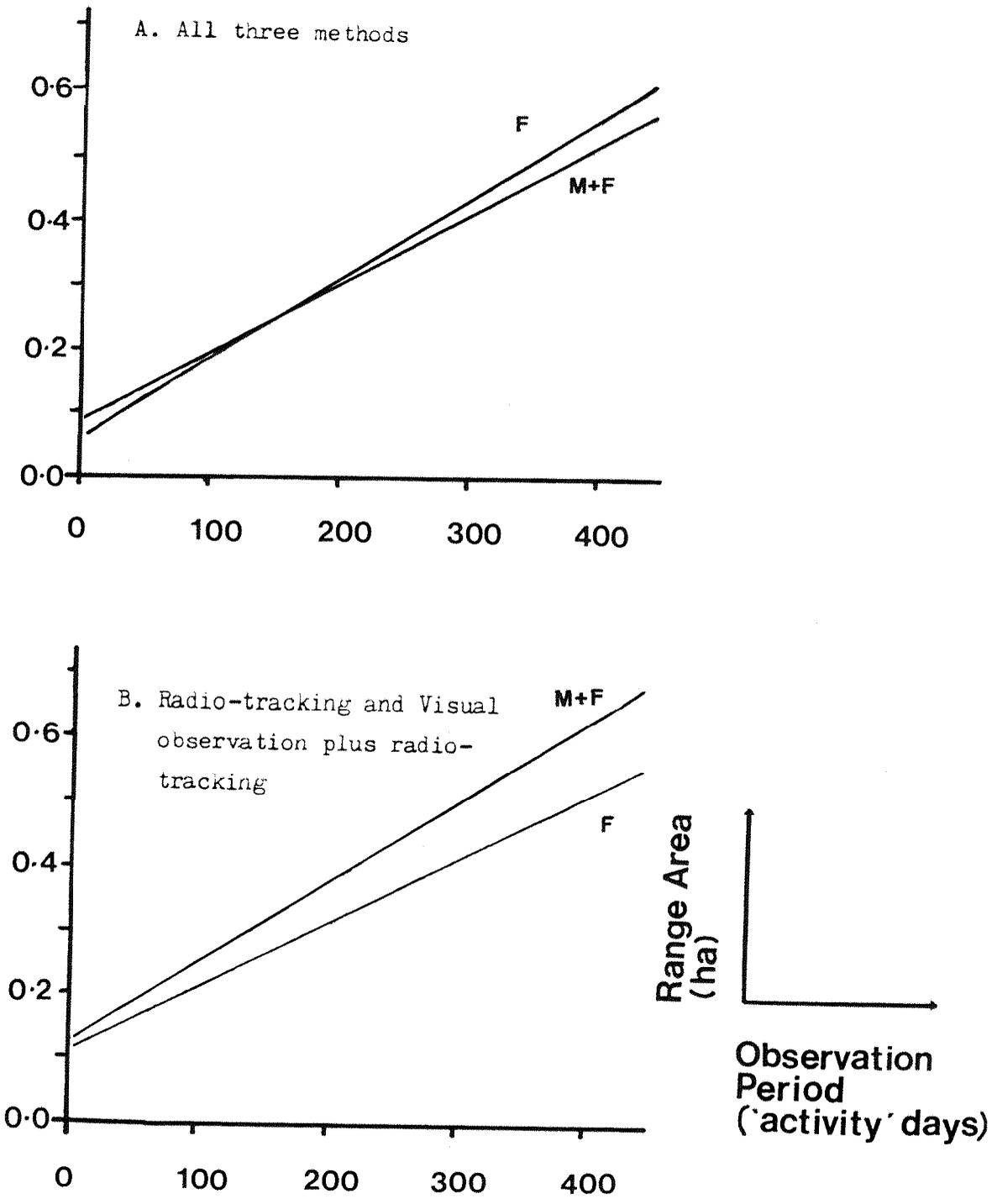


Fig. 5.11A and B : Regression lines for the relationship between home range area (ha) and the Period of observation ('activity' days) for *C. austriaca* as determined by A. All three methods and B. Radio-tracking and Visual observation plus Radio-tracking. M+F represents male and female specimens, F represents female specimens only.

equation:

$$\text{Area} = (12.51 \times \text{No. Days}) + 505.74$$

(where Area is given in m^2 and No. Days equals the number of 'activity days'). The regression line of this equation is presented in Fig. 5.11 A.

No significant correlations were observed between range area and observation period for male snakes ($r_m = 0.321$, $n = 7$, $p > 0.05$), female snakes ($r_m = 0.110$, $n = 11$, $p > 0.05$) or for both sexes together ($r_m = -0.149$, $n = 18$, $p > 0.05$) when 'Visual location only' data were analysed.

The analysis of 'Visual location and radio-tracking' and 'Radio-tracking only' data combined showed a significant positive correlation between estimated range area and observation period for both sexes together ($r_m = 0.389$, $n = 37$, $p < 0.02$) and for female snakes ($r_m = 0.536$, $n = 15$, $p < 0.05$). These relationships were described by the regression equations:

$$\text{Both sexes: Area} = (12.69 \times \text{No. Days}) + 1198.57$$

$$\text{Females: Area} = (9.86 \times \text{No. Days}) + 1096.27$$

(where Area is given in m^2 and No. Days represents the period of observation in 'activity days'). The regression lines for these relationships are illustrated in Fig. 5.11 B. No correlation was observed between range area and observation period for male snakes using 'Visual location and radio-tracking' and 'Radio-tracking only' data combined ($r_m = 0.329$, $n = 22$, $p > 0.05$).

vi. Relationship between range area and snake body length

The relationship between range area (ha) and body length (snout to vent length) (mm) is presented in Fig. 5.12 (see also Tables 5.1 to 5.4). No significant correlation was observed when data from all methods of location were combined for both sexes together ($r_m = -0.122$, $n = 55$,

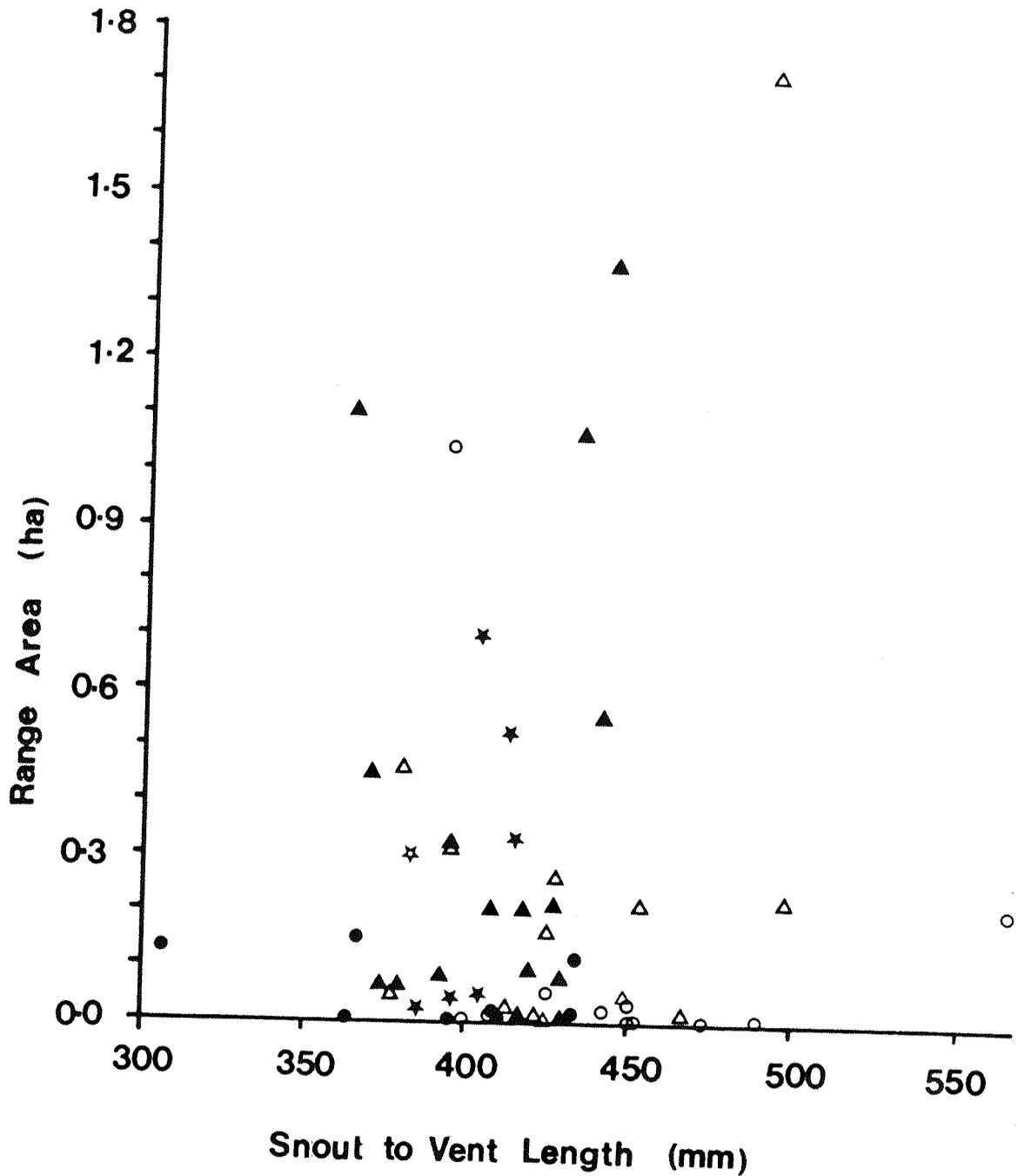


Fig. 5.12 : Estimated home range area (ha) against snout to vent length (mm) for *C. austriaca* at Sites One and Two. Closed symbols represent male snakes, open symbols represent female snakes:

★☆ Radio-tracking only, ●○ Visual location only, ▲△ Visual location and radio-tracking.

$p > 0.05$) or for either of the sexes when analysed separately (males: $r_m = 0.144$, $n = 29$, $p > 0.05$; females: $r_m = -0.291$, $n = 26$, $p > 0.05$).

Home range area estimates calculated from 'Visual location only' data were not correlated with snout to vent length when analysed using results for both sexes together ($r_m = -0.176$, $n = 18$, $p > 0.05$) or for male ($r_m = -0.143$, $n = 7$, $P > 0.05$) or female snakes ($r_m = -0.193$, $n = 11$, $p > 0.05$) separately.

No significant correlations were detected between range area and body size using data collected via 'Visual location and radio-tracking' and 'Radio-tracking only' combined (both sexes together: $r_m = 0.025$, $n = 37$, $p > 0.05$; male snakes: $r_m = 0.172$, $n = 22$, $p > 0.05$; female snakes: $r_m = 0.020$, $n = 15$, $p > 0.05$).

5.3.2. Vegetation use

a. Vegetation categories occupied in the field

i. Vegetation category use (33 categories)

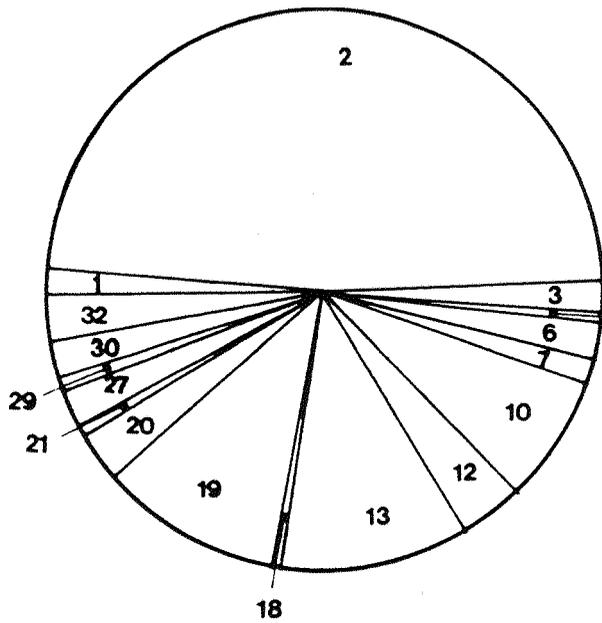
The frequency and relative frequency of observations of smooth snakes within each of the defined vegetation categories at Site One is presented, for each sex and each method of location, in Table 5.5. The vegetation categories in the 0.25 m^2 quadrats associated with 419 radio-locations of males and 215 radio-locations of females and 87 visual locations of males, 108 visual locations of females and eight visual locations of juveniles were recorded at Site One (these totals include three, zero, three, one and four cases respectively where snakes were located under tin or tile such that the surrounding vegetation could not be classified). Relative use of each vegetation category (omitting observations below tin/ tile) by radio-tagged males and females, by visually located males and females and the relative occurrence of each vegetation type in the random sample is illustrated in Figs. 5.13 A. to C.

	SITE ONE										
	Radio-tracking				Visual observation				Random		
	Males		Females		Males		Females		Juveniles	No. obs:	
	No. obs	%	No. obs	%	No. obs	%	No. obs	%	No. obs	(%)	
Dry heath I : <u>Calluna</u> >90%	86	20.5	28	13.0	2	2.3	1	0.9	0	0.0	6
Dry heath II : <u>Calluna</u> and <u>E. cinerea</u>	126	30.1	115	53.5	33	37.9	58	53.7	3	37.5	6
Humid heath : <u>Calluna</u> and <u>E. tetralix</u>	11	2.6	13	6.0	3	3.4	1	0.9	0	0.0	3
Grass and Dry heath	1	0.2	10	4.7	0	0.0	0	0.0	1	12.5	0
Grass and Wet-humid heath	8	1.9	3	1.3	1	1.1	0	0.0	0	0.0	0
Grass I : <u>Agrostis</u> & similar	2	0.5	6	2.8	2	2.3	2	1.9	0	0.0	2
Grass II : <u>Molinia</u>	1	0.2	8	3.7	1	1.1	2	1.9	0	0.0	4
Grass III : 'lawn'	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	7
Bog / Wet heath	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0
Gorse, <u>Ulex europaeus</u>	66	15.8	13	6.0	13	14.9	1	0.9	0	0.0	5
Bracken, <u>Pteridium aquilinum</u>	15	3.6	1	0.5	0	0.0	0	0.0	0	0.0	1
Bryophytes	2	0.5	2	0.9	3	3.4	4	3.7	0	0.0	0
Bare ground	5	1.2	2	0.9	8	9.2	13	12.0	0	0.0	10
Deciduous tree / litter	5	1.2	1	0.5	0	0.0	0	0.0	0	0.0	6
Pine tree / litter, <u>Pinus</u> spp.	15	3.6	3	1.4	0	0.0	0	0.0	0	0.0	30
Other conifer spp. / litter	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	16
Bramble, <u>Rubus fruticosus</u>	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1
Deciduous and Heath	4	1.0	0	0.0	1	1.1	0	0.0	0	0.0	1
Dry heath and Open / Prostrate spp.	6	1.4	5	2.3	3	3.4	17	15.7	0	0.0	0
Gorse and Understorey	30	7.2	5	2.3	5	5.7	1	0.9	0	0.0	0
Gorse and Bramble with Other spp.	0	0.0	0	0.0	1	1.1	0	0.0	0	0.0	0
Deciduous and Understorey	2	0.5	0	0.0	0	0.0	0	0.0	0	0.0	0
Bracken and Tree spp.	4	1.0	0	0.0	0	0.0	0	0.0	0	0.0	1
Heath and Bracken / Catmint	3	0.7	0	0.0	0	0.0	0	0.0	0	0.0	0
Bracken and Understorey	5	1.2	0	0.0	0	0.0	0	0.0	0	0.0	1
Deciduous and Bramble with Understorey	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0
Grass spp. with Open / Moss	1	0.2	0	0.0	1	1.1	3	2.8	0	0.0	0
Bramble and Understorey	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0
Prostrate spp. and Bare ground	4	1.0	0	0.0	1	1.1	1	0.9	0	0.0	0
Dry heath and Pine	13	3.1	0	0.0	2	2.3	2	1.9	0	0.0	0
Fern spp.	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0
Catmint, <u>Nepeta cataria</u>	1	0.2	0	0.0	4	4.6	1	0.9	0	0.0	0
Tin / Tile	3	0.7	0	0.0	3	3.4	1	0.9	4	50.0	0
Totals	419	100.1	215	99.8	87	99.4	108	99.9	8	100.0	100

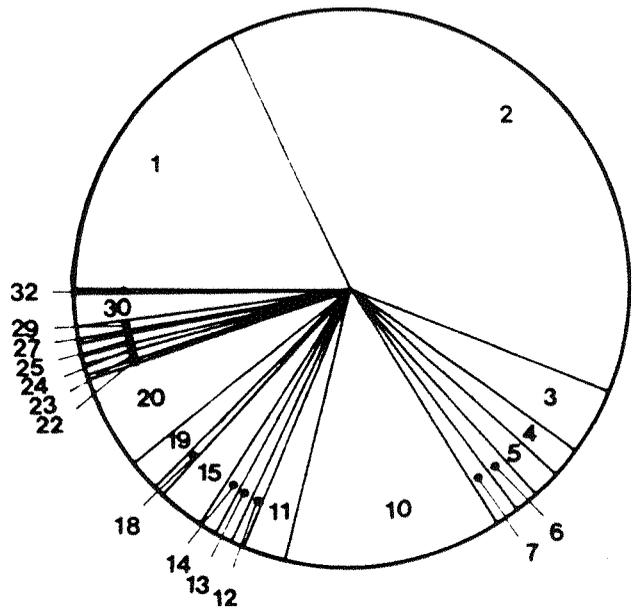
Table 5.5 : Number of observations (No. obs) and percentages of observations (%) of Male, Female and Juvenile specimens of C. austriaca in each vegetation category at Site One as determined from 0.25 m² quadrats at radio-tracking and visual observation locations during April 1984 to July 1986 inclusive. The relative abundance of each vegetation category as determined from 100 randomly positioned 0.25 m² quadrats is presented under the heading 'Random'.

SITE ONE

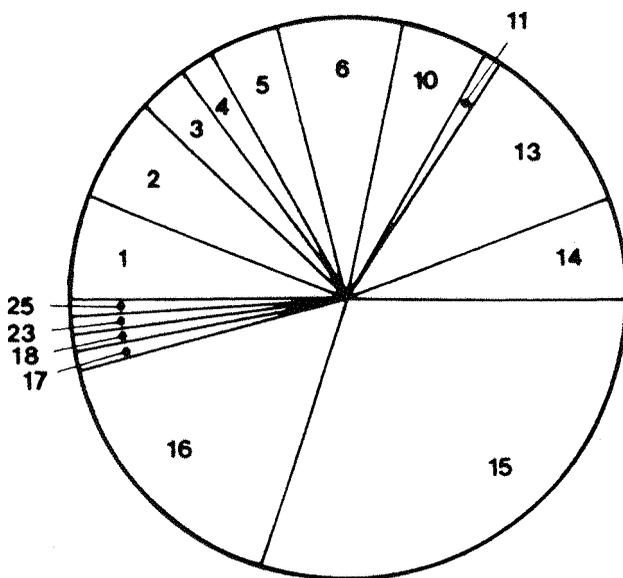
A. Visual Location



B. Radio-location



C. Random



KEY

- | | |
|--------------------------|----------------------------------|
| 1 Dry Heath I | 16 Other conifer spp./ litter |
| 2 Dry Heath II | 17 Bramble |
| 3 Humid Heath | 18 Deciduous & Heath |
| 4 Grass/ Dry Heath | 19 Dry Heath & Open/ Prost. spp. |
| 5 Grass/ Humid Heath | 20 Gorse & Understorey |
| 6 Grass I | 21 Gorse & Bramble & other spp. |
| 7 Grass II | 22 Deciduous & Understorey |
| 8 Grass III | 23 Bracken & Tree spp. |
| 10 Gorse | 24 Heath & Bracken/ Catmint |
| 11 Bracken | 25 Bracken & Understorey |
| 12 Bryophytes | 27 Grass sp(p). with Open/ Moss |
| 13 Bare Ground | 29 Prostrate spp. & Bare ground |
| 14 Deciduous tree/Litter | 30 Dry Heath & Pine |
| 15 Pine tree/ litter | 32 Catmint |

Figs. 5.13 A. to C. : Relative usage of 32 defined vegetation categories by *C. austriaca* (both sexes combined) at Site One for A. Visually located specimens (n= 191), B. Radio-located specimens (n= 631) and C. the relative abundance of each of the vegetation categories at Site One as revealed by 100 randomly positioned quadrats. Data were collected during 1984 to 1986 inclusive.

respectively.

Of the 32 defined vegetation categories (excluding tin/tile), 27 were found at Site One and smooth snakes were recorded in 24 of these. In three cases vegetation categories were found by random sampling that were never occupied by C. ausriaca, namely Grass III ('lawn'), Other conifer spp. (i.e. not Pinus spp.)/ litter and Bramble (Rubus fruticosus). At this site, the most frequently used habitat category for each sex and each of the methods of location was Dry Heath II (Calluna vulgaris and Erica cinerea dominated heathland) (see Table 5.5). Dry heath I (C. vulgaris dominated heathland) was also frequently occupied by smooth snakes. The combination of Dry heath I and Dry heath II accounted for 50.6% and 66.5% respectively of all radio-locations of male and female snakes and 40.2%, 54.6% and 37.5% respectively of all visual locations of male, female and juvenile snakes at Site One. Only small percentages of sightings at Site One were associated with Humid heath (heathland dominated by C. vulgaris and E. tetralix) for radio-tagged (males= 2.6%, females= 6.0%) and visually located (males= 3.4%, females= 0.9%) animals.

Scrub layer vegetation was frequently used by smooth snakes. Most notably, Gorse Ulex europaeus, both on its own (radio-tagged males= 15.8%, radio-tagged females= 6.0%; visually located males= 14.9%, visually located females= 0.9%) and when associated with an understorey of other plant species (radio-tagged males= 7.2%, radio-tagged females= 2.3%; visually located males= 5.7%, visually located females= 0.9%), was often used. Bracken Pteridium aquilinum was also used by C. austriaca, both where the species is dominant (radio-tagged males= 3.6%, radio-tagged females= 0.5%) and where it occurs with other plant species including understorey plants, heath species and deciduous trees.

Various herb layer plant communities were occupied, particularly Agrostis and Molinia grasses both alone and in association with heath species (the combination of these

categories accounting for 2.9% of locations of radio-tagged males, 12.5% of radio-tagged females, 4.5% of visually located males and 3.8% of visually located females). Smooth snakes were also observed in association with open ground and prostrate vegetation, most notably mosses or grass species. A greater proportion of locations of visually located snakes were found in these more open vegetation types than of radio-tagged specimens.

A small proportion of radio-locations of C. austriaca at Site One were associated with trees. Male snakes were located under Pinus spp. on 15 occasions (3.6%) and where pine and dry heath were found together on a further 13 occasions (3.1%). A further five observations (1.2%) of radio-tagged male snakes were associated with Deciduous trees/ litter. Females were found in close proximity to trees on fewer occasions than were males, with three locations (1.5%) being below pine trees and a single location (0.5%) being associated with deciduous trees.

Random quadrats showed that coniferous trees dominated the study area at Site One, with 46% of the sample occurring in these habitats (Fig. 5.13 C.). A further 6% of the site was covered by deciduous tree species. Bare ground accounted for 10% of the area, this including gravelled tracks, earth between vegetation and a major metalled road. A large grazing strip surrounded the Inclosure and 7% of the random quadrats were of 'lawn grass', located in this area. Other grass species dominated 6% of the site, with 4% being Molinia caerulea and 2% being Agrostis spp. Dry heath I and Dry heath II each were found in six quadrats (6% each) and Humid heath was found in three (3%). Gorse was fairly abundant, being dominant in five quadrats (5%).

At Site Two, 431 and 329 quadrats were classified for radio-locations of males and females respectively and 77, 115 and three quadrats classified for visual locations of males, females and juveniles respectively (these totals include four, nine, 14, three and zero cases respectively where snakes were recorded below tin or tile and the

vegetation within the quadrat could not be classified). The frequency, and relative frequency, of observations within each vegetation category at Site Two are presented in Table 5.6 (for each method of location and each sex). Relative use of each vegetation category (other than observations below tin/ tile) by radio-tagged snakes (males and females combined) and visually located snakes (males and females combined) is illustrated in Fig. 5.14 (A. and B. respectively) together with the relative abundance of each vegetation category within the study area as revealed by 100 randomly positioned quadrats (Fig. 5.14 C.).

Site two was dominated by humid heathland, this vegetation category accounting for 18% of the randomly positioned quadrats (see Fig. 5.14 C.). Molinia grassland and Bog/ wet heath were also abundant, yielding a further 17% and 13% respectively. Seven more quadrats were of a combination of Grassland and wet-humid heath. Thus 55% of Site Two was covered by Humid heath and bog type vegetation. Dry heath I was dominant in 9% of the quadrats and Grass and dry heath represented a further 4% of the area. Whilst Dry heath II was present at Site Two it was not present in any of the random samples and therefore assumed to have occupied less than 1% of the study area. Both Gorse and Bracken were abundant, covering 9% and 8% of the study area respectively, and Bracken and understorey was found dominating an additional four quadrats (4%). Five per cent of the area of the study site was Bare ground. In contrast to Site One, Site Two had very little tree cover. Although self-sown pine trees were found at this site neither they nor any other species of conifer were represented in any of the randomly positioned quadrats and deciduous trees were represented in only 3% of the sample.

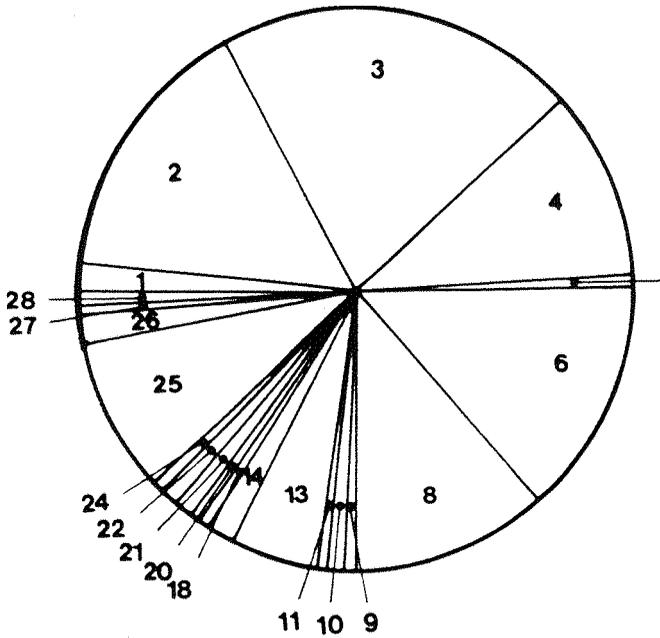
At Site Two smooth snakes were recorded in 26 of the 32 defined vegetation categories (excluding tin/ tile). In no cases were vegetation categories found by random sampling that were never occupied by C. austriaca. The three defined heath vegetation categories were frequently used by C. austriaca at Site Two. Of the 431 radio-locations of male

	SITE TWO									
	Radio-tracking				Visual observation				Random	
	Males		Females		Males		Females		Juveniles	No. obs:
	No. obs	%	No. obs	%	No. obs	%	No. obs	%	No. obs	(%)
Dry heath I : <u>Calluna</u> >90%	77	17.9	14	4.3	2	2.6	1	0.9	0	0.0
Dry heath II : <u>Calluna</u> and <u>E. cinerea</u>	39	9.0	47	14.3	16	20.8	11	9.6	0	0.0
Humid heath : <u>Calluna</u> and <u>E. tetralix</u>	91	21.1	21	6.4	29	37.7	8	7.0	0	0.0
Grass and Dry heath	7	1.6	51	15.5	3	3.9	16	13.9	1	33.3
Grass and Wet-humid heath	35	8.1	1	0.3	0	0.0	1	0.9	0	0.0
Grass I : <u>Agrostis</u> & similar	12	2.8	26	7.9	0	0.0	24	20.9	1	33.3
Grass II : <u>Molinia</u>	43	10.0	10	3.0	0	0.0	0	0.0	0	0.0
Grass III : 'lawn'	1	0.2	0	0.0	0	0.0	20	17.4	0	0.0
Bog / Wet heath	67	15.5	7	2.1	1	1.3	0	0.0	0	0.0
Gorse, <u>Ulex europaeus</u>	10	2.3	11	3.3	1	1.3	1	0.9	0	0.0
Bracken, <u>Pteridium aquilinum</u>	18	4.2	65	19.8	0	0.0	1	0.9	0	0.0
Bryophytes	1	0.2	0	0.0	0	0.0	0	0.0	0	0.0
Bare ground	0	0.0	5	1.5	2	2.6	7	6.1	1	33.3
Deciduous tree / litter	0	0.0	0	0.0	0	0.0	3	2.6	0	0.0
Pine tree / litter, <u>Pinus</u> spp.	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Other conifer spp. / litter	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Bramble, <u>Rubus fruticosus</u>	5	1.2	2	0.6	0	0.0	0	0.0	0	0.0
Deciduous and Heath	0	0.0	0	0.0	1	1.3	0	0.0	0	0.0
Dry heath and Open / Prostrate spp.	0	0.0	11	3.3	0	0.0	0	0.0	0	0.0
Gorse and Understorey	5	1.2	3	0.9	0	0.0	1	0.9	0	0.0
Gorse and Bramble with Other spp.	0	0.0	0	0.0	2	2.6	0	0.0	0	0.0
Deciduous and Understorey	0	0.0	0	0.0	2	2.6	0	0.0	0	0.0
Bracken and Tree spp.	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Heath and Bracken / Catmint	5	1.2	11	3.3	1	1.3	0	0.0	0	0.0
Bracken and Understorey	3	0.7	30	9.1	2	2.6	14	12.2	0	0.0
Deciduous and Bramble with Understorey	0	0.0	0	0.0	0	0.0	3	2.6	0	0.0
Grass spp. with Open / Moss	2	0.4	4	1.2	1	1.3	0	0.0	0	0.0
Bramble and Understorey	6	1.4	0	0.0	0	0.0	1	0.9	0	0.0
Prostrate spp. and Bare ground	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Dry heath and Pine	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Fern spp.	0	0.0	1	0.3	0	0.0	0	0.0	0	0.0
Catmint, <u>Nepeta cataria</u>	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Tin / Tile	4	0.9	9	2.7	14	18.2	3	2.6	0	0.0
Totals	431	99.9	329	99.8	77	100.1	115	100.3	3	99.9

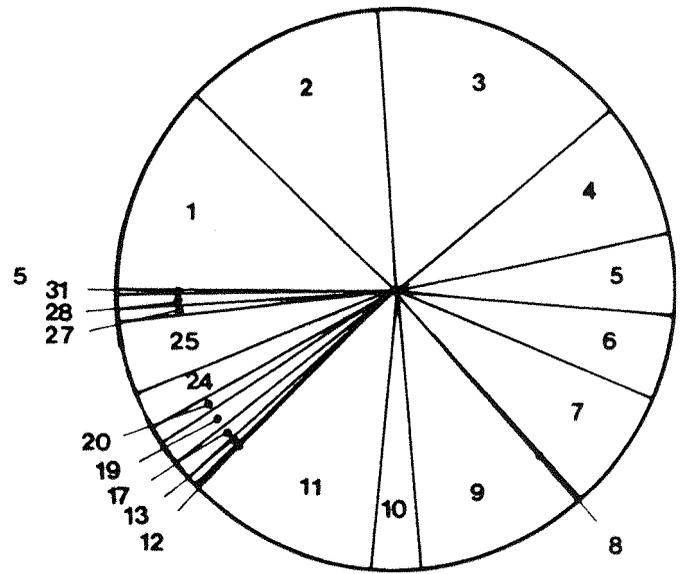
Table 5.6 : Number of observations (No. obs) and percentage of observations (%) of Male, Female and Juvenile specimens of C. austriaca in each vegetation category at Site Two as determined from 0.25m² quadrats at radio-tracking and visual observation locations during June 1984 to July 1986 inclusive. The relative abundance of each vegetation category as determined from 100 randomly positioned 0.25 m² quadrats is presented under the heading 'Random'.

SITE TWO

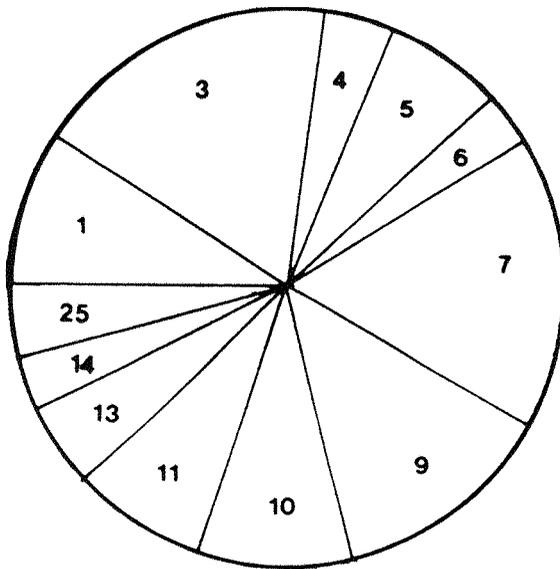
A. Visual Location



B. Radio-location



C. Random



KEY

- | | |
|----------------------|-----------------------------------|
| 1 Dry Heath I | 14 Deciduous tree/ litter |
| 2 Dry Heath II | 17 Bramble |
| 3 Humid Heath | 18 Deciduous and Heath |
| 4 Grass/ Dry Heath | 19 Dry Heath & Open/ prost. spp. |
| 5 Grass/ Humid Heath | 20 Gorse and Understorey |
| 6 Grass I | 21 Gorse & Bramble & other spp. |
| 7 Grass II | 22 Deciduous & Understorey |
| 8 Grass III | 24 Heath & Bracken/ Catmint |
| 9 Bog/ Wet Heath | 25 Bracken & Understorey |
| 10 Gorse | 26 Decid. & Bramble & Understorey |
| 11 Bracken | 27 Grass spp. with Open/ Moss |
| 12 Bryophytes | 28 Bramble & Understorey |
| 13 Bare Ground | 31 Fern spp. |

Figs. 5.14 A. to C. : Relative usage of 32 defined vegetation categories by *C. austriaca* (both sexes combined) at Site Two for A. Visually located specimens (n= 175), B. Radio-located specimens (n= 747) and C. the relative abundance of each of the vegetation categories at Site Two as revealed by 100 randomly positioned quadrats. Data collected during 1984 to 1986 inclusive.

snakes 21.1% were in Humid heath, 17.9% in Dry heath I and 9.0% in Dry heath II. The respective percentages for the 329 radio-locations of female snake were 6.4%, 4.3% and 14.3%. Visually located snakes were found in the three heath categories in the following relative frequencies: for male snakes 37.7%, 2.6% and 20.8% and for females 7.0%, 0.9% and 9.6% for Humid heath, Dry heath I and Dry heath II respectively. Thus the use of heath vegetation accounted for 48.0%, 25.0%, 61.1% and 17.5% of observations of radio-tagged males, radio-tagged females, visually located males and visually located females respectively at Site Two.

Bog vegetation was used particularly often by radio-tagged male snakes, this vegetation category accounting for 15.5% of observations. Bog was used only infrequently by radio-tagged females (1.3%) and visually located males (2.1%) and on no occasion by visually located females (0.0%). Bracken, both alone and in association with an understorey, was used particularly frequently by females with 28.9% of radio-locations and 13.1% of visual locations of this sex being associated with these two vegetation categories. The use of bracken by males was less prominent, with 4.9% of radio-locations and 2.6% of visual locations being in association with Bracken or Bracken and understorey. Other scrub-layer plant communities were also inhabited by smooth snakes, most notably Gorse and Bramble. Neither of these vegetation categories was frequently used, with only 2.3% of radio-locations and 1.3% of visual locations of male snakes and 3.3% of radio-locations and 0.9% of visual locations of females snakes being found in Gorse. Only radio-tagged snakes were found in Bramble with 1.2% of observations of males and 0.6% of observations of females being found in this vegetation category.

At Site Two, Agrostis spp. and Molinia spp. dominated grass communities and mixed grass and heathland were used often by C. austriaca. Agrostis dominated and Grass/ dry heath (where the grass species were most frequently Agrostis spp.) communities were used more frequently by females than males. For radio-tagged specimens the percentage of

observations in the two vegetation categories were 7.9% and 15.5% for females and 2.8% and 1.6% for males respectively whilst the percentage of visual observations were 20.9% and 13.9% for females and 0.0% and 3.9% for males respectively. Conversely Molinia and Grass/ wet-humid heath (where the grass species was most usually Molinia caerulea) communities were more often used by males. Radio-tagged males were found in Molinia during 10.0% of locations and in Grass/ wet-humid heath during 8.1% of locations. The corresponding percentages for radio-tagged females were 3.0% and 0.3%. No males were visually located in either vegetation category and females were not visually located in Molinia. Only 0.9% of visual locations of females were in Grass/ wet-humid heath.

Open ground and areas covered by sparse or prostrate vegetation cover were only used occasionally by smooth snakes at Site Two. Use of Dry heath and open was only observed for radio-tagged females (3.3% of observations) whereas occupancy of Bare ground was observed in radio-tagged females (1.5% of observations), visually located males (2.6% of locations) and visually located females (6.1% of locations). The use of 'Lawn' (Grass III) was most notable in visually located female snakes (where 17.4% of sightings were in this vegetation type), although radio-tagged males were also recorded in this habitat type (0.2% of observations).

Combining the Humid heath, Bog, Molinia and grass and wet/ humid heath categories to form a single 'Humid habitats' category and the Dry heath I, Dry heath II, Agrostis and Grass and dry heath category to form a 'Dry habitats' category, showed that 54.8% of radio-tagged and 39.0% of visually located male snakes were found in the former habitat category and 31.3% of radio-tagged and 27.3% of visually observed males were found in the latter category. The equivalent percentages for radio-tagged and visually located female snakes were 11.8% and 7.9% in 'Humid habitats' and 51.1% and 45.3% in 'Dry habitats' respectively. Male snakes were, therefore, observed more

frequently in the humid and damper vegetation categories than female snakes at Site Two.

ii. Vegetation category use (ten categories)

In order to perform statistical analysis upon the vegetation category data, it was necessary to reduce the number of categories. This reduction was achieved through the amalgamation of the previously defined categories (32 in number), based upon taxonomic similarity, species association in the field and the structural similarity of the categories. In two cases (namely Heath and bracken/catmint and Bracken and tree spp.) the original category was subdivided prior to amalgamation into different habitat groupings. Thus ten new categories were produced for further analysis. The new categories, and the component vegetation categories used to create them, are presented in Table 5.7.

The absolute and relative numbers of observations of radio-tagged and visually located male, female and juvenile C. austriaca in each of the ten defined habitat categories at Site One are presented in Table 5.8. The relative occurrence of each habitat type within the study areas, based upon their representation in a sample of 100 randomly positioned quadrats, is also presented in Table 5.8. Smooth snakes were found in nine out of the ten defined habitat types, and these nine were the only habitat categories to be represented within the randomly located sample at Site One.

Dry Heath was the most frequently used vegetation category in each of the five sub-divisions of the data at Site One. Of the radio-locations of smooth snakes at Site One, 53.1% of the observations of males and 73.5% of the observation of females were found in Dry Heath. The percentages of observations in Dry Heath for visually located snakes were 45.2% for males, 71.0% for females and 100.0% for juveniles. Scrub vegetation was the next most frequently used vegetation category by radio-tagged specimens of both

<u>Category</u>	<u>Composition categories</u>
Dry Heath	Dry heath I : <u>Calluna</u> >90%, Dry heath II : <u>Calluna</u> and <u>E. cinerea</u> . Grass and Dry heath, Dry heath and Open/ Prostrate spp., Heath and Bracken/ Catmint (Dry heath spp. only).
Humid Heath	Humid heath : <u>Calluna</u> and <u>E. tetralix</u> , Grass and Wet-humid heath, Heath and Bracken/ Catmint (Humid heath spp. only).
Bog	Bog/ Wet heath.
Fine Grass	Grass I: <u>Agrostis</u> & similar, Grass III: 'lawn', Grass spp. with Open/ Moss.
Coarse Grass	Grass II: <u>Molinia</u>
Scrub	Gorse <u>Ulex europaeus</u> , Gorse and Understorey, Bramble <u>Rubus fruticosus</u> , Bramble and Understorey, Catmint <u>Nepeta cataria</u> , Gorse and Bramble with Other spp..
Bracken	Bracken <u>Pteridium aquilinum</u> , Bracken and Understorey, Fern spp..
Open	Bryophytes, Bare ground, Prostrate spp. and Bare ground.
Deciduous Wood	Deciduous tree/ litter, Deciduous and Heath, Deciduous and Understorey, Deciduous and Bramble with Understorey, Bracken and Tree spp. (Deciduous tree spp. only).
Coniferous Wood	Pine tree/ litter, <u>Pinus</u> spp., Other conifer spp./ litter, Dry heath and Pine, Bracken and Tree spp. (Coniferous tree spp. only).

Table 5.7 : Re-classification of habitat categories, by amalgamation of vegetation categories, for the purpose of statistical analysis.

SITE ONE										
	Radio-tracking				Visual observation				Random	
	Males		Females		Males		Females		Juveniles	No. obs
	No. obs	%	No. obs	%	No. obs	%	No. obs	%	No. obs	(%)
Dry Heath	221	53.1	158	73.5	38	45.2	76	71.0	4	100.0
Humid Heath	20	4.8	16	7.4	4	4.8	1	0.9	0	0.0
Bog	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Fine Grass	3	0.7	6	2.8	3	3.6	5	4.7	0	0.0
Coarse Grass	1	0.2	8	3.7	1	1.2	2	1.9	0	0.0
Scrub	97	23.3	18	8.4	23	27.4	3	2.8	0	0.0
Bracken	20	4.8	1	0.5	0	0.0	0	0.0	0	0.0
Open	11	2.6	4	1.9	12	14.3	18	16.8	0	0.0
Deciduous Wood	15	3.6	1	0.5	1	1.2	0	0.0	0	0.0
Coniferous Wood	28	6.7	3	1.4	2	2.4	2	1.9	0	0.0
Totals	416	99.8	215	100.1	84	100.1	107	100.0	4	100.0

Table 5.8 : Number of observations (No. obs) and percentage of observations (%) of Male, Female and Juvenile specimens of *C. austriaca* in each habitat category at Site One as determined from 0.25m² quadrats at radio-tracking and visual observation locations during June 1984 to July 1986 inclusive. The relative abundance of each habitat category as determined from 100 randomly positioned 0.25 m² quadrats is presented under the heading 'Random'.

sexes and by visually located males. The percentages of observations in this vegetation category were 23.3%, 8.4%, 27.4% and 2.8% for radio-tagged males and females and visually located males and females respectively.

The relative importance of the remainder of the habitat categories varied between the different sexes and the different method employed for location at Site One. For radio-tagged males, the third most frequently used habitat category was Coniferous Wood (6.7% of observations), followed by Humid Heath and Bracken (each used during 4.8% of locations). Deciduous Wood (occupied in 3.6% of locations) and Open (2.6%) were the sixth and seventh most frequently occupied vegetation categories by radio-tagged males at Site One.

Radio-tagged females were found in Humid Heath in 7.4% of cases and in Coarse Grass in 3.7% of cases. Fine Grass was occupied in 2.8% and Open Ground in 1.9% of radio-locations of females at Site One. Coniferous Wood (1.4%) and Deciduous Wood (0.5%) were both used only infrequently by radio-tagged females.

Habitat use demonstrated by visually located snakes differed between the sexes. Open vegetation was used during 16.8% of observations by females and 14.3% of observations of males. Humid Heath was used relatively more by males (4.8%) than females (0.9%). Fine Grass was used fairly frequently by both sexes with 3.6% of observations of males and 4.7% of observations of females being in this habitat category. Coarse Grass was occupied by males during 1.2% and females during 1.9% of observations. Snakes were only infrequently visually observed in woodland, with 2.4% of observations of males and 1.9% of observations of females occurring in Coniferous Wood and 1.2% and 0.0% of observations respectively being located in Deciduous Wood.

Coniferous Wood represented the dominant vegetation at Site One, occurring in 47% of the randomly positioned quadrats. Dry Heath was the next most abundant vegetation category

(12% of quadrats), closely followed by Open and Fine Grass with 10% and 9% of quadrats respectively. Deciduous Wood and Scrub were both fairly common (7% and 6%). Coarse Grass was observed in 4% of the sample and Humid Heath in 3% of the quadrats. Bracken (2%) was the least common of the habitat categories detected by random quadrat sampling at Site One.

The frequency and relative frequencies of habitat category use by radio-tagged and visually located males, females and juvenile smooth snakes at Site Two are presented in Table 5.9, together with the relative abundances of each vegetation category at the site based upon randomly positioned quadrats. Nine habitat categories were represented in the randomly positioned samples and each of these categories were occupied by smooth snakes at Site Two.

The habitat category in which radio-tagged males (30.2% of locations) and visually located males (46.0% of locations) were most frequently found, at Site Two, was Humid Heath. Humid Heath, however, was relatively much less important to radio-tagged (6.9% of observations, the fourth most used category) or visually located females (8.0% of sightings, being ranked fourth). For both methods the habitat category next most frequently occupied by males was Dry Heath (29.3% of radio-locations and 34.9% of visual locations of males). Radio-tagged females were found most often in Dry Heath (41.9% of observations) with the second greatest number of observations being in Bracken (30.0% of observations). Visually located females, however, were most frequently encountered in Fine Grass (39.3% of observations) and Dry Heath (25.0% of observations). Fine Grass was, in addition, often associated with radio-locations of female snakes at Site Two (9.4% of radio-locations) but was used less often by males, as indicated by radio-tracking (3.5%) or visual location (1.6%).

Radio-tagged males were found in Bog vegetation relatively more often (15.7% of locations) than radio-tagged females

		SITE TWO											
		Radio-tracking				Visual observation				Random			
		Males		Females		Males		Females		Juveniles	No. obs:		
		No. obs	%	No. obs	%	No. obs	%	No. obs	%	No. obs	%	(%)	
Dry heath	:	125	29.3	134	41.9	22	34.9	28	25.0	1	33.3	13	:
Humid Heath	:	129	30.2	22	6.9	29	46.0	9	8.0	0	0.0	25	:
Bog	:	67	15.7	7	2.2	1	1.6	0	0.0	0	0.0	13	:
Fine Grass	:	15	3.5	30	9.4	1	1.6	44	39.3	1	33.3	3	:
Coarse Grass	:	43	10.1	10	3.1	0	0.0	0	0.0	0	0.0	17	:
Scrub	:	26	6.1	16	5.0	3	4.8	3	2.7	0	0.0	9	:
Bracken	:	21	4.9	96	30.0	2	3.2	15	13.4	0	0.0	12	:
Open	:	1	0.2	5	1.6	2	3.2	7	6.3	1	33.3	5	:
Deciduous Wood	:	0	0.0	0	0.0	3	4.8	6	5.4	0	0.0	3	:
Coniferous Wood	:	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	:
Totals	:	427	100.0	320	100.1	63	100.1	112	100.1	3	99.9	100	:

Table 5.9 : Number of observations (No. obs) and percentage of observations (%) of Male, Female and Juvenile specimens of *C. austriaca* in each habitat category at Site Two as determined from 0.25m² quadrats at radio-tracking and visual observation locations during June 1984 to July 1986 inclusive. The relative abundance of each habitat category as determined from 100 randomly positioned 0.25 m² quadrats is presented under the heading 'Random'.

(2.2%) or visually located snakes of either sex (1.6% of observations of males and 0.0% of visual locations of females). Coarse Grass was used in 10.1% of the radio-locations of male snakes and 3.1% of radio-locations of females. No snakes were visually located in Coarse Grass at Site Two. Both Scrub and Bracken were commonly occupied by radio-tagged and visually located snakes. Males were found in association with Scrub relatively more often than were females (6.1% of radio-locations of males and 4.8% of visual locations of males compared to 5.0% and 2.7% of radio- and visual locations of females respectively). Bracken was occupied relatively more often by females (30.0% of radio-locations and 13.4% of visual locations) than by males (4.9% of radio-locations and 3.2% of visual locations).

Open habitats were, in general, only infrequently occupied by radio-tagged (0.2% of locations of males and 1.6% of locations of females) or visually located snakes (3.2% and 6.2% of observations of males and females respectively). Neither Deciduous Wood nor Coniferous Wood were used by radio-tagged snakes of either sex although small percentages of visually located animals were found in association with Deciduous Wood (4.8% and 5.4% of visual locations of males and females respectively).

Humid Heath was the most abundant habitat category at Site Two with this category representing 25% of the randomly positioned quadrats. Coarse Grass, present in 17% of the quadrats, was the second most abundant habitat type. Dry Heath and Bog each represented 13% of the sample and Bracken was the fifth most common category, occurring in 12% of the quadrats. Scrub, Open and Fine Grass were less abundant and represented 9%, 5% and 3% respectively. In contrast to Site One, trees were sparse at Site Two. Only 3% of the sample were Deciduous Wood whilst no Coniferous Wood was detected by random sampling.

- iii. Comparison of vegetation use between methods of location (ten categories)

The number of observations of radio-tagged snakes (for both males and females combined) and visually located snakes (males and females combined) are presented in Tables 5.10 A. and B. for Sites One and Two respectively. The expected frequencies of observations, based upon the relative totals from each method, are presented for each habitat type and these used as a basis for comparison between the vegetation use as revealed by the two methods. The G-test statistic and associated significance level are, additionally, presented in Tables 5.10 A. and B.

Significant variation in habitat use was indicated by the different methods at each of the sites studied (At Site One $G = 65.811$ with 8 d.f., $p < 0.001$ and at Site Two $G = 139.338$ with 8 d.f., $p < 0.001$). Significant differences in vegetation use were observed between the two methods in four of the nine categories that were occupied at that site. Fine Grass was occupied slightly less by radio-tagged snakes, and slightly more by visually located snakes, than would have been expected from the numbers of locations made by each of the methods ($G = 4.471$ with 1 d.f., $p < 0.05$). Open habitat yielded considerably fewer observations of radio-tagged, and more of visually located, snakes than would have been predicted from the expected values ($G = 38.002$ with 1 d.f., $p < 0.001$). Conversely, radio-tagged snakes were observed in Deciduous Wood slightly more and in Bracken considerably more than were visually located animals ($G = 3.872$ with 1 d.f., $p < 0.05$ and $G = 11.160$ with 1 d.f., $p < 0.001$ for Deciduous Wood and Bracken respectively).

At Site Two significant variation was observed in the number of locations made by the two methods in five of the nine habitat categories that were used at that site. A relatively greater number of locations of snakes were made in Bog vegetation ($G = 23.772$ with 1 d.f., $p < 0.001$) and Coarse Grass ($G = 22.410$ with 1 d.f., $p < 0.001$) using radio-

A. SITE ONE

	<u>Radio-tagged</u>		<u>Visual locn.</u>		Total	G	p
	Obs.	Exp.	Obs.	Exp.			
Dry Heath	379	378.4	114	114.6	493	0.004	NS
Humid Heath	36	31.5	5	9.5	41	3.196	NS
Bog	0	0.0	0	0.0	0	n/a	
Fine Grass	9	13.0	8	4.0	17	4.471	*
Coarse Grass	9	9.2	3	2.8	12	0.018	NS
Scrub	115	108.2	26	32.8	141	1.931	NS
Bracken	21	16.1	0	4.9	21	11.160	***
Open	15	34.5	30	10.5	45	38.002	***
Deciduous Wood	16	13.0	1	4.0	17	3.872	*
Coniferous Wood	31	26.9	4	8.1	35	3.151	NS
Totals	631	630.8	191	191.2	822	65.811	***

B. SITE TWO

	<u>Radio-tagged</u>		<u>Visual locn.</u>		Total	G	p
	Obs.	Exp.	Obs.	Exp.			
Dry Heath	259	250.4	50	58.6	309	1.621	NS
Humid Heath	151	153.1	38	35.9	189	0.149	NS
Bog	74	60.8	1	14.2	75	23.772	***
Fine Grass	45	72.9	45	17.1	90	43.664	***
Coarse Grass	53	42.9	0	10.1	53	22.410	***
Scrub	42	38.9	6	9.1	48	1.428	NS
Bracken	117	108.6	17	25.4	134	3.781	NS
Open	6	12.2	9	2.8	15	12.501	***
Deciduous Wood	0	7.3	9	1.7	9	29.999	***
Coniferous Wood	0	0.0	0	0.0	0	n/a	.
Totals	747	747.1	175	174.9	922	139.338	***

Tables 5.10 A. and B. : Observed (Obs.) and expected (Exp.) frequencies of observations of radio-tagged and visually located C. austriaca in each of the ten defined habitat categories (see Table 5.7 for details) at Sites One and Two. G-test statistics (G) and their significance levels (p) are presented (NS= $p > 0.05$, *= $p < 0.05$, **= $p < 0.01$, ***= $p < 0.001$). Expected frequencies are based on a hypothesis of the same pattern of habitat category use being shown by each of the two methods. Data are for male and female specimens observed between April 1984 and July 1986 inclusive.

location than using visual location. Smooth snakes were observed relatively more frequently by visual observation in Fine Grass ($G= 43.664$ with 1 d.f., $p<0.001$), Open ($G= 12.501$ with 1 d.f., $p<0.001$) and Deciduous Wood ($G= 29.999$ with 1 d.f., $p<0.001$) than by radio-tracking.

As the two methods of observation showed differences in range use, further analysis was restricted to data collected by radio-location only. This latter method was selected since it was deemed to be less susceptible to observer bias and therefore more likely to be representative of habitat usage by C.austriaca.

iv. Comparison of vegetation use between sexes (ten categories)

The frequency of radio-locations of male and female snakes in each of the ten defined habitat categories are presented in Tables 5.11 A. and B. for Site One and Two respectively. Expected frequencies of observation are presented in each case and these are used as a basis for comparison between the sexes using the G-test (G values and significance levels are also presented in Tables 5.11 A. and B.). Significant variation in habitat use was observed between radio-tagged male and female C. austriaca at both Site One ($G= 75.166$ with 8 d.f., $p<0.001$) and Site Two ($G= 209.676$ with 1 d.f., $p<0.001$).

At Site One significant differences were observed in the number of observations made of male and female snakes in seven of the nine categories occupied by snakes at that site. Only Humid Heath and Open habitats were used to the same degree by males and females ($G= 1.626$ and $G= 0.374$ respectively, with 1 d.f. and $p>0.05$ in each case). Males were observed relatively more frequently than females in Scrub ($G= 19.823$ with 1 d.f., $p<0.001$), Bracken ($G= 10.894$ with 1 d.f., $p<0.001$), Coniferous Wood ($G= 10.160$ with 1 d.f., $p<0.001$) and Deciduous Wood ($G= 7.291$ with 1 d.f., $p<0.01$). Females, on the other hand, were observed relatively more often than males in Dry Heath ($G= 9.513$

A. SITE ONE

	<u>Males</u>		<u>Females</u>		Total	G	p
	Obs.	Exp.	Obs.	Exp.			
Dry Heath	221	249.9	158	129.1	379	9.513	***
Humid Heath	20	23.7	16	12.3	36	1.626	NS
Bog	0	0.0	0	0.0	0	n/a	
Fine Grass	3	5.9	6	3.1	9	3.866	*
Coarse Grass	1	5.9	8	3.1	9	11.619	***
Scrub	97	75.8	18	39.2	115	19.823	***
Bracken	20	13.8	1	7.2	21	10.894	***
Open	11	9.9	4	5.1	15	0.374	NS
Deciduous Wood	15	10.5	1	5.5	16	7.291	**
Coniferous Wood	28	20.4	3	10.6	31	10.160	***
Totals	416	415.8	215	215.2	631	75.166	***

B. SITE TWO

	<u>Males</u>		<u>Females</u>		Total	G	p
	Obs.	Exp.	Obs.	Exp.			
Dry Heath	125	148.0	134	111.0	259	8.242	**
Humid Heath	129	86.3	22	64.7	151	56.248	***
Bog	67	42.3	7	31.7	74	40.482	***
Fine Grass	15	25.7	30	19.3	45	10.312	**
Coarse Grass	43	30.3	10	22.7	53	13.709	***
Scrub	26	24.0	16	18.0	42	0.393	NS
Bracken	21	66.9	96	50.1	117	76.198	***
Open	1	3.4	5	2.6	6	4.092	*
Deciduous Wood	0	0.0	0	0.0	0	n/a	
Coniferous Wood	0	0.0	0	0.0	0	n/a	
Totals	427	426.9	320	320.1	747	209.676	***

Tables 5.11 A. and B. : Observed (Obs.) and expected (Exp.) frequencies of observations of male and female C. austriaca in each of the ten defined habitat categories (see Table 5.7 for details) at Sites One and Two. G-test statistics (G) and their significance levels (p) are presented (NS= $p > 0.05$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$). Expected frequencies are based on a hypothesis of each habitat category being used to the same degree by each sex. Data are for radio-tagged specimens observed between April 1984 and July 1986 inclusive.

with 1 d.f., $p < 0.001$), Coarse Grass ($G = 11.619$ with 1 d.f., $p < 0.001$) and Fine Grass ($G = 3.866$ with 1 d.f., $p < 0.05$).

At Site Two smooth snakes were radio-located in eight different habitat categories and in all but one of these, namely Scrub ($G = 0.393$ with 1 d.f., $p > 0.05$), significant differences were observed in the relative number of observations of the two sexes. Vegetation associated with damper ground was used more frequently by male snakes than by female snakes at Site Two, with relative more observations of males being found in Humid Heath ($G = 56.248$ with 1 d.f., $p < 0.001$), Bog ($G = 40.482$ with 1 d.f., $p < 0.001$) and Coarse Grass ($G = 13.709$ with 1 d.f., $p < 0.001$). Females were associated more with the 'drier' habitats, with relative more observations of females than males being observed in Bracken ($G = 76.198$ with 1 d.f., $p < 0.001$), Dry Heath ($G = 8.242$ with 1 d.f., $p < 0.01$) and Fine Grass ($G = 10.312$ with 1 d.f., $p < 0.001$). Females were also more frequently observed in Open habitats than males at Site Two ($G = 4.092$ with 1 d.f., $p < 0.05$).

Other than Dry Heath and Fine Grass, which were occupied by females relatively more often than males at both Sites One and Two, differences in habitat category use between the sexes were not, in general, consistent between the two study sites. Male snakes used Humid Heath, Bog, Scrub, Deciduous Wood and Coniferous Wood more than females at one of the sites but there was either no significant difference between the sexes, or there were no observations of C. austriaca associated with these habitat types, at the other. Open vegetation was used relatively more by females than males at Site Two but no difference was observed in the use of this habitat category at Site One. In two cases, namely Coarse Grass and Bracken, habitat categories were used more by males than females at one site but more by females than males at the other.

Since differences in habitat use were detected between the sexes, data for male and female C. austriaca are kept separate in further analysis.

v. Comparison of vegetation use with relative abundance of vegetation categories in the field (ten categories)

The frequencies of observations of radio-tagged snakes in each of the ten vegetation categories are presented separately for males and females in Table 5.12 A. for Site One and Table 5.12 B. for Site Two. In addition, the expected frequencies, based upon a hypothesis that the use of each category was in direct proportion to its availability in the environment, are presented. Observed and expected frequencies were compared via a G-test and the respective G value and significance level are furnished in Tables 5.12 A. and B.

Radio-tagged males at Site One showed highly a significant deviation from 'expected' habitat category use ($G= 796.040$ with 8 d.f., $p<0.001$). Significant variation was observed against the expected frequency of use in all nine habitat categories that were located at Site One. Radio-tagged males were found more frequently in Dry Heath ($G= 412.095$ with 1 d.f., $p<0.001$), Humid Heath ($G= 3.940$ with 1 d.f., $p<0.05$), Scrub ($G= 133.188$ with 1 d.f., $p<0.001$) and Bracken ($G= 12.118$ with 1 d.f., $p<0.001$) than would have been expected from the relative abundance of these habitat categories in the environment. Conversely fewer than 'expected' observations of radio-tagged males were made in Fine Grass ($G= 56.697$ with 1 d.f., $p<0.001$), Coarse Grass ($G= 26.183$ with 1 d.f., $p<0.001$), Open ($G= 34.371$ with 1 d.f., $p<0.001$) and Deciduous ($G= 8.827$ with 1 d.f., $p<0.01$) and Coniferous Wood ($G= 329.656$ with 1 d.f., $p<0.001$).

Females that were radio-tracked at Site One showed a marked difference in habitat use compared to habitat availability ($G= 555.335$ with 8 d.f., $p<0.001$). In six of the nine habitat categories at Site One females showed significant over- or under-use against 'expected'. Females were radio-located considerably more often in Dry Heath than would have been expected from its abundance ($G= 435.890$ with 1 d.f., $p<0.001$) and also more often in Humid Heath ($G=$

A. SITE ONE

	Males				Females			
	Obs.	Exp.	G	p	Obs.	Exp.	G	p
Dry Heath	221	49.9	412.095	***	158	25.8	435.890	***
Humid Heath	20	12.5	3.940	*	16	6.5	10.265	***
Bog	0	0.0	n/a		0	0.0	n/a	
Fine Grass	3	37.4	56.697	***	6	19.4	13.616	***
Coarse Grass	1	16.1	26.183	***	8	8.6	0.045	NS
Scrub	97	25.0	133.188	***	18	12.9	1.923	NS
Bracken	20	8.3	12.118	***	1	4.3	3.734	NS
Open	11	41.6	34.371	***	4	21.5	23.033	***
Deciduous Wood	15	29.1	8.827	**	1	15.1	23.743	***
Coniferous Wood	28	195.5	329.656	***	3	101.1	242.312	***
Totals	416	415.4	796.040	***	215	215.2	555.335	***

B. SITE TWO

	Males				Females			
	Obs.	Exp.	G	p	Obs.	Exp.	G	p
Dry Heath	125	55.5	77.881	***	134	41.6	163.458	***
Humid Heath	129	106.8	5.900	*	22	80.0	72.204	***
Bog	67	55.5	2.593	NS	7	41.6	48.382	***
Fine Grass	15	12.8	0.370	NS	30	9.6	28.937	***
Coarse Grass	43	72.6	16.562	***	10	54.4	61.965	***
Scrub	26	38.4	4.914	*	16	28.8	13.183	***
Bracken	21	51.2	25.333	***	96	38.4	73.407	***
Open	1	21.4	35.682	***	5	16.0	10.762	**
Deciduous Wood	0	12.8	25.992	***	0	9.6	19.494	***
Coniferous Wood	0	0.0	n/a		0	0.0	n/a	
Totals	427	427.0	172.819	***	320	320.0	411.713	***

Tables 5.12 A. and B. : Observed (Obs.) and expected (Exp.) frequencies of observations of male and female C. austriaca in each of the ten defined habitat categories (see Table 5.7 for details) at Sites One and Two. G-test statistics (G) and their significance levels (p) are presented (NS= $p > 0.05$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$). Expected frequencies are based upon a hypothesis of use of each category being in direct proportion to its availability in the environment (based on random quadrats). Data are for radio-tagged specimens observed between April 1984 and July 1986 inclusive.

10.265 with 1 d.f., $p < 0.001$). Fine Grass, Open, Deciduous Wood and Coniferous Wood were all used less frequently than would have been predicted from their abundance at Site One ($G = 13.616, 23.033, 23.743$ and 242.312 respectively with 1 d.f. and $p < 0.001$ in each case). No difference was observed in the use of Coarse Grass ($G = 0.045$ with 1 d.f., $p > 0.05$), Scrub ($G = 1.923$ with 1 d.f., $p > 0.05$) or Bracken ($G = 3.734$ with 1 d.f., $p > 0.05$) when compared against expected use by females at Site One.

A highly significant difference between expected and observed use of the habitat categories was found for radio-tagged males at Site Two ($G = 172.819$ with 8 d.f., $p < 0.001$). Nine habitat categories were found at Site Two and in seven of these variation between observed and expected frequencies of observation were recorded. Dry Heath ($G = 77.881$ with 1 d.f., $p < 0.001$) and Humid Heath ($G = 5.900$ with 1 d.f., $p < 0.05$) were used more often than would have been expected. Coarse Grass ($G = 16.562$ with 1 d.f., $p < 0.001$), Scrub ($G = 4.914$ with 1 d.f., $p < 0.05$), Bracken ($G = 25.333$ with 1 d.f., $p < 0.001$), Open ($G = 35.682$ with 1 d.f., $p < 0.001$) and Deciduous Wood ($G = 25.992$ with 1 d.f., $p < 0.001$), however, were used less frequently than expected. Bog and Fine Grass were used by radio-tagged males with a frequency proportional to their abundance at Site Two ($G = 2.593$ and 0.370 respectively with 1 d.f. and $p > 0.05$ in both cases).

Observed habitat category use by radio-tagged females differed from expected at Site Two ($G = 411.713$ with 8 d.f., $p < 0.001$). In all nine categories found at Site Two significant differences between observed and expected frequencies of observation were found. Dry Heath, Fine Grass and Bracken were used more often than would have been predicted from their relative abundance at the site ($G = 163.458, 28.937$ and 73.407 respectively with 1 d.f., $p < 0.001$ in each case). Humid Heath ($G = 72.204$ with 1 d.f., $p < 0.001$), Bog ($G = 48.382$ with 1 d.f., $p < 0.001$), Coarse Grass ($G = 61.965$ with 1 d.f., $p < 0.001$), Scrub ($G = 13.183$ with 1 d.f., $p < 0.001$), Open ($G = 10.762$ with 1 d.f., $p < 0.01$)

and Deciduous Wood ($G = 19.494$ with 1 d.f., $p < 0.001$) were used less than would have been expected by females at Site Two.

vi. Comparison of vegetation use between seasons (ten categories)

The number (and percentage) of observations of smooth snakes in each of the ten defined habitat categories during each of the three seasons at Site One are presented in Tables 5.13 A. and B. for males and females respectively. The respective numbers of observations in the different habitat categories at Site Two during each of the three seasons for males and females are presented in Tables 5.14 A. and B. As sample sizes in each vegetation category were small in most cases, the Spearman's rank correlation test was used for comparisons between seasons within each sex at each site.

At Site One significant correlation was only observed between the ranked orders of vegetation category use between Spring and Autumn for female snakes and in this case the correlation was negative ($r_s = -0.695$, $n = 10$, $p < 0.05$). No significant correlations were observed between vegetation use in any of the seasons for radio-tagged males at Site One (between Spring and Summer, $r_s = 0.647$; between Summer and Autumn, $r_s = 0.648$ and between Spring and Autumn, $r_s = 0.599$, $n = 10$ and $p > 0.05$ in each case) and no correlation was detected between vegetation use in Spring and Summer ($r_s = 0.215$, $n = 10$, $p > 0.05$) or between vegetation use in Summer and Autumn ($r_s = 0.181$, $n = 10$, $p > 0.05$) for females. At Site One, therefore, variation in habitat category use was suggested between the seasons for both sexes.

Dry Heath and Scrub vegetations were the two most frequently occupied habitat categories by male snakes at Site One in all seasons, although their rank order varied between the seasons (Table 5.13 A.). In Spring, Scrub was most commonly used by males (54.0% of radio-locations) and,

SITE ONE

A. Males

	<u>Spring</u>		<u>Summer</u>		<u>Autumn</u>	
	n	%	n	%	n	%
Dry Heath	16	32.0	122	62.6	83	48.5
Humid Heath	1	2.0	6	3.1	13	7.6
Bog	0	0.0	0	0.0	0	0.0
Fine Grass	1	2.0	1	0.5	1	0.6
Coarse Grass	0	0.0	1	0.5	0	0.0
Scrub	27	54.0	44	22.6	26	15.2
Bracken	0	0.0	14	7.2	6	3.5
Open	4	8.0	5	2.6	2	1.2
Deciduous Wood	0	0.0	1	0.5	14	8.2
Coniferous Wood	1	2.0	1	0.5	26	15.2
Totals	50	100.0	195	100.1	171	100.0

B. Females

	<u>Spring</u>		<u>Summer</u>		<u>Autumn</u>	
	n	%	n	%	n	%
Dry Heath	0	0.0	135	91.8	23	46.9
Humid Heath	11	57.9	5	3.4	0	0.0
Bog	0	0.0	0	0.0	0	0.0
Fine Grass	0	0.0	4	2.7	2	4.1
Coarse Grass	7	36.8	1	0.7	0	0.0
Scrub	0	0.0	0	0.0	18	36.7
Bracken	1	5.3	0	0.0	0	0.0
Open	0	0.0	2	1.4	2	4.1
Deciduous Wood	0	0.0	0	0.0	1	2.0
Coniferous Wood	0	0.0	0	0.0	3	6.1
Totals	19	100.0	147	100.0	49	99.9

Tables 5.13 A. and B. : Frequencies (n) and percentage frequencies (%) of usage of the ten defined habitat categories (see Table 5.7 for details) by radio-tagged C. austriaca at Site One for male and female specimens. Data were collected between April 1984 and July 1986 inclusive.

SITE TWO

A. Males

	<u>Spring</u>		<u>Summer</u>		<u>Autumn</u>	
	n	%	n	%	n	%
Dry Heath	19	25.0	77	28.9	29	34.1
Humid Heath	17	22.4	75	28.2	37	43.5
Bog	0	0.0	67	25.2	0	0.0
Fine Grass	8	10.5	5	1.9	2	2.4
Coarse Grass	28	36.8	15	5.6	0	0.0
Scrub	3	3.9	20	7.5	3	3.5
Bracken	1	1.3	6	2.3	14	16.5
Open	0	0.0	1	0.4	0	0.0
Deciduous Wood	0	0.0	0	0.0	0	0.0
Coniferous Wood	0	0.0	0	0.0	0	0.0
Totals	76	99.9	266	100.0	85	100.0

B. Females

	<u>Spring</u>		<u>Summer</u>		<u>Autumn</u>	
	n	%	n	%	n	%
Dry Heath	0	0.0	75	39.7	59	45.0
Humid Heath	0	0.0	8	4.2	14	10.7
Bog	0	0.0	7	3.7	0	0.0
Fine Grass	0	0.0	13	6.9	17	13.0
Coarse Grass	0	0.0	8	4.2	2	1.5
Scrub	0	0.0	15	7.9	1	0.8
Bracken	0	0.0	61	32.3	35	26.7
Open	0	0.0	2	1.1	3	2.3
Deciduous Wood	0	0.0	0	0.0	0	0.0
Coniferous Wood	0	0.0	0	0.0	0	0.0
Totals	0	0.0	189	100.0	131	100.0

Tables 5.14 A. and B. : Frequencies (n) and percentage frequencies (%) of usage of the ten defined habitat categories (see Table 5.7 for details) by radio-tagged C. austriaca at Site Two for male and female specimens. Data were collected between June 1984 and July 1986 inclusive.

other than Dry Heath (32.0% of locations), other vegetation categories were used to only a small degree (with the next most commonly used vegetation type, namely 'Open', being occupied in only 8.0% of locations). During Summer these two categories were, again, predominant, with Dry Heath being most frequently used (62.6% of observations) and Scrub being used second most commonly (22.6%). Bracken was the third most occupied category by males in Summer and represented 7.2% of sightings. In Autumn, Dry Heath was the most commonly used vegetation category (found in 48.5% of locations). Scrub and Coniferous Wood were the next most commonly used categories (each being occupied in 15.2% of locations) and Deciduous Wood and Humid Heath were both used often (8.2% and 7.6% respectively).

Female snakes were radio-located most often in Humid Heath and Coarse Grass during the Spring at Site One (57.9% and 36.8% respectively) with only one other category, namely Bracken (5.3%), being occupied during this season (Table 5.13 B.). In Summer nearly all observations of female snakes (91.8%) were in Dry Heath with a small number of sightings occurring in Humid Heath (3.4%), Fine and Coarse Grass (2.7% and 0.7% respectively) and Open ground (1.4%). Dry Heath and Scrub were most frequently used by radio-tagged females during the Autumn, and these categories represented a total of 83.6% (46.9% and 36.7% respectively) of the observations during this season. Coniferous Wood was used in 6.1% of locations and Open and Fine Grass each accounted for 4.1% of locations of females at Site One during Autumn.

At Site Two significant rank correlations were observed between the frequency of use of the ten habitat categories during Summer and Autumn by both male ($r_s = 0.655$, $n = 10$, $p < 0.05$) and female ($r_s = 0.796$, $n = 10$, $p < 0.05$) smooth snakes. There was no correlation detected between the habitat use during Spring and Summer or Spring and Autumn for males ($r_s = 0.621$ and 0.567 respectively, $n = 10$ and $p > 0.05$ in both cases). No data for habitat use by female snakes during Spring were available and consequently no

comparisons between this season and the other seasons were possible at Site Two.

Coarse grass was most frequently used by males at Site Two during Spring (accounting for 36.8% of locations) with Dry Heath and Humid Heath being the next most commonly used (25.0% and 22.4% respectively) (Table 5.14 A.). Other than Fine Grass (which represented 10.5% of locations), other habitat categories were used infrequently during the Spring. During Summer and Autumn Dry Heath and Humid Heath were most frequently used by radio-tagged males at Site Two (representing 28.9% and 28.2% in Summer and 34.1% and 43.5% in Autumn). In Summer Bog was also commonly used (25.2% of sightings), although this vegetation type was not occupied in either Spring or Autumn. Scrub and Coarse Grass were also used often in Summer (7.5% and 5.6%). Bracken was commonly used in Autumn by males (16.5% of sightings), but less frequently so in either Spring or Summer.

Females at Site Two used Dry Heath most frequently and Bracken next most frequently in both Summer and Autumn (Dry Heath representing 39.7% and 45.0% and Bracken representing 32.3% and 26.7% of observations in Summer and Autumn respectively) (Table 5.14 B.). Scrub and Fine Grass were the next most commonly used vegetation categories during the Summer (7.9% and 6.9% respectively) and Fine Grass and Humid Heath were the next most often occupied during Autumn (13.0% and 10.7% respectively). All other categories in both Summer and Autumn were each used during less than 5% of locations.

vii. Comparison of vegetation use between day and night
(ten categories)

Radio-tracking data were subdivided into two categories; those final observations during a day's observation where the snake could not be visually located and was assumed to have been occupying its over-night refuge were termed 'over-night' observations and those throughout the remainder of the day were termed 'day-time' observations. A

total of 72 over-night observations were obtained for radio-tagged males at Site One, 34 for females at Site One, 65 for males at Site Two and 45 for females at Site Two. The respective numbers of day-time observations were 344, 181, 362 and 275. The frequencies of observation in each of the ten vegetation categories for each of the sexes during the day-time and over-night are presented in Tables 5.15 A. and B. for Sites One and Two respectively. As sample sizes were too small to permit the use of the G-test, pairwise comparison were made between the number of over-night and day-time observations in each vegetation category (separately for each sex at each site) using the Spearman's rank correlation coefficient.

A similar use of vegetation categories during the day-time and over-night was shown by each sex at each site. Dry Heath was most commonly used during the night at all sites by both sexes and was most commonly used during the day by both males and females at Site One and by females at Site Two. At Site Two males used Humid Heath most often during the day and Dry Heath second most commonly; the relative importance of these habitats was reversed over-night. At Site One, both males and females occupied Scrub vegetation second most commonly during both the day-time and over-night and Humid Heath was frequently used by both sexes during both time periods. Males at Site One were also often found in association with Coniferous Wood at night, these observations related to snakes that occupied heather spp. at the base of coniferous trees. Bracken was the second most frequently occupied vegetation type by females at Site Two during both the day-time and over-night. Fine Grass and Humid Heath were both commonly used during the day-time and over-night by females at Site Two, and males at this site often used Bog and Coarse Grass during both time periods. In all cases, a significant correlation between day-time vegetation use and night-time vegetation use was detected ($r_{\text{m}} = 0.921$, $n = 10$, $p < 0.01$ for males at Site One; $r_{\text{m}} = 0.846$, $n = 10$, $p < 0.02$ for females at Site One; $r_{\text{m}} = 0.966$, $n = 10$, $p < 0.005$ for males at Site Two, $r_{\text{m}} = 0.942$, $n = 10$, $p < 0.005$ for females at Site Two).

A. SITE ONE

	<u>. Males .</u>		<u>. Females .</u>	
	Day	Night	Day	Night
Dry Heath	190	31	133	25
Humid Heath	17	3	13	3
Bog	0	0	0	0
Fine Grass	3	0	6	0
Coarse Grass	0	1	7	1
Scrub	79	18	14	4
Bracken	17	3	1	0
Open	8	3	4	0
Deciduous Wood	12	3	1	0
Coniferous Wood	17	11	2	1
Totals	344	72	181	34

B. SITE TWO

	<u>. Males .</u>		<u>. Females .</u>	
	Day	Night	Day	Night
Dry Heath	100	25	116	18
Humid Heath	117	12	18	4
Bog	59	8	6	1
Fine Grass	13	2	26	4
Coarse Grass	34	9	9	1
Scrub	20	6	14	2
Bracken	18	3	83	13
Open	1	0	3	2
Deciduous Wood	0	0	0	0
Coniferous Wood	0	0	0	0
Totals	362	65	275	45

Tables 5.15 A. and B. : Day-time (Day) and over-night (Night) frequencies of observations of male and female C. austriaca in each of the ten defined habitat categories (see Table 5.7 for details) at Sites One and Two. Data are for radio-tagged specimens observed between April 1984 and July 1986 inclusive.

b. Vegetation species composition used in the field

The relative abundances of each plant species were described separately for radio-tagged males and females and visually located males, females and juveniles at both Site One and Site Two. In addition, the species composition of 100 randomly positioned quadrats at each of the sites was recorded. Relative abundance was expressed as the total percentage of ground area covered by each species in all 0.25 m² quadrats combined. The species composition of quadrats from a total of 339 radio-locations of males, 220 radio-locations of females, 85 visual locations of males, 108 visual locations of females and eight visual locations of juveniles were described for Site One (Table 5.16). Due to the small number of locations of juvenile snakes, only the vegetation associated with adult snakes is described below.

At Site One, Calluna vulgaris was the plant species found in the greatest abundance in association with observations of C. austriaca. Of the total area of all 0.25 m² quadrats centred on radio-locations of male smooth snakes, 40.80% was covered by C. vulgaris and 31.24% of the area of quadrats associated with radio-locations of females was covered by this species. Calluna vulgaris was also abundant in quadrats associated with visual locations of smooth snakes, covering 19.51% of the area for males and 30.31% for females. Erica cinerea was also frequently associated with sightings of smooth snakes, representing 11.08% of the ground cover for radio-tagged males, 30.19% for radio-tagged females, 17.68% for visually located males and 18.74% for visually located females. The third species of heather, Erica tetralix, was less frequently encountered in association with C. austriaca at Site One. Only 0.50%, 3.97%, 0.88% and 0.32% of the areas immediately surrounding radio-tagged males and females and visually located males and females respectively were covered by this latter species.

Gorse, Ulex europaeus, was an important element in the

	SITE ONE					
	Radio-tracking		Visual observation			Random
	Males	Females	Males	Females	Juv's	
	%	%	%	%	%	%
European gorse, <u>Ulex europaeus</u>	12.40	5.55	16.76	0.69	0.00	4.10
Dwarf gorse, <u>Ulex minor</u>	0.06	0.02	0.88	0.02	0.00	0.15
Ling, <u>Calluna vulgaris</u>	40.80	31.24	19.51	30.31	1.88	11.06
Cross-leaved heath, <u>Erica tetralix</u>	0.50	3.97	0.88	0.32	0.00	0.80
Bell heather, <u>Erica cinerea</u>	11.08	30.19	17.68	18.74	12.50	1.69
Bare ground	3.57	4.94	10.07	20.06	13.13	10.40
Moss sp(p).	3.98	5.00	8.15	15.63	0.00	0.85
Lichen sp(p).	0.48	0.55	1.53	2.43	0.63	0.20
Bramble, <u>Rubus fruticosus</u>	0.33	0.27	0.55	0.09	0.00	0.70
Bracken, <u>Pteridium aquilinum</u>	4.18	0.25	0.45	0.12	0.00	1.50
Catmint, <u>Nepeta cataria</u>	0.96	0.12	5.91	0.76	0.00	0.00
Pine tree, <u>Pinus</u> sp(p).	2.70	0.93	0.53	0.28	0.00	3.27
Other coniferous tree sp(p).	0.00	0.00	0.00	0.00	0.00	7.60
Deciduous tree sp(p).	0.50	0.23	0.06	0.00	0.00	0.53
Bog myrtle, <u>Myrica gale</u>	0.00	0.00	0.00	0.00	0.00	0.00
Rush, <u>Juncus</u> sp(p).	0.00	0.00	0.00	0.00	0.00	0.00
Bent grass, <u>Agrostis</u> sp(p).	0.54	4.55	0.94	1.97	0.00	1.78
Purple moor grass, <u>Molinia caerulea</u>	2.04	4.72	1.72	1.62	2.50	5.38
Other/ unidentified grass sp(p).	1.32	0.05	3.48	0.91	2.50	4.93
Gorse litter	2.19	1.43	2.47	1.11	0.00	0.50
Bracken litter	1.48	0.66	0.24	0.14	0.63	1.63
Heather sp(p). litter	2.96	3.66	0.18	2.27	16.25	0.35
Deciduous tree litter	2.34	1.12	0.00	0.17	0.00	6.05
Pine tree litter	4.33	0.59	2.29	0.28	0.00	25.40
Other coniferous tree litter	0.00	0.00	0.00	0.00	0.00	7.60
Tin/ tile	0.81	0.00	4.59	2.08	50.00	0.00
Other herbaceous dicotyledonous spp.	0.23	0.00	0.65	0.02	0.00	3.23
Other herbaceous monocotyledonous spp.	0.00	0.00	0.12	0.00	0.00	0.00
Dead wood	0.13	0.00	0.36	0.00	0.00	0.00
Fern sp(p).	0.00	0.00	0.00	0.00	0.00	0.00
Sedge, <u>Carex</u> sp(p).	0.00	0.00	0.00	0.00	0.00	0.00
Fungus sp(p).	0.00	0.00	0.00	0.00	0.00	0.00
Reed, <u>Phragmites australis</u>	0.00	0.00	0.00	0.00	0.00	0.10
Bilberry, <u>Vaccinium myrtillus</u>	0.00	0.00	0.00	0.00	0.00	0.15
Holly, <u>Ilex aquifolium</u>	0.00	0.00	0.00	0.00	0.00	0.05
Totals	99.91	100.04	100.02	100.02	100.00	100.00
Number of Quadrats	399	220	85	108	8	100

Table 5.16 : Percentage cover of each plant species (%) associated with observations of Male, Female and Juvenile specimens of C. austriaca at Site One as determined from 0.25 m² quadrats at radio-tracking and visual observation locations during April 1984 to July 1986 inclusive. The relative abundance of each plant species, determined from 100 randomly positioned quadrats is presented under the heading 'Random'.

ground cover for smooth snakes at Site One, particularly for males where 12.40% of ground cover was provided by this species for radio-tagged specimens and 16.76% for visually located specimens. The respective percentages of ground cover by U. europaeus for females was 5.55% for radio-tagged specimens and 0.69% for visually located specimens. Bracken Pteridium aquilinum was most commonly associated with radio-tagged male snakes (4.18% of ground cover) but used only in small amounts by radio-tagged females (0.25%) and visually located males (0.45%) and females (0.12%).

Open ground and prostrate species were used not infrequently by smooth snakes at Site One and such habitats were particularly associated with visually located specimens. Bare ground represented 3.57% and 4.94% of the ground cover associated with radio-located males and females respectively and 10.07% and 20.06% for males and females that were located visually. Similarly moss sp(p). covered 3.98% and 5.00% of ground associated with radio-locations and 8.15% and 15.63% of ground for visual locations of males and females respectively. Grass species, such as Agrostis sp(p). and Molinia caerulea, were most often associated with radio-locations of females at Site One although these species accounted for a small percentage of ground cover for males and females located by both methods.

The litter of various plant species was often observed in association with sightings of smooth snakes and accounted for a notable proportion of ground cover for radio-tagged and visually located snakes of both sexes. Pine tree litter was the most abundant form of litter associated with male snakes (4.33% of cover for radio-tagged animals and 2.29% for visually located animals, whereas Heather litter was the most abundant litter for both radio-tagged (3.66% of ground cover) and visually located (2.27% of ground cover) females. Tree species were only rarely encountered within quadrats occupied by smooth snakes. Pine trees were most frequently associated with radio-tagged males but this vegetation type represented only 2.70% of ground cover.

Less than 1.0% of ground cover was Pinus sp(p). for visual locations of snakes of both sexes and radio-locations of females. Deciduous trees also accounted for less than 1.0% of ground cover for all groupings of C. austriaca.

Tin sheeting and tiles were positioned around the site to aid the capture of smooth snakes. However, these objects contributed only a small amount to the total percentage area at Site One indicating that they were only infrequently used. Radio-tagged snakes were associated with a notably smaller percentage cover of tin/ tile (0.81% for males and 0.00% for females) than was associated with visual locations of C. austriaca (4.59% and 2.08% for males and females respectively).

Randomly positioned quadrats at Site One showed that the majority of the site was dominated by Pinus sp(p)., (3.27%) Other conifers (particularly norway Picea abies and sitka spruce P. sitchensis, larch Larix kaemferi or cypresses (family Cupressaceae)) (7.60%) or the litter of trees of these two vegetation categories (Pine tree litter (25.40%) and Other coniferous tree litter (7.60%)). Deciduous trees and their associated leaf litter were not as abundant as conifers and represented 0.53% and 6.05% of the ground cover respectively.

Heath species were abundant in the study area with Calluna vulgaris covering 11.06% and Erica cinerea covering 1.69% of the total area of the randomly positioned quadrats. Erica tetralix, however, represented a mere 0.80% of ground cover at Site One. Ulex europaeus was found covering 4.10% of area whereas other shrub layer plants, such as Pteridium aquilinum (1.5%) and Rubus fruticosus (0.70%), were less common. Of the grasses, Molinia caerulea was the most abundant (covering 5.38%). Other/ unidentified grass sp(p)., which were associated particularly with the large grazing strip around the Inclosure, covered 4.93% of the area whilst the less abundant Agrostis sp(p). totalled 1.78% of the ground cover.

A large proportion (10.40%) of the study area was covered by bare ground, this included quadrats sampled on a major road and others located on rides within the Inclosure. Prostrate species, such as Moss sp(p). and Lichen sp(p). and various herbaceous dicotyledonous species (including Belis perenis, Plantago major and Taraxacum spp.) accounted for a small percentage of ground cover at Site One.

At Site Two quadrats associated with 430 and 326 observations of radio-tagged males and females respectively and 74, 114 and three visual locations of male, female and juvenile snakes are described in Table 5.17. Due to the small number of locations of juvenile snakes, only the vegetation associated with adult snakes is described below.

No single vegetation category was most frequently used by all sub-divisions of snakes at Site Two. Calluna vulgaris covered the greatest proportion of the area of quadrats associated with radio-tagged males (36.07%), Pteridium aquilinum was the most widespread category associated with radio-tagged females (18.06%) whereas Tin/ tile (28.78%) and Other/ unidentified grass sp(p). (18.37%) were the most widespread categories for visually located males and females respectively.

Certain categories were, however, commonly associated in with locations of smooth snakes of both sexes and located by both methods. Calluna vulgaris covered a large proportion of the area of quadrats in which males and females were located by both radio- and visual location (36.07% of total quadrat area associated with radio-tagged males, 26.62% of the area of quadrats associated with visually located males, 14.37% of total quadrat area associated with radio-tagged females and 8.04% of the area of quadrats associated with visually located females). Erica cinerea was also commonly found in association with C. austriaca, representing 5.08%, 11.64%, 8.78% and 7.69% of the ground cover for radio-tagged males and females and visually located males and females respectively.

	SITE TWO					
	Radio-tracking		Visual observation			Random
	Males	Females	Males	Females	Juv's	
	%	%	%	%	%	%
European gorse, <u>Ulex europaeus</u>	2.58	3.37	1.96	1.34	0.00	8.25
Dwarf gorse, <u>Ulex minor</u>	0.15	0.01	0.57	0.20	0.00	0.06
Ling, <u>Calluna vulgaris</u>	36.07	14.37	26.62	8.04	13.33	21.86
Cross-leaved heath, <u>Erica tetralix</u>	9.32	2.72	6.91	0.92	0.00	7.02
Bell heather, <u>Erica cinerea</u>	5.08	11.64	8.78	7.69	0.00	0.86
Bare ground	1.03	6.28	7.15	14.87	21.67	5.95
Moss sp(p).	1.51	1.16	1.55	0.61	0.00	3.80
Lichen sp(p).	0.32	0.16	0.74	0.04	0.00	0.00
Bramble, <u>Rubus fruticosus</u>	1.50	0.08	1.04	3.15	0.00	0.00
Bracken, <u>Pteridium aquilinum</u>	4.66	18.06	1.22	3.11	3.33	0.80
Catmint, <u>Nepeta cataria</u>	0.43	0.92	0.27	0.90	0.00	0.15
Pine tree, <u>Pinus</u> sp(p).	0.00	0.00	0.00	0.00	0.00	0.00
Other coniferous tree sp(p).	0.00	0.00	0.00	0.00	0.00	0.00
Deciduous tree sp(p).	0.00	0.06	0.61	3.11	0.00	2.25
Bog myrtle, <u>Myrica gale</u>	5.37	0.69	0.00	0.00	0.00	2.93
Rush, <u>Juncus</u> sp(p).	4.57	0.50	0.00	0.00	0.00	3.10
Bent grass, <u>Agrostis</u> sp(p).	2.85	14.84	6.08	11.05	46.67	5.61
Purple moor grass, <u>Molinia caerulea</u>	17.80	5.22	2.65	1.82	6.67	21.75
Other/ unidentified grass sp(p).	2.45	5.27	0.99	18.37	0.00	4.00
Gorse litter	0.22	0.02	0.68	0.28	0.00	0.80
Bracken litter	1.76	6.56	0.70	1.20	0.00	7.20
Heather sp(p). litter	0.00	2.90	0.34	1.71	8.33	0.00
Deciduous tree litter	0.00	0.00	0.74	0.22	0.00	0.40
Pine tree litter	0.00	0.15	0.00	0.53	0.00	0.00
Other coniferous tree litter	0.00	0.00	0.00	0.00	0.00	0.00
Tin/ tile	1.44	2.98	28.78	12.11	0.00	0.00
Other herbaceous dicotyledonous spp.	0.56	1.16	1.42	8.73	0.00	2.16
Other herbaceous monocotyledonous spp.	0.28	0.01	0.00	0.00	0.00	0.05
Dead wood	0.13	0.00	0.00	0.00	0.00	0.00
Fern sp(p).	0.00	0.60	0.14	0.00	0.00	0.00
Sedge, <u>Carex</u> sp(p).	0.00	0.21	0.07	0.00	0.00	0.00
Fungus sp(p).	0.01	0.00	0.00	0.00	0.00	0.00
Reed, <u>Phragmites australis</u>	0.02	0.00	0.00	0.00	0.00	0.95
Bilberry, <u>Vaccinium myrtillus</u>	0.00	0.00	0.00	0.00	0.00	0.05
Holly, <u>Ilex aquifolium</u>	0.00	0.00	0.00	0.00	0.00	0.00
Totals	100.11	100.27	100.01	100.00	100.00	100.00
Number of Quadrats	430	326	74	114	3	100

Table 5.17 : Percentage cover of each plant species (%) associated with observations of Male, Female and Juvenile specimens of C. austriaca at Site Two as determined from 0.25 m² quadrats at radio-tracking and visual observation locations during April 1984 to July 1986 inclusive. The relative abundance of each plant species, determined from 100 randomly positioned quadrats is presented under the heading 'Random'.

Wet and humid heathland and bog vegetation were used more frequently by male, than female, C. austriaca at Site Two. This was demonstrated by the greater use of Erica tetralix by radio-tagged (9.32% of ground cover) and visually located (6.91% of ground cover) males compared with the relative use by females (2.72% and 0.92% for radio-locations and visual locations respectively). No visual locations of C. austriaca were made in either Myrica gale or Juncus sp(p). (both species associated with wet ground), but these categories represented 5.37% and 4.57% of vegetation cover for radio-tagged males and 0.69% and 0.50% for radio-tagged females respectively.

Use of Bare ground was most notable by visually located snakes, and in particular females (14.87% of ground cover). For visually located males Bare ground represented 7.15% of ground area with the respective figures for radio-tagged males and females being 1.03% and 6.28%. Both Moss sp(p). and Lichen sp(p). yielded only small percentages of ground cover for all sub-divisions of the snake data (ranging from 0.61 to 1.55% and 0.04 to 0.74% respectively). Various herbaceous dicotyledonous plants were found in close proximity to smooth snakes at Site Two, including Potentilla erecta, Lonicera periclymenum, Achillea millefolium and Taraxacum sp(p).. This latter category of plant species accounted for only a small proportion of the total ground cover associated with observations of C. austriaca (0.56% for radio-tagged males, 1.16% for radio-tagged females, 1.42% for visually located males and 8.73% for visually located females).

Tin/ tile was only rarely used by radio-tagged snakes (1.44% of ground cover for males and 2.98% for females) but this category provided a large proportion of the total quadrat area associated with visually located male (28.78%) and female (12.11%) snakes.

Grasses were often used by C. austriaca, with Molinia caerulea being particularly common in association with radio-locations of males (17.80% of ground cover was this

species). Molinia caerulea was used relatively less often by radio-tagged females (5.22%) and visually located males (2.65%) and females (1.82%). Agrostis sp(p). was used relatively most often by radio-tagged females (representing 14.84% of the total area of quadrats). Both visually located males and females were often found amongst Agrostis sp(p). (representing 6.08% and 11.05% of ground cover respectively) and this category yielded 2.85% of the ground cover associated with locations of radio-tagged males. Other/ unidentified grass sp(p). was the most abundant category associated with visually located females (18.37% of total area), and was also common in association with radio-tagged females (5.27%). Radio-tagged and visually located males, however, used this latter 'grass' category relatively less often (2.45% and 0.99% of ground cover respectively).

Pteridium aquilinum was particularly associated with radio-locations of females at Site Two, where it represented 18.06% of the ground cover. Bracken litter accounted for a further 6.56% of the quadrat area associated with radio-tagged females. For radio-tagged males P. aquilinum covered 4.66% of the quadrat area with a further 1.76% being Bracken litter. Smooth snakes that were located visually were associated with relatively smaller quantities of P. aquilinum and Bracken litter (1.22% and 0.70% of ground cover for males and 3.11% and 1.20% for females respectively). Other shrub layer plant species accounted for only a small proportion of the vegetation associated with C. austriaca. Ulex europaeus represented 2.58% of ground cover for radio-tagged males, 3.37% for radio-tagged females, 1.96% for visually located males and 1.34% for visually located females whilst the respective percentages for Rubus fruticosus were 1.50%, 0.08%, 1.04% and 3.15%.

Trees were only infrequently encountered by C. austriaca at Site Two with Deciduous trees only being encountered by radio-tagged females and visually located males and females (0.06%, 0.61% and 3.11% of ground cover respectively) and with Pine and Other conifers not being recorded in quadrats

associated with either radio-tagged or visually located snakes. Deciduous tree litter further indicated association with deciduous trees by increasing the percentage of quadrat area by 0.74% and 0.22% for visual locations of males and females. Pine tree litter was found in quadrats occupied by radio-tagged and visually located females only (0.15% and 0.53% respectively).

Randomly positioned quadrats showed that Site Two was dominated by two species of plant, namely Calluna vulgaris (21.86%) and Molinia caerulea (21.75%). Ulex europaeus was abundant (8.25% of ground cover) with the litter of this species accounting for an additional 0.80%. Pteridium aquilinum and its associated litter represented 8.00% of the total area of the random sample (0.80% and 7.20% respectively). Erica tetralix was abundant, covering 7.02% of the area, although E. cinerea was relatively uncommon (representing only 0.86% of the area). Much of the ground area was devoid of plant cover (5.95% was Bare ground) which included a wide gravel and soil track, sandy pathways, an asphalt road and numerous patches of bare ground between plants. Moss species, including Sphagnum sp. in bog areas and small prostrate species on the drier ground, represented 3.80% of the area of the random sample.

Various species of grass (other than Molinia caerulea which is mentioned above) were common at Site Two, including Agrostis sp(p). (which covered 5.61% of the area). Other/ unidentified grass species accounted for an additional 4.00% of the ground cover. Various herbaceous dicotyledonous plants were found throughout the site, these totalling 2.16% of the area. Bog related species were quite abundant: Myrica gale covered 2.93% of the ground area sampled, Juncus sp(p). covered 3.10% and Phragmites australis represented a further 0.95%.

Trees were not abundant at Site Two and only 2.25% of the sample area was Deciduous trees (with a further 0.40% Deciduous leaf litter). Neither Pinus sp(p). nor Other coniferous tree species were observed in the random sample,

nor was any litter associated with these species.

c. Height of vegetation occupied in the field

i. Proportion of ground cover in different height categories

Vegetation heights were assessed at each location of smooth snakes during the 1985 and 1986 field seasons (see below and Chapter 2, section 2.2.4. a.). The proportion of vegetation cover in each of the sixteen defined height categories was summed and expressed as a percentage of the total for all observations of C. austriaca in each of four groupings at each site. These groupings were defined by sex (males and females) and the method employed for location (radio-tracking and visual observation). At Site One, 67 locations of female snakes and 121 locations of male snakes made by radio-tracking were assessed for vegetation height composition. A further 75 quadrats were assessed for females and 43 for males using data from visually located animals (two quadrats described for juvenile snakes at Site One have been excluded from this analysis).

At Site Two, radio-tracking yielded 120 locations of female and 288 locations of male C. austriaca for which the vegetation height was assessed. Height composition was also determined for a further 72 quadrats in which female snakes were located by visual observation and 33 quadrats in which male snakes were visually located (one quadrat in which a juvenile snake was found at Site Two has been excluded from this analysis). Vegetation height estimates where snakes were found below tin sheeting or tiles were discarded (49 cases).

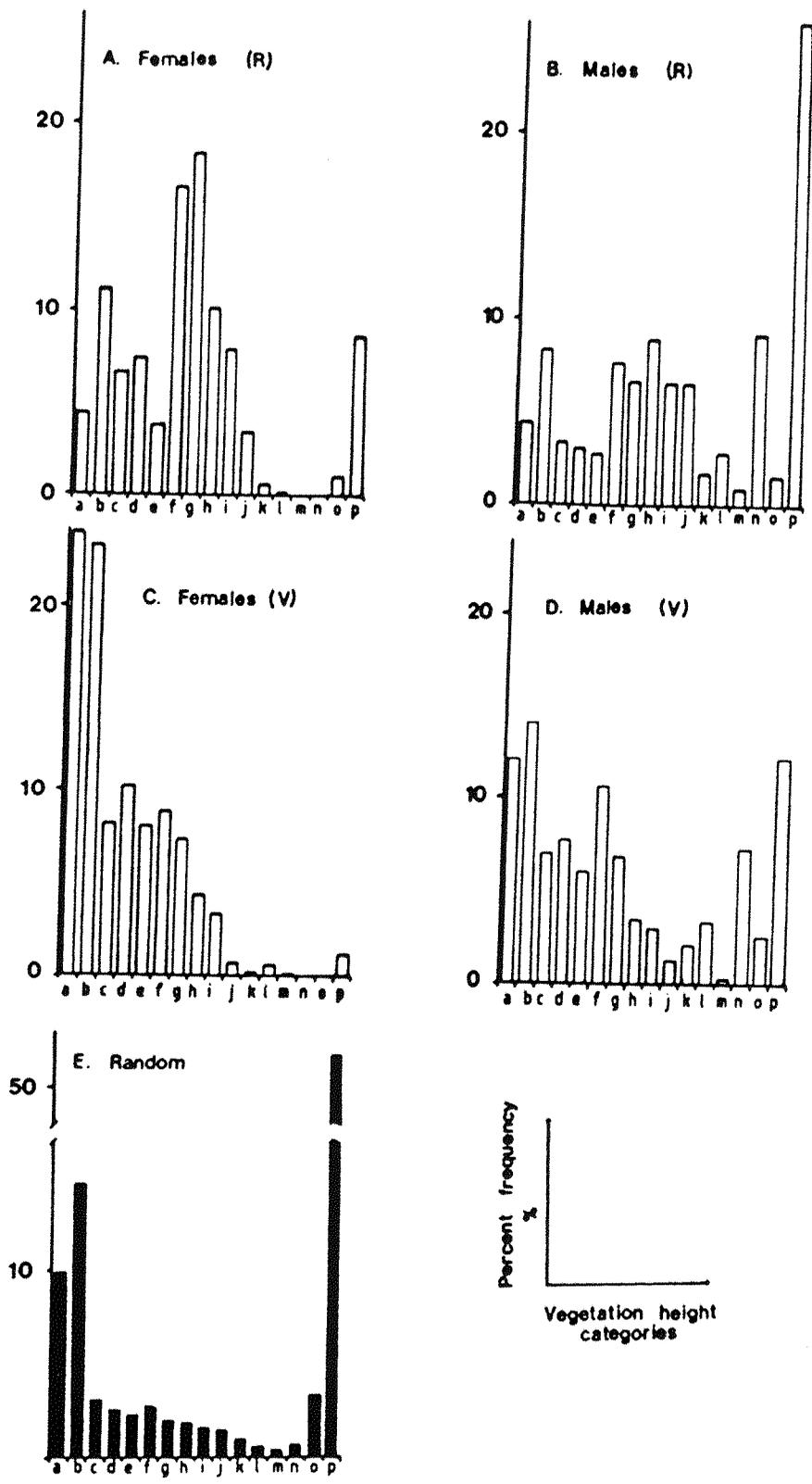
In addition, vegetation heights were assessed for 100 randomly positioned quadrats at both Site One and Site Two to allow the vegetation structure at each site to be described.

The percentage cover of each vegetation height category for

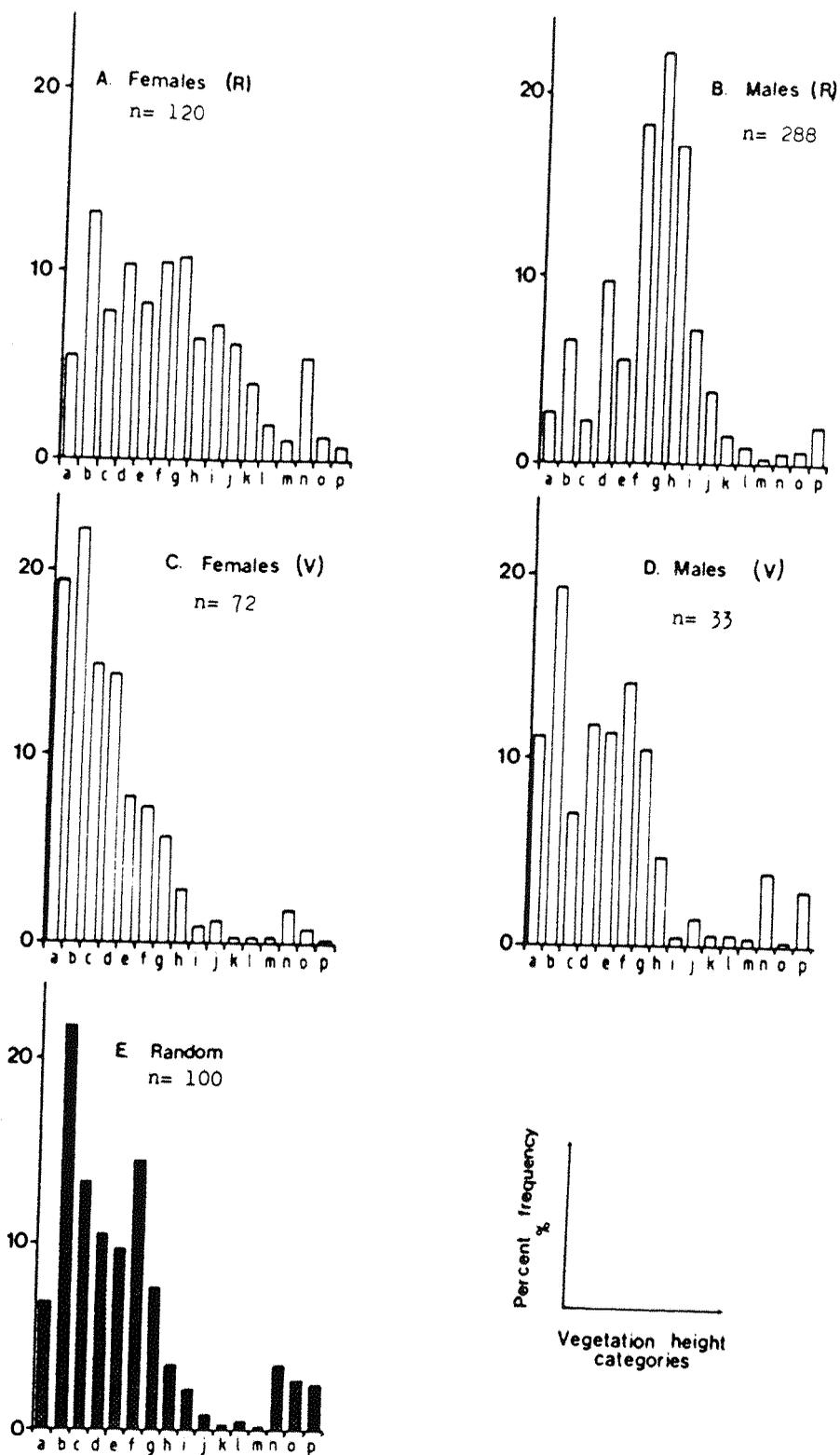
combined data for each of the four groupings and for the 100 random quadrats at each site are presented in Figs. 5.15 A. to E. and 5.16 A. to E. for Sites One and Two respectively. The sixteen vegetation categories, represented by the lower case letters a to p inclusive, were as follows: a= 0 cm, b= between 0 and 5 cm, c= between 5 and 10 cm, d= between 10 and 15 cm, e= between 15 and 20 cm, f= between 20 and 30 cm, g= between 30 and 40 cm, h= between 40 and 50 cm, i= between 50 and 60 cm, j= between 60 and 70 cm, k= between 70 and 80 cm, l= between 80 and 90 cm, m= between 90 and 100 cm, n= between 100 and 150 cm, o= between 150 and 200 cm and p= over 200 cm. Frequency of use of the vegetation height categories appeared inconsistent between groupings, with no height category or range of categories being predominant.

At Site One, radio-tagged females were found most frequently in association with vegetation between 30 and 40 cm tall (category 'g') which represented 18.4% of the total quadrat area (see Fig. 5.15 A.). In general vegetation categories below this height range were used with decreasing frequency as vegetation height decreased (category 'f'= 16.6% of ground cover, 'e'= 3.8%, 'd'= 7.4%, 'c'= 6.6%, 'b'= 11.1% and 'a'= 4.4%). Increasing vegetation heights from the 40 to 50 cm category to 100 to 150 cm category were used progressively less frequently ('h'= 10.1%, 'i'= 7.9%, 'j'= 3.4%, 'k'= 0.6% and 'l'= 0.1%), with 0.0% cover being found in both group 'm' (90 to 100 cm) and group 'n' (100 to 150 cm). A small percentage of ground was covered by vegetation between 150 and 200 cm (1.0%) with an increased percentage being in excess of 200 cm in height (8.6%).

The most abundant height category associated with radio-tagged males at Site One was 'p' (greater than 200 cm) which accounted for 26.1% of the area of the combined quadrats (see Fig. 5.15 B.). Each of the other categories represented less than 10.0% of the total area and the distribution of height categories indicated that no particular range of heights below 200 cm was favoured by



Figs. 5.15 A. to E. : Percentage cover of different vegetation height categories totalled for 0.25 m² quadrats occupied by *C. austriaca* at Site One as follows : A. Females located by radio-tracking (R), B. Males located by radio-tracking (R), C. Females located by visual observation (V), D. Males located by visual observation (V) and E. that shown by 100 randomly positioned quadrats at Site One. Vegetation height categories represent increasing vegetation heights from a. to p. (as described in section 5.3.2. c. (i)). Data were collected during 1985 and 1986 inclusive, sample sizes (n) are given in each case.



Figs. 5.16 A. to E. : Percentage cover of different vegetation height categories totalled for 0.25 m² quadrats occupied by *C. austriaca* at Site Two as follows : A. Females located by radio-tracking (R), B. Males located by radio-tracking (R), C. Females located by visual observation (V), D. Males located by visual observation (V) and E. that shown by 100 randomly positioned quadrats at Site Two, during 1985 and 1986 inclusive. Vegetation height categories represent increasing vegetation heights from a. to p. (as described in section 5.3.2. c. (i)). Sample sizes (n) are given in each case.

radio-tagged males at Site One. The three next most abundant vegetation height categories were 'n' (100 to 150 cm) (9.2% cover), 'h' (40 to 50 cm) (8.9% cover) and 'b' (0 to 5 cm) (8.3% cover). Of the remaining 12 categories the most widespread occurred within the height range between 20 to 70 cm (categories 'f' to 'j') as follows: 'f' (20 to 30 cm)= 7.6% cover, 'g' (30 to 40 cm)= 6.6%, 'i' (50 to 60 cm)= 6.5% and 'j' (60 to 70 cm)= 6.5%. All other categories combined represented 20.3% of ground cover, with each representing less than 5%. Bare ground (category 'a', i.e. 0 cm height) accounted for 4.3% of the area of quadrats occupied by radio-tagged males at Site One with the three categories between 5 and 20 cm ('c'= 5 to 10cm, 'd'= 10 to 15 cm and 'e'= 15 to 20 cm) covering 3.3%, 3.0% and 2.7% respectively. Only small a percentage of ground cover was between 70 and 100 cm ('k'= 1.7%, 'l'= 2.8%, 'm'= 0.9%) and 1.6% of ground cover was between 150 and 200 cm in height (category 'o').

Visually located females were found most frequently in association with bare ground (0 cm height) or short (less than 5 cm tall) vegetation at Site One ('a'= 23.9%, 'b'= 23.2%) (see Fig. 5.15 C.). Vegetation of intermediate height, between 5 and 40 cm, was used often ('c'= 8.1%, 'd'= 10.2%, 'e'= 8.0%, 'f'= 8.8% and 'g'= 7.3%). Vegetation of increasing height above 40 cm became less abundant ('h'= 4.3%, 'i'= 3.3%, 'j'= 0.7%, 'k'= 0.2%, 'l'= 0.6% and 'm'= 0.1%) and heights between 100 and 200 cm (categories 'n' and 'o') were not represented in the quadrats associated with visually located female snakes at Site One. A small proportion (1.2%) of ground cover associated with females snakes was in excess of 200 cm in height.

The most widespread vegetation category in quadrats associated with visually located males at Site One was 'b' (between 0 and 5 cm) which represented 14.1% of the area (see Fig. 5.15 D.). Both categories 'a' (0 cm) and 'p' (greater than 200 cm) were common (each occupying 12.2% of the total quadrat area). Between these two extremes of vegetation height there was a tendency for vegetation

between 5 and 40 cm to be used most often with the most abundant category in this range being 'f' (20 to 30 cm) ('c'= 6.9%, 'd'= 7.7%, 'e'= 6.0%, 'f'= 10.7% and 'g'= 6.8%). Heights between 40 and 200 cm were, in general, encountered only to a small degree, with the two least abundant height categories being 'j' and 'm'. However, a notably high value was associated category 'n', i.e. 100 to 150 cm height (categories 'h' to 'o' represented 3.5%, 2.9%, 1.3%, 2.1%, 3.3%, 0.3%, 7.3% and 2.6% of the area respectively).

Randomly positioned quadrats showed that vegetation in excess of 200 cm was most abundant at Site One where it covered 51.7% of the area (see Fig. 5.15 E.). Of the remainder of the area the majority was covered by the two categories representing bare ground and vegetation less than 5 cm in height ('a'= 9.9% and 'b'= 14.7% of the total area). Vegetation between 5 and 150 cm became, on the whole, progressively less abundant with increasing vegetation height (with categories 'c' to 'n' representing 3.1%, 2.6%, 2.3%, 2.8%, 2.0%, 1.9%, 1.6%, 1.0%, 0.6%, 0.4% and 0.7% of total area respectively). Vegetation between 150 and 200 cm (category 'o') covered 3.4% of Site One.

At Site Two, radio-tagged females were found most often in association with vegetation above 0 cm and up to 40 cm in height ('b'= 13.2%, 'c'= 7.8%, 'd'= 10.4%, 'e'= 8.3%, 'f'= 10.5% and 'g'= 10.8%) (see Fig. 5.16 A.). Vegetation between 40 and 70 cm was also encountered often, and represented a total of 19.6% of the quadrat area, ('h'= 6.4%, 'i'= 7.1% and 'j'= 6.1%) as was bare ground (category 'a', i.e. 0 cm, = 5.4%). Only 14.1% of the quadrat area associated with radio-locations of females at Site Two was vegetation of 70 cm or over, and of this 5.4% (of the total area) was between 100 and 150 cm in height (category 'n') ('k'= 4.0%, 'l'= 1.8%, 'm'= 1.0%, 'n'= 5.4%, 'o'= 1.2% and 'p'= 0.7%).

Quadrats associated with radio-locations of males at Site Two (see Fig. 5.16 B.) were dominated by intermediate

height vegetation, between 20 and 50 cm in height ('f'= 18.3%, 'g'= 23.2% and 'h'= 17.1%). In general, vegetation height below 20 cm became increasingly abundant with increasing vegetation height ('a'= 2.6%, 'b'= 4.5%, 'c'= 2.2%, 'd'= 9.7% and 'e'= 5.5%) whilst those in excess of 50 cm became decreasingly abundant with increasing vegetation height (vegetation height categories 'i' to 'p' inclusive represented 7.1%, 3.8%, 1.5%, 0.9%, 0.3%, 0.6%, 0.7% and 2.0% respectively).

Visually located females were most often associated with bare ground and vegetation of less than 5 cm in height ('a'= 19.4% and 'b'= 22.2%) (see Fig. 5.16 C.). Vegetation above 5 cm accounted for progressively smaller proportions of the quadrat area associated with female snakes as vegetation height increased up to 100 cm ('c'= 14.9%, 'd'= 14.4%, 'e'= 7.7%, 'f'= 7.2%, 'g'= 5.6%, 'h'= 2.8%, 'i'= 0.9%, 'j'= 1.2%, 'k'= 0.3%, 'l'= 0.3% and 'm'= 0.3%). Vegetation between 100 and 150 cm in height represented 1.8% of the total quadrat area and diminishing quantities were found in the 150 to 200 cm (0.8% cover) and greater than 200 cm (0.2% cover) categories.

Quadrats associated with male snakes located by visual observation at Site Two (see Fig. 5.16 D.) were mostly dominated by vegetation cover less than 50 cm in height, these categories representing 90.0% of the total area of these quadrats. Very short vegetation (category 'b', i.e. 0 to 5 cm in height) was especially abundant (covering 19.3% of the area). Vegetation in the height range 10 to 40 cm was notably widespread ('d'= 11.8%, 'e'= 11.4%, 'f'= 14.1% and 'g'= 10.5%). Bare ground (category 'a') represented 11.2% of the area and categories 'c' and 'h' covered 7.0% and 4.7% respectively. Only small percentages of the total area of quadrats associated with visually located males were in excess of 50 cm ('i'= 0.5%, 'j'= 1.5%, 'k'= 0.6%, 'l'= 0.6%, 'm'= 0.5%, 'n'= 3.9%, 'o'= 0.3% and 'p'= 2.3%).

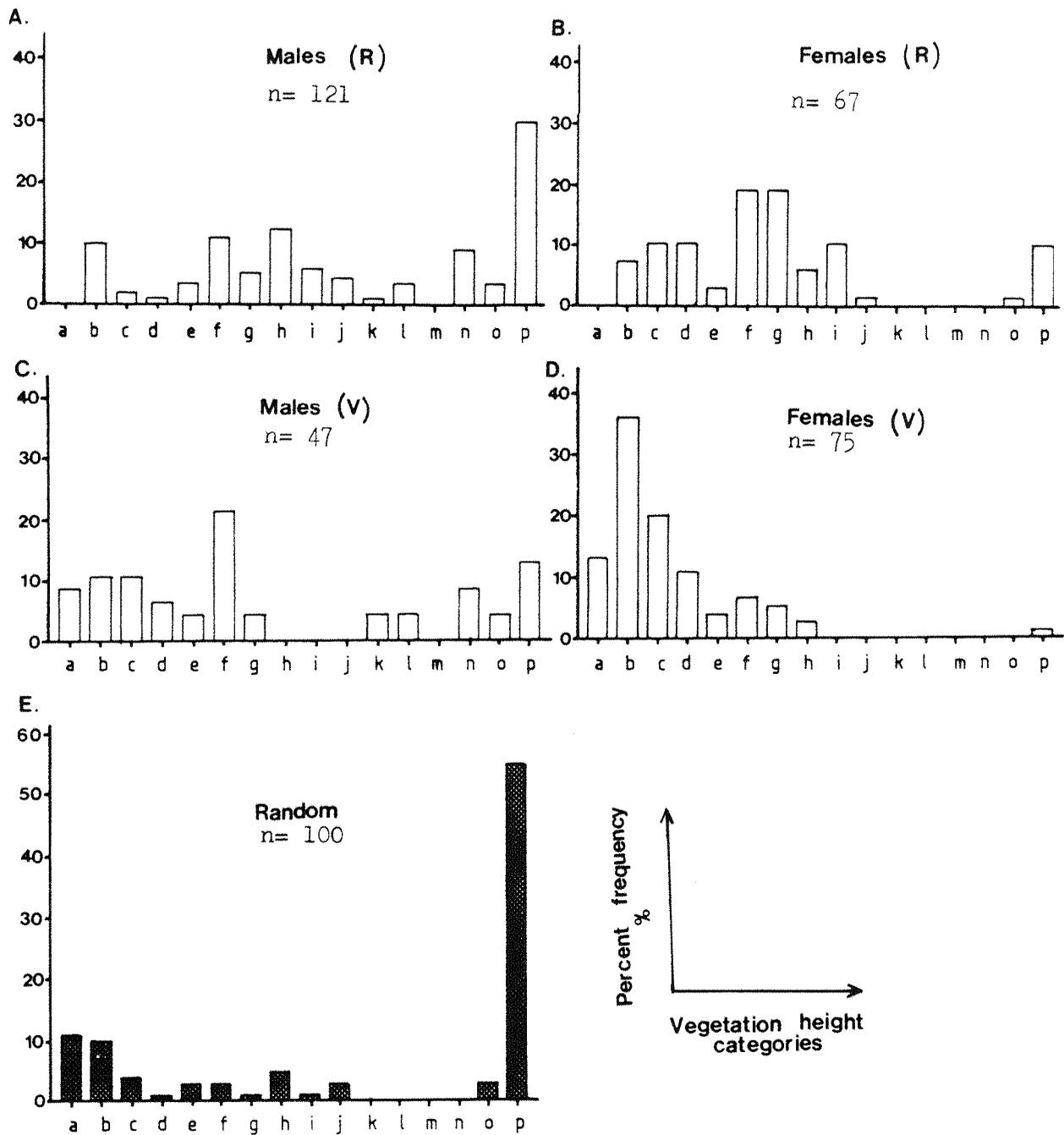
Site Two was mostly covered by vegetation above 0 and less than 40 cm in height, this range representing 77.3% of the

area of the 100 randomly positioned quadrats (see Fig. 5.16 E.). On the whole, there is a diminishing quantity of ground cover associated with increasing vegetation height between 0 to 5 cm and 100 to 150 cm (the percentage of ground covered by each of the categories in this range were as follows: 'b'= 21.7%, 'c'= 13.3%, 'd'= 10.5%, 'e'= 9.7%, 'f'= 14.5%, 'g'= 7.6%, 'h'= 3.5%, 'i'= 2.2%, 'j'= 0.8%, 'k'= 0.3%, 'l'= 0.5% and 'm'= 0.2%). Bare ground was widespread at Site Two with height category 'a' representing 6.8% of the area. Vegetation in excess of 100 cm was not uncommon and represented a total of 8.7% of the area ('n'= 3.5%, 'o'= 2.7% and 'p'= 2.5%).

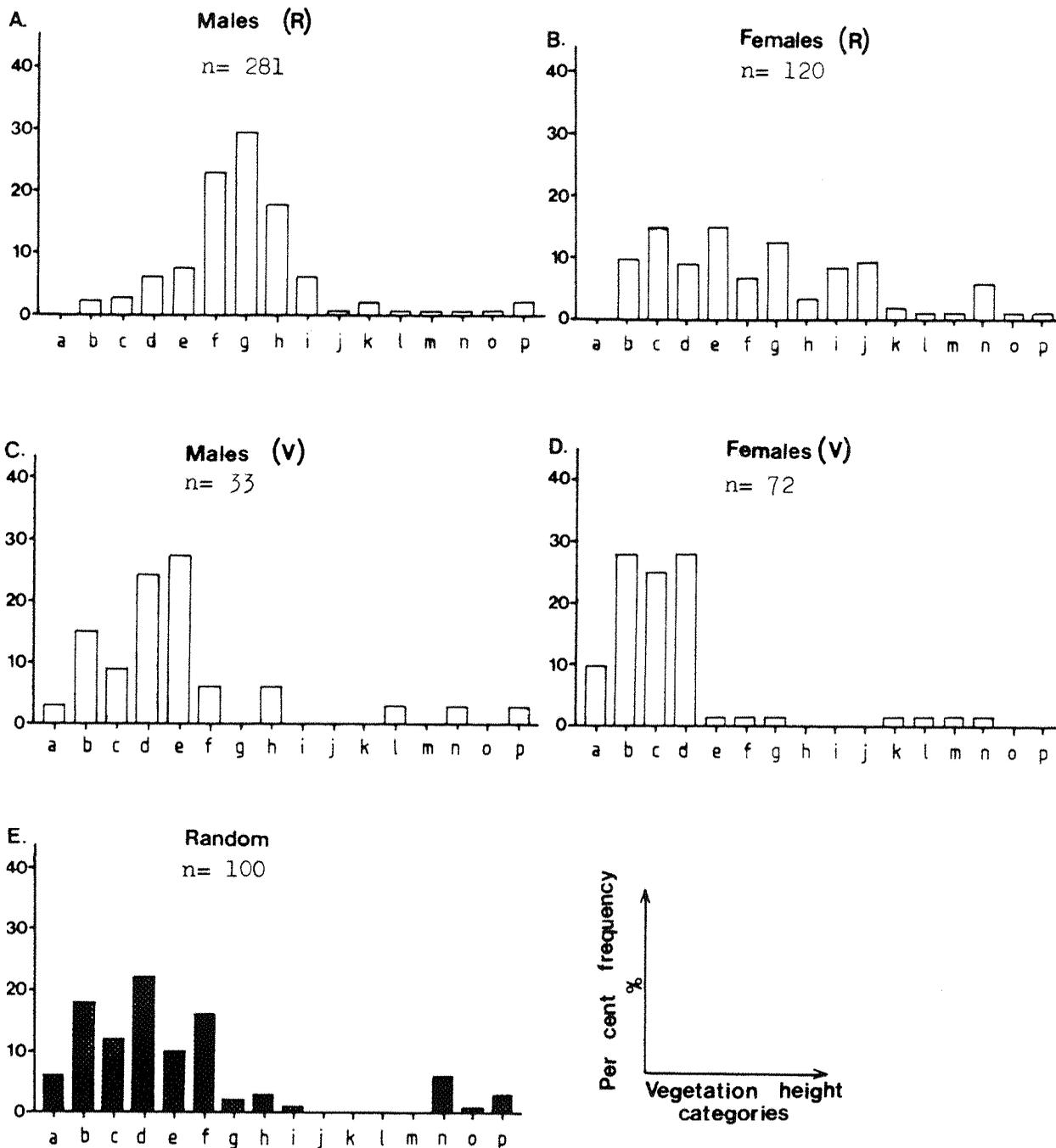
ii. Median vegetation height categories

The median vegetation height of each quadrat was calculated and assigned to one of the above 16 categories ('a' to 'p' inclusive) and the relative frequency with which each median category occurred used as the basis for statistical comparisons. Median heights were calculated for quadrats associated with 281 radio-locations of males, 120 radio-locations of females, 33 visual locations of males and 72 visual locations of females at Site One. Median heights were also calculated for quadrats associated with 121 radio-locations of males, 67 radio-locations of females, 47 visual locations of males and 75 visual locations of females at Site Two. In addition, median heights were calculated for the 100 randomly positioned quadrats at both Sites One and Two. The relative frequencies of each of the median categories for males and females recorded by both radio-tracking and visual observation are illustrated in Figs. 5.17 A. to E. for Site One and Figs. 5.18 A. to E. for Site Two.

The most frequently occurring median vegetation height associated with radio-tagged males was category 'p' (greater than 200 cm) which accounted for 29.8% of the quadrats (see Fig. 5.17 A.). There was no pronounced trend in the relative occurrence of median quadrat heights below 200 cm with the next four most frequently observed



Figs. 5.17 A. to E. : Relative frequency distributions of median vegetation height categories for 0.25 m² quadrats occupied by *C. austriaca* at Site One as follows: A. Males located by radio-tracking (R), B. Females located by radio-tracking (R), C. Males located by visual observation (V), D. Females located by visual observation (V) and E. that shown by 100 randomly positioned quadrats at Site One, during 1985 and 1986 inclusive. Vegetation height categories represent increasing heights from a. to p. (as described in section 5.3.2. c. (i)). Sample sizes (n) are given in each case.



A. to E.

Figs. 5.18/: Relative frequency distributions of median vegetation height categories for 0.25 m² quadrats occupied by *C. austriaca* at Site Two as follows: A. Males located by radio-tracking (R), B. Females located by radio-tracking (R), C. Males located by visual location (V), D. Females located by visual location (V) and E. that shown by 100 randomly positioned quadrats at Site Two, during 1985 to 1986 inclusive. Vegetation height categories represent increasing heights from a. to p. (as described in section 5.3.2. c. (i)). Sample size (n) is given in each case.

categories occurring throughout the range of median height classes (12.4% of quadrats had a median within category 'h', 10.7% were within category 'f', 9.9% were in category 'b' and 9.1% were in category 'n'). Relatively small percentages of median heights occurred within the remaining height classes ('c'= 1.7%, 'd'= 0.8%, 'e'= 3.3%, 'g'= 5.0%, 'i'= 5.8%, 'j'= 4.1%, 'k'= 0.8%, 'l'= 3.3% and 'o'= 3.3%), however, the majority of these tended to occur within the range 15 to 70 cm (categories 'e' to 'j' inclusive). No quadrats associated with radio-locations of males at Site One had a median height of 0 cm (category 'a') or that fell in the range 90 to 100 cm (category 'm').

Radio-tagged females at Site One were found most commonly in quadrats with a median height between 20 and 40 cm (categories 'f' and 'g' each representing 19.4% of the sample) (see Fig. 5.17 B.). On the whole, there was an increase in the number of quadrats with increasing median height between 0 cm and 20 cm ('a'= 0.0%, 'b'= 7.5%, 'c'= 10.5%, 'd'=10.5% and 'e'= 3.0%). At heights over 40 cm, but below 70 cm there is, in general, a decrease in the number of quadrats with increasing median height ('h'= 6.0%, 'i'= 10.4% and 'j'= 1.5%) and no quadrats were found in association with females with a median height between 70 and 150 cm. A small percentage (1.5%) of quadrats had a median height in the range 150 to 200 cm (category 'o') and 10.5% had a median height of 200 cm or more (category 'p').

The most frequently encountered median quadrat height category associated with visually located males at Site One (see Fig. 5.17 C.) was 'f' (20 to 30 cm), which represented 21.3% of observations. Within the remaining categories no clear trend was evident but approximately half of these sightings (40.4% of the total) had a median value of less than 20 cm ('a'= 8.5%, 'b'= 10.6%, 'c'= 10.6%, 'd'= 6.4% and 'e'= 4.3%) and approximately half (38.3% of the total) had a median value of greater than 30 cm ('g'= 4.3%, 'k'= 4.3%, 'l'= 4.3%, 'n'= 8.5%, 'o'= 4.3% and 'p'= 12.8%). No quadrats were found with median values in categories 'h', 'i', 'j' or 'm' in association with visually located males

at Site One.

Visually located females were most often found in quadrats with a median value between 0 and 5 cm (36.0% of sightings) at Site One. A median value of 0 cm (bare ground representing over half the quadrat area, i.e. category 'a') was observed in 13.3% of the quadrats. Decreasing numbers of locations were found in association with increasing median heights of vegetation between 5 cm and 50 cm ('c'= 20.0%, 'd'= 10.7%, 'e'= 4.0%, 'f'= 6.7%, 'g'= 5.6% and 'h'= 2.7%). No sightings of female snakes were made in quadrats with median height values between 50 and 200 cm. A small number (1.3%) of sightings were in quadrats with median heights in excess of 200 cm.

The majority of randomly positioned quadrats (55%) at Site One had median values of 200 cm or more (see Fig. 5.17 E.). Median values of 0 cm represented 11% of the area and medians between 0 and 5 cm represented 10%. Of the remainder nearly all had median values less than 70 cm ('c'= 4%, 'd'= 1%, 'e'= 3%, 'f'= 3%, 'g'= 1%, 'h'= 5%, 'i'= 1% and 'j'= 3%). No quadrats were located by random sampling with a median value between 70 and 150 cm at Site One. Quadrats with median values of 200 cm or more accounted for 3% of the random sample.

At Site Two male snakes were most frequently radio-located in vegetation with a median height between 20 and 30 cm (category 'g'= 29.2%) (see Fig. 5.18 A.). An increasing number of quadrats were found as median vegetation height increased up to a value of 20 cm ('a'= 0.0%, 'b'= 2.1%, 'c'= 2.5%, 'd'= 6.0%, 'e'= 7.5% and 'f'= 22.8%). Progressively decreasing numbers of quadrats were found with increasing median vegetation heights in excess of 40 cm ('h'= 17.8%, 'i'= 6.0%, 'j'= 0.4%, 'k'= 1.8%, 'l'= 0.4%, 'm'= 0.4%, 'n'= 0.4%, 'o' = 0.7% and 'p'= 2.1%).

Radio-tagged females at Site Two (see Fig. 5.18 B.) were found commonly in quadrats with median height between 5 and 40 cm, with the most frequently encountered categories

being 'c' (5 to 10 cm) and 'e' (15 to 20 cm) in each case representing 15.0% of all locations (category 'd' = 9.2%). On the whole there was an increase in the number of observations with increasing vegetation height up to 5 cm ('a' = 0.0% and 'b' = 10.0%) and a decrease in the number of observations with increasing median vegetation height above 20 cm ('f' = 6.7%, 'g' = 12.5%, 'h' = 3.3%, 'i' = 8.3%, 'j' = 9.2%, 'k' = 1.7%, 'l' = 0.8%, 'm' = 0.8%, 'n' = 5.8%, 'o' = 0.8% and 'p' = 0.8%).

Visually located *C. austriaca* of both sexes were found most frequently in quadrats with median heights less than 20 cm in height at Site Two (see Figs. 5.18 C. and D. for males and females respectively). Relatively small proportions of the observations were in quadrats with a median height of 0 cm (3% of quadrats for males and 9.7% for females), but a greater number of quadrats were found with median heights up to 20 cm for males (category 'b' = 15.2%, 'c' = 9.1%, 'd' = 24.2% and 'e' = 27.3%) and up to 15 cm for females (category 'b' = 27.8%, 'c' = 25.0% and 'd' = 27.8%). Only relatively small numbers of quadrats were found with median values above these latter heights (for males: 'f' = 6.1%, 'g' = 0.0%, 'h' = 6.1%, 'i' = 0.0%, 'j' = 0.0%, 'k' = 0.0%, 'l' = 3.0%, 'm' = 0.0%, 'n' = 3.0%, 'o' = 0.0% and 'p' = 3.0%; for females: 'e' = 1.4%, 'f' = 1.4%, 'g' = 1.4%, 'h' = 0.0%, 'i' = 0.0%, 'j' = 0.0%, 'k' = 1.4%, 'l' = 1.4%, 'm' = 1.4%, 'n' = 1.4%, 'o' = 0.0% and 'p' = 0.0%).

Random quadrats showed that Site Two was predominantly covered by vegetation less than 30 cm in height, with the most commonly represented median vegetation heights occurring in category 'd' (10 to 15 cm = 22% of the quadrats) (see Fig. 5.18 E.). Below this category there was a trend towards increasing abundance with increasing median vegetation height ('a' = 6%, 'b' = 18% and 'c' = 12%), and above this category there were generally fewer quadrats as median height increased ('e' = 10%, 'f' = 16%, 'g' = 2%, 'h' = 3% and 'i' = 1%). No quadrats were found with median values between 60 and 100 cm at Site Two. Quadrats with median values of 100 cm or more were found in 10% of the random

sample ('n' = 6%, 'o' = 1% and 'p' = 3%).

iii. Comparison of vegetation height usage between methods of location

Pooling of data, such that adequate 'expected frequencies' were obtained for statistical comparison between radio-tagged and visually located snakes (males and females combined), yielded 12 vegetation height categories at Site One. Median heights were assessed for each quadrat and the frequencies at which these median heights occurred in each height category at Site One are presented in Table 5.18 A. Overall, there was a significant difference between vegetation height category usage indicated by the two methods ($G = 102.224$ with 11 d.f., $p < 0.001$). Of the 12 categories, a significant difference was observed in the frequency of occurrence between radio-located and visually located animals in 6 cases, and in 6 cases (10 to 15 cm, 15 to 20 cm, 20 to 30 cm, 30 to 40 cm, 70 to 100 cm and 100 to 200 cm) no difference was observed between the methods. Radio-tagged animals were found relatively more frequently in vegetation with median heights in the 40 to 50 cm, 50 to 70 cm and over 200 cm categories ($G = 9.615$, $p < 0.01$; $G = 20.101$, $p < 0.001$ and $G = 15.619$, $p < 0.001$ respectively, with 1 d.f. in each case) than were visually located animals. Visually located snakes were found relatively more often in shorter vegetation (median height less than 20 cm) than were radio-tagged snakes with significant differences being observed at 0 cm ($G = 26.161$ with 1 d.f., $p < 0.001$), 0 to 5 cm ($G = 13.391$ with 1 d.f., $p < 0.001$) and 5 to 10 cm ($G = 10.108$ with 1 d.f., $p < 0.01$).

At Site Two, nine height categories were compared between methods and, overall, a significant difference was observed between height category use by radio-tagged and visually located snakes ($G = 160.644$ with 8 d.f., $p < 0.001$) (Table 5.18 B.). Visually located snakes were found relatively more often in shorter vegetation, with median heights below 15 cm (0 cm and 0 to 5 cm: $G = 45.849$; 5 to 10 cm: $G = 14.394$ and 10 to 15 cm: $G = 23.529$ with 1 d.f. and $p < 0.001$ in all

A. SITE ONE

Height category (cm)	<u>Radio-tagged</u>		<u>Visual locn.</u>		Total	G	p
	Obs.	Exp.	Obs.	Exp.			
0	0	8.5	14	5.5	14	26.161	***
0 to 5	17	29.7	32	19.3	49	13.391	***
5 to 10	9	17.9	20	11.4	29	10.108	**
10 to 15	8	11.5	11	7.5	19	2.619	NS
15 to 20	6	6.7	5	4.3	11	0.184	NS
20 to 30	26	24.9	15	16.1	41	0.125	NS
30 to 40	19	15.2	6	9.8	25	2.592	NS
40 to 50	19	12.7	2	8.3	21	9.615	**
50 to 60	14)-	12.1	0)-	7.9	14)-	20.101	***
60 to 70	6)		0)		6)		
70 to 80	1)-	5.5	2)-	3.5	3)-	0.115	NS
80 to 90	4)		2)		6)		
90 to 100	0)		0)		0)		
100 to 150	11)-	13.3	4)-	8.6	15)-	1.594	NS
150 to 200	5)		2)		7)		
Over 200	43	30.3	7	19.7	50	15.619	***
Totals	188	188.3	122	121.9	310	102.224	***

B. SITE TWO

Height category (cm)	<u>Radio-tagged</u>		<u>Visual locn.</u>		Total	G	p
	Obs.	Exp.	Obs.	Exp.			
0	0)-	40.4	8)-	10.6	8)-	45.849	***
0 to 5	18)		25)		43)		
5 to 10	25	36.5	21	9.5	46	14.394	***
10 to 15	28	44.4	28	11.6	56	23.529	***
15 to 20	39	38.8	10	10.2	49	0.005	NS
20 to 30	72	59.4	3	15.6	75	17.810	***
30 to 40	97	77.7	1	20.3	98	37.019	***
40 to 50	54	44.4	2	11.6	56	14.109	***
50 to 60	27)-	42.8	0)-	11.2	27)-	7.312	**
60 to 70	12)		0)		12)		
70 to 80	7)		1)		8)		
80 to 90	2)		2)		4)		
90 to 100	2)		1)		3)		
100 to 150	8)-	16.6	2)-	4.4	10)-	0.617	NS
150 to 200	3)		0)		3)		
Over 200	7)		1)		8)		
Totals	401	401.0	105	105.0	506	160.644	***

Tables 5.18 A. and B. : Observed (Obs.) and expected (Exp.) frequencies of observations of radio-tagged and visually located C. austriaca in each median height category at Sites One and Two. G-test statistics (G) and their significance levels (p) are presented (NS= $p > 0.05$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$). Expected frequencies are based on a hypothesis of the same pattern of habitat category use being shown by each of the two methods. Data are for male and female specimens observed between April 1985 and July 1986 inclusive.

cases) than were radio-tagged snakes. Observations made by radio-tracking were, on the other hand, relatively more frequently in vegetation with median heights between 20 and 100 cm (20 to 30 cm: $G= 17.810$; 30 to 40 cm: $G= 37.019$ and 40 to 50 cm: $G= 14.109$ with 1 d.f. and $p<0.001$ in each case and 50 to 100 cm: $G= 7.312$ with 1 d.f., $p<0.01$). No significant differences were observed between the use of vegetation with median heights in the 15 to 20 cm ($G= 0.005$ with 1 d.f., $p>0.05$) and the 100 to over 200 cm ($G= 0.617$ with 1 d.f., $p>0.05$) categories as indicated by the two methods.

The two methods of observation showed difference in vegetation height category use and, as such, further analysis was restricted to data collected by radio-location only. These latter data were used as they were assumed to be less susceptible to observer bias.

iv. Comparison of vegetation height usage between sexes

Nine categories of vegetation height were created by pooling data such that adequate sample sizes could be obtained for statistical analysis and these were used in the comparison of height category usage between radio-tagged males and females at Site One (Table 5.19 A.). Overall a significant difference in height category use was observed between the sexes ($G= 102.224$ with 8 d.f., $p<0.001$). No difference was observed in four of the combined height categories (namely 0 cm and 0 to 5 cm ($G= 0.319$), 20 to 30 cm ($G= 2.196$), 40 to 50 cm ($G= 1.953$) and 50 to 100 cm ($G= 0.144$) (all G values with 1 d.f., and $p>0.05$)). Females were radio-located relatively more frequently than males in the shorter (5 to 10 cm ($G= 6.70$ with 1 d.f., $p<0.01$) and 10 to 20 cm ($G= 4.702$ with 1 d.f., $p<0.05$)) and intermediate (30 to 40 cm ($G= 8.333$ with 1 d.f., $p<0.01$) height vegetation, whilst males were found relatively more often than females in quadrats with median height in excess of 100 cm (100 to 150 cm: $G= 7.796$ and over 200 cm: $G= 7.923$, with 1.d.f. and $p<0.01$ in both cases).

A. SITE ONE

Height category (cm)	. Males .		. Females .		Total	G	p
	Obs.	Exp.	Obs.	Exp.			
0	0)-	10.9	0)-	6.1	0)-	0.319	NS
0 to 5	12)		5)		17)		
5 to 10	2	5.8	7	3.2	9	6.700	**
10 to 15	1)-	9.0	7)-	5.0	8)-	4.702	*
15 to 20	4)		2)		6)		
20 to 30	13	16.7	13	9.3	26	2.196	NS
30 to 40	6	12.2	13	6.8	19	8.333	**
40 to 50	15	12.2	4	6.8	19	1.953	NS
50 to 60	7)-	16.1	7)-	8.9	14)-	0.144	NS
60 to 70	5)		1)		6)		
70 to 80	1)		0)		1)		
80 to 90	4)		0)		4)		
90 to 100	0)		0)		0)		
100 to 150	11)-	10.3	0)-	5.7	11)-	7.796	**
150 to 200	4)		1)		5)		
Over 200	36	27.7	7	15.3	43	7.923	**
Totals	121	120.9	67	67.1	188	40.066	***

B. SITE TWO

Height category (cm)	. Males .		. Females .		Total	G	p
	Obs.	Exp.	Obs.	Exp.			
0	0)-	12.6	0)-	5.4	0)-	10.261	**
0 to 5	6)		12)		18)		
5 to 10	7	17.5	18	7.5	25	18.689	***
10 to 15	17	19.6	11	8.4	28	1.094	NS
15 to 20	21	27.3	18	11.7	39	4.489	*
20 to 30	64	50.5	8	21.5	72	14.507	***
30 to 40	82	68.0	15	29.0	97	10.925	***
40 to 50	50	37.8	4	16.2	54	16.782	***
50 to 60	17	18.9	10	8.1	27	0.612	NS
60 to 70	1)-	16.1	11)-	6.9	12)-	12.106	***
70 to 80	5)		2)		7)		
80 to 90	1)		1)		2)		
90 to 100	1)		1)		2)		
100 to 150	1)-	12.6	7)-	5.4	8)-	3.138	NS
150 to 200	2)		1)		3)		
Over 200	6)		1)		7)		
Totals	281	280.9	120	120.1	401	92.603	***

Tables 5.19 A. and B. : Observed (Obs.) and expected (Exp.) frequencies of observations of male and female C. austriaca in each median height category at Sites One and Two. G-test statistics (G) and their significance levels (p) are presented (NS= $p > 0.05$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$). Expected frequencies are based on a hypothesis of each height category being used to the same degree by each sex. Data are for radio-tagged specimens observed between April 1985 and July 1986 inclusive.

At Site Two combining data created 10 vegetation height categories (Table 5.19 B.). A significant difference in the use of these categories was observed between the sexes ($G=92.603$ with 9 d.f., $p<0.001$). Females were found relatively more often than males in the shorter vegetation (0 cm and 0 to 5 cm ($G=10.261$ with 1 d.f., $p<0.01$) and 5 to 10 cm ($G=18.689$ with 1 d.f., $p<0.001$) and in vegetation between 15 and 20 cm ($G=4.489$ with 1 d.f., $p<0.05$). No difference was, however, observed between the sexes in the use of vegetation with median heights between 10 and 15 cm ($G=1.094$ with 1 d.f., $p>0.05$). Quadrats with median height between 20 and 50 cm were used proportionally more often by males than females (20 to 30 cm: $G=14.507$. 30 to 40 cm: $G=10.925$ and 40 to 50 cm: $G=16.782$ with 1 d.f. and $p<0.001$ in each case). No difference was observed in the relative frequency of sightings of males and females in quadrats with median heights between 50 and 60 cm ($G=0.612$ with 1 d.f., $p>0.05$) or above 100 cm (100 cm to over 200 cm: $G=3.138$ with 1 d.f., $p>0.05$). Females were radio-located relatively more frequently than males in quadrats with median heights between 60 cm and 100 cm (60 to 100 cm: $G=12.106$ with 1 d.f., $p<0.001$).

There was, therefore, no clear or consistent pattern of vegetation height category use by either of the sexes at the two sites. However, as a difference in vegetation use was detected between the males and females at each site, data for the two sexes were kept separate in further analysis.

v. Comparison of vegetation height usage to abundance in the habitat (median heights)

The observed number of radio-locations in each vegetation height category are presented (separately for each sex), together with expected frequencies based upon the relative abundance recorded in 100 random quadrats, for each of Sites One and Two in Tables 5.20 A. and B. respectively. Five median height categories were compared between

A. SITE ONE

Height category	Males				Females			
	Obs.	Exp.	G	p	Obs.	Exp.	G	p
0	0)	25.4	10.600	**	0)	14.1	9.315	**
0 to 5	12)				5)			
5 to 10	2)	9.6	0.838	NS	7)	5.4	15.497	***
10 to 15	1)				7)			
15 to 20	4)				2)			
20 to 30	13)	10.9	36.383	***	13)	6.1	58.699	***
30 to 40	6)				13)			
40 to 50	15)				4)			
50 to 60	7)	4.8	19.925	***	7)	2.7	7.228	**
60 to 70	5)				1)			
70 to 80	1)				0)			
80 to 90	4)				0)			
90 to 100	0)				0)			
100 to 150	11)	70.2	12.293	***	0)	38.9	62.224	***
150 to 200	4)				1)			
Over 200	36)				7)			
Totals	121	120.9	65.343	***	67	67.2	112.039	***

B. SITE TWO

Height category	Males				Females			
	Obs.	Exp.	G	p	Obs.	Exp.	G	p
0	0)	67.5	110.179	***	0)	28.8	15.509	***
0 to 5	6)				12)			
5 to 10	7	33.7	34.182	***	18)	14.4	0.957	NS
10 to 15	17	61.8	54.306	***	11	26.4	13.945	***
15 to 20	21	28.1	2.165	NS	18	12.0	2.936	NS
20 to 30	64	45.0	8.657	**	8	19.2	9.595	**
30 to 40	82	5.6	310.850	***	15)	6.0	19.344	***
40 to 50	50	8.4	101.878	***	4)			
50 to 60	17)	19.7	1.982	NS	10)	8.4	43.785	***
60 to 70	1)				11)			
70 to 80	5)				2)			
80 to 90	1)				1)			
90 to 100	1)				1)			
100 to 150	1)				7)			
150 to 200	2)	11.2	1.054	NS	1)	4.8	2.166	NS
Over 200	6)				1)			
Totals	281	281.0	565.514	***	120	120.0	94.215	***

Tables 5.20 A. and B. : Observed (Obs.) and expected (Exp.) frequencies of observations of male and female C. austriaca in each median height category at Sites One and Two. G-test statistics (G) and their significance levels (p) are presented (NS= $p > 0.05$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$). Expected frequencies are based upon a hypothesis of use of each category being in direct proportion to its availability in the environment (based on random quadrats). Data are for radio-tagged specimens observed between April 1985 and July 1986 inclusive.

observed usage and the relative abundance in the field for radio-tagged males at Site One (Table 5.20 A.). Overall there was a difference between the observed and expected use of these height categories ($G= 65.343$ with 4 d.f., $p<0.001$). In four height categories significant variation between observed and expected frequencies was found. Radio-tagged male C. austriaca were found more frequently in vegetation with a median height between 20 and 50 cm ($G= 36.383$ with 1 d.f., $p<0.001$) and between 50 and 100 cm ($G= 19.925$ with 1 d.f., $p<0.001$), but less in vegetation with median heights between 0 cm and 5 cm ($G= 10.600$ with 1 d.f., $p<0.01$) and in excess of 100 cm (100 to over 200 cm: $G= 12.293$ with 1 d.f., $p<0.001$), than would have been expected from the relative abundance in the environment. No significant difference was observed between the observed and expected frequencies for quadrats with median heights between 5 and 20 cm.

Female snakes at Site One showed a significantly different use of height categories compared to the relative abundance in the habitat ($G= 112.039$ with 4 d.f., $p<0.001$) (see Table 5.20 A.). In all five height categories, significant deviations from the expected frequency were observed. Quadrats with median height of less than 5 cm (0 cm and 0 to 5 cm combined) and those with medians above 100 cm (100 to over 200 cm) were used less frequently by radio-tagged female smooth snakes ($G= 9.315$ with 1 d.f., $p<0.01$ and $G= 62.224$ with 1 d.f., $p<0.001$ respectively) than 'expected'. The three height categories between 5 cm and 100 cm were used more often than would have been predicted on the basis of their relative abundance (5 to 20 cm: $G= 15.497$, $p<0.001$; 20 to 50 cm: $G= 58.699$, $p<0.001$ and 50 to 100 cm: $G= 7.228$, $p<0.01$ with 1 d.f. in each case).

At Site Two nine height categories were created for radio-tagged male C. austriaca and the observed usage of these was compared against the abundance of each in the field (see Table 5.20 B.). Overall a highly significant deviation from expected height category use was observed ($G= 565.514$ with 8 d.f., $p<0.001$). In three height categories (namely

15 to 20 cm, 50 to 150 cm and 150 to over 200 cm) the relative frequencies of usage were in proportion to the abundance as revealed from the 100 random quadrats ($G=2.165$, 1.982 and 1.054 respectively with 1 d.f. and $p>0.05$ in each case). Vegetation with median heights between 0 and 5cm, 5 and 10 cm and 10 and 15 cm were used much less frequently than would have been expected for the given abundance at Site Two ($G=110.179$, 34.182 and 54.306 respectively with 1 d.f. and $p<0.001$ in each case). Quadrats with median vegetation heights of 20 to 30 cm, 30 to 40 cm and 40 to 50 cm were used more frequently than expected on the grounds of relative abundance ($G=8.657$, $p<0.01$; $G=310.850$, $p<0.001$ and $G=101.878$, $p<0.001$ respectively with 1 d.f. in each case).

Eight height categories were used for radio-tagged females at Site Two (see Table 5.20 B.). Overall there was a significant deviation from the expected frequencies of use in the median height categories ($G=94.215$ with 7 d.f., $p<0.001$). In three cases, namely 0 to 5 cm, 10 to 15 cm and 20 to 30 cm, observed use was less than would have been expected for their abundance at the site ($G=15.509$, $p<0.001$; $G=13.945$, $p<0.001$ and $G=9.593$, $p<0.01$ with 1 d.f. in each case). A greater number of the quadrats occupied by female snakes had median heights between 30 and 50 cm ($G=19.344$ with 1 d.f., $p<0.001$) and 50 and 150 cm ($G=43.785$ with 1 d.f., $p<0.001$) than would have been expected. A further three height classes were used by females in proportion to their relative abundance at Site Two, namely 5 to 10 cm, 15 to 20 cm and 150 to over 200 cm ($G=0.957$, 2.936 and 2.166 respectively, with 1 d.f. and $p>0.05$ in each case).

vi. Comparison of median vegetation height category use between seasons

The number (and percentage) of observations of median vegetation heights recorded in association with male and female smooth snakes at Site One are presented in Tables 5.21 A. and B. respectively and for males and females at

SITE ONE

A. Males

Height category (cm)	<u>Spring</u>		<u>Summer</u>		<u>Autumn</u>	
	n	%	n	%	n	%
0	0	0.0	0	0.0	0	0.0
0 to 5	0	0.0	11	30.6	1	1.2
5 to 10	0	0.0	1	2.8	1	1.2
10 to 15	0	0.0	0	0.0	1	1.2
15 to 20	0	0.0	0	0.0	4	4.7
20 to 30	0	0.0	0	0.0	13	15.3
30 to 40	0	0.0	0	0.0	6	7.1
40 to 50	0	0.0	4	11.1	11	12.9
50 to 60	0	0.0	2	5.6	5	5.9
60 to 70	0	0.0	2	5.6	3	3.5
70 to 80	0	0.0	0	0.0	1	1.2
80 to 90	0	0.0	2	5.6	2	2.4
90 to 100	0	0.0	0	0.0	0	0.0
100 to 150	0	0.0	9	25.0	2	2.4
150 to 200	0	0.0	0	0.0	4	4.7
Over 200	0	0.0	5	13.9	31	36.5
Totals	0	0.0	36	100.2	85	100.2

B. Females

Height category (cm)	<u>Spring</u>		<u>Summer</u>		<u>Autumn</u>	
	n	%	n	%	n	%
0	0	0.0	0	0.0	0	0.0
0 to 5	0	0.0	5	7.5	0	0.0
5 to 10	0	0.0	7	10.4	0	0.0
10 to 15	0	0.0	7	10.4	0	0.0
15 to 20	0	0.0	2	3.0	0	0.0
20 to 30	0	0.0	13	19.4	0	0.0
30 to 40	0	0.0	13	19.4	0	0.0
40 to 50	0	0.0	4	6.0	0	0.0
50 to 60	0	0.0	7	10.4	0	0.0
60 to 70	0	0.0	1	1.5	0	0.0
70 to 80	0	0.0	0	0.0	0	0.0
80 to 90	0	0.0	0	0.0	0	0.0
90 to 100	0	0.0	0	0.0	0	0.0
100 to 150	0	0.0	0	0.0	0	0.0
150 to 200	0	0.0	1	1.5	0	0.0
Over 200	0	0.0	7	10.4	0	0.0
Totals	0	0.0	67	99.9	0	0.0

Tables 5.21 A. and B. : Frequencies (n) and percentage frequencies (%) of usage of the sixteen median vegetation height categories by radio-tagged male and female C. austriaca at Site One. Data were collected between April 1985 and July 1986 inclusive.

Site Two in Tables 5.22 A. and B. respectively. Due to the small sample sizes encountered in each height category, comparisons between vegetation height category usage between seasons was undertaken using the Spearman's rank correlation coefficient.

No vegetation height data were recorded at Site One for either male or female snakes during Spring or for female snakes during Autumn. As such, comparisons were limited to observations of males made in Summer and Autumn. No significant correlation was observed between height category use by males in Summer and that observed in Autumn ($r_s = 0.201$, $n = 16$, $p > 0.05$). Median vegetation heights associated with males at Site One were most commonly between 0 and 5 cm during Summer (30.6% of radio-locations) with the next most frequently encountered median heights being 100 to 150 cm (25.0% of locations), over 200 cm (13.9%) and 40 to 50 cm (11.1%) during this season (Table 5.21 A.). During Autumn, the most commonly observed median height category associated with male snakes at Site One was over 200 cm (36.5% of radio-locations) with 20 to 30 cm (15.3%), 40 to 50 cm (12.9%) and 30 to 40 cm (7.1%) representing the next most frequently encountered categories.

Female C. austriaca at Site One were most often found in quadrats with median vegetation heights between 20 and 30 cm and 30 and 40 cm (each representing 19.4% of the locations) during the Summer (Table 5.21 B.). Quadrats with median heights between 5 and 10 cm, 10 and 15 cm, 50 and 60 cm and over 200 cm were also commonly found in association with females at Site One (these categories each representing 10.4% of the radio-locations). No observations were made of females during either Spring or Autumn.

At Site Two, a significant correlation was observed between the use of the different vegetation height categories by male smooth snakes in Spring and Summer ($r_s = 0.567$, $n = 16$, $p < 0.05$), but not between that observed in Spring and Autumn ($r_s = 0.359$, $n = 16$, $p > 0.05$) or Summer and Autumn ($r_s = 0.467$,

SITE TWO

A. Males

Height category (cm)	<u>Spring</u>		<u>Summer</u>		<u>Autumn</u>	
	n	%	n	%	n	%
0	0	0.0	0	0.0	0	0.0
0 to 5	4	5.6	1	0.5	1	6.7
5 to 10	0	0.0	6	3.1	1	6.7
10 to 15	6	8.5	9	4.6	2	13.3
15 to 20	1	1.4	18	9.2	2	13.3
20 to 30	23	32.4	39	20.0	2	13.3
30 to 40	31	43.7	50	25.6	1	6.7
40 to 50	4	5.6	45	23.1	1	6.7
50 to 60	0	0.0	17	8.7	0	0.0
60 to 70	0	0.0	1	0.5	0	0.0
70 to 80	0	0.0	3	1.5	2	13.3
80 to 90	1	1.4	0	0.0	0	0.0
90 to 100	0	0.0	0	0.0	1	6.7
100 to 150	0	0.0	0	0.0	1	6.7
150 to 200	1	1.4	1	0.5	0	0.0
Over 200	0	0.0	5	2.6	1	6.7
Totals	71	100.0	195	99.9	15	100.1

B. Females

Height category (cm)	<u>Spring</u>		<u>Summer</u>		<u>Autumn</u>	
	n	%	n	%	n	%
0	0	0.0	0	0.0	0	0.0
0 to 5	0	0.0	9	8.9	3	15.8
5 to 10	0	0.0	13	12.9	5	26.3
10 to 15	0	0.0	9	8.9	2	10.5
15 to 20	0	0.0	13	12.9	5	26.3
20 to 30	0	0.0	8	7.9	0	0.0
30 to 40	0	0.0	15	14.8	0	0.0
40 to 50	0	0.0	4	4.0	0	0.0
50 to 60	0	0.0	8	7.9	2	10.5
60 to 70	0	0.0	9	8.9	2	10.5
70 to 80	0	0.0	2	2.0	0	0.0
80 to 90	0	0.0	1	1.0	0	0.0
90 to 100	0	0.0	1	1.0	0	0.0
100 to 150	0	0.0	7	6.9	0	0.0
150 to 200	0	0.0	1	1.0	0	0.0
Over 200	0	0.0	1	1.0	0	0.0
Totals	0	0.0	101	100.0	19	99.9

Tables 5.22 A. and B. : Frequencies (n) and percentage frequencies (%) of usage of the sixteen median vegetation height categories by radio-tagged male and female C. austriaca at Site Two. Data were collected between June 1985 and July 1986 inclusive.

n= 16, $p>0.05$). Males were found most frequently in association with quadrats with a median height between 30 to 40 cm during the Spring (43.7%) and Summer (25.6%), with the second most frequently encountered height categories being 20 to 30 cm (32.4%) and 40 to 50 cm (23.1%) in Spring and Summer respectively (Table 5.21 A.). In addition, 20.0% of quadrats located during the Summer had median heights between 20 and 30 cm. During the Autumn vegetation with median heights between 10 and 15 cm, 15 and 20 cm, 20 and 30 cm and 70 and 80 cm were occupied most commonly (13.3% of sightings in each case). The small sample size in this latter season, however, may not truly reflect the correct distribution within the height categories and therefore these data should be treated with caution.

A significant correlation was observed between the rank orders of vegetation height usage during Summer and Autumn by female C. austriaca at Site Two ($r_s = 0.693$, $n = 16$, $p < 0.01$) (Table 5.21 B.). No data were collected for vegetation height use by females at Site Two during Spring. In Summer the most commonly occupied vegetation height category by radio-tagged females was 30 to 40 cm (14.8% of locations) with 5 to 10 cm and 15 to 20 cm being used next most often (12.9% of locations in each case). During the Autumn the most commonly occurring height categories associated with females at Site Two were 5 to 10 cm and 15 to 20 cm (each representing 26.3% of observations) and 0 to 5 cm was the next most common height category (15.8%). However, only a small sample size was obtained during this latter season and, as such, these observations should be treated with caution.

vii. Comparison of vegetation height usage between day and night

Median vegetation heights associated with radio-located snakes were subdivided into those observations that were collected during 'day-time' and those collected 'over-night' (see 5.3.2. a. vii. for details). The number of observations in each median height class for 'day-time' and

'over-night' vegetation use are presented separately for male and female snakes in Tables 5.23 A. and B. for Sites One and Two respectively. A total of 22 median values for over-night vegetation heights were recorded for males at Site One, 11 for females at Site One, 44 for males at Site Two and 17 for females at Site Two. The respective numbers of 'day-time' median height records were 99, 56, 237 and 103.

With the exception of females at Site Two, a similar pattern of vegetation height category usage was observed during 'day-time' and 'over-night' in each case and significant correlations were obtained between the vegetation use in the two time periods ($r_s = 0.714$, $n = 16$, $p < 0.01$ for males at Site One; $r_s = 0.561$, $n = 16$, $p < 0.05$ for females at Site One and $r_s = 0.552$, $n = 16$, $p < 0.05$ for males at Site Two). The most commonly encountered height category for male snakes at Site One was 'over 200 cm' during both day and night. Female snakes were radio-located at Site One most frequently in association with vegetation that had a median height of 20 to 30 cm and 30 to 40 cm during the day, and these categories were two of the three most frequently encountered 'over-night' vegetation heights. Males at Site Two were most commonly radio-located in vegetation with a median height of 30 to 40 cm during the day and over-night with the two adjacent categories (20 to 30 cm and 40 to 50 cm) being used second and third most frequently during the day and night (although their relative positions were reversed between the time periods).

No significant correlation was observed between vegetation height category use during the day and over-night for females at Site Two ($r_s = 0.476$, $n = 16$, $p > 0.05$). During the day short vegetation (with a median height between 5 and 40 cm) was used most often. Small sample sizes prevent any clear pattern of over-night vegetation use being determined although the most commonly encountered median height category was 60 to 70 cm during this latter time period.

A. SITE ONE

Height category (cm)	<u>. Males .</u>		<u>. Females .</u>	
	Day	Night	Day	Night
0	0	0	0	0
0 to 5	11	1	4	1
5 to 10	2	0	6	1
10 to 15	1	0	7	0
15 to 20	4	0	1	1
20 to 30	11	2	11	2
30 to 40	4	2	11	2
40 to 50	13	2	3	1
50 to 60	5	2	5	2
60 to 70	5	0	1	0
70 to 80	1	0	0	0
80 to 90	2	2	0	0
90 to 100	0	0	0	0
100 to 150	9	2	0	0
150 to 200	3	1	0	1
Over 200	28	8	7	0
Totals	99	22	56	11

B. SITE TWO

Height category (cm)	<u>. Males .</u>		<u>. Females .</u>	
	Day	Night	Day	Night
0	0	0	0	0
0 to 5	5	1	9	3
5 to 10	7	0	16	2
10 to 15	17	0	10	1
15 to 20	20	1	18	0
20 to 30	58	6	8	0
30 to 40	66	16	13	2
40 to 50	38	12	3	1
50 to 60	15	2	9	1
60 to 70	0	1	7	4
70 to 80	3	2	1	1
80 to 90	0	1	1	0
90 to 100	1	0	1	0
100 to 150	1	0	5	2
150 to 200	1	1	1	0
Over 200	5	1	1	0
Totals	237	44	103	17

Tables 5.23 A. and B. : Day-time (Day) and over-night (Night) frequencies of usage of the sixteen median vegetation height categories by radio-tagged male and female C. austriaca at Sites One and Two. Data were collected between April 1985 and July 1986 inclusive.

d. Abundance of smooth snakes in different vegetation communities

Three study sites were used (Sites Four, Nine and Ten) at which eight, seven and six vegetation categories respectively were defined. A total of 24 visits were made to Site Four (between 15th April and 9th October 1986), nine visits to Site Nine (between 25th April and 2nd October 1986) and eight visits to Site Ten (between 25th April and 9th September 1986). The plant species composition and mean heights of each category are described in Tables 5.24, 5.25 and 5.26 for the three sites respectively.

All reptilian species observed in each vegetation category at each site were recorded. The total numbers of each species observed throughout the study period are presented in Tables 5.27, 5.28 and 5.29 for Sites Four, Nine and Ten respectively. Observations of animals on or below the tins (T.) were recorded separately from those that were made on the transects between the tins (B.). Two specimens of C. austriaca were recorded at Site Four, these being a female snake below tin in mature/ degenerate dry heath (on 18th July 1986) and a male specimen between tin sheeting in mature wet/ humid heathland (on 28th August 1986). No smooth snakes were observed at either Site Nine or Site Ten.

No other snake species were observed on the transects at any of the three sites during the study period and only small numbers of lizards were recorded. At Site Four two L. vivipara were observed, one each in mature/ degenerate dry heath and mature dry/ humid heath. Nine observations of L. vivipara were made at Site Nine with three each in wet bog, mature wet/ humid heath and bog. Seven records of A. fragilis were made at Site Nine; five of these were in mature wet/ humid heath, one in a pine plantation and the other in bog. Six records of L. vivipara and two of A. fragilis were made at Site Ten. The sightings of L. vivipara were equally divided among three vegetation types,

Site number	Vegetation type	% cover (%)	Species composition (%)	Mean height (± 1 s.d.) (cm)	Biomass (dry wt.) (kg/m ²)
IV.	Pioneer humid heath (cut)	92.5	Et=34.5 Mc=30.5 Cv=12.0 Mo=12.0 Ba= 7.5 Li= 2.0 Lh= 1.0 Ju= 0.5	5.8 \pm 3.0	0.8
IV.	Building dry heath	94.5	Cv=89.0 Ba= 5.5 Lh= 3.0 Li= 1.5 Et= 1.0	17.2 \pm 6.0	0.6
IV.	Mature/ degenerate dry heath	98.0	Cv=75.5 Mc=14.0 Et= 6.5 Ba= 2.0 Li= 1.5 Mo= 0.5	39.0 \pm 14.8	1.6
IV.	Mature wet/ humid heath	96.5	Cv=44.5 Mc=30.5 Et=19.0 Ba= 3.5 Mo= 2.0 Pi= 0.5	20.8 \pm 10.1	1.0
IV.	Bracken	100.0	Pa=96.2 Lp= 2.3 Gr= 1.5	20.0 \pm 10.3 *130.0 \pm 32.3	1.6 -
IV.	Burnt dry heath	27.0	Ba=73.0 Mo=11.5 Lh=11.4 Mc= 2.0 Cv= 1.9 Pi= 0.2	2.5 \pm 3.8	0.4
IV.	Mature dry/ humid heath	98.8	Cv=72.0 Mc=21.9 Et= 4.1 Ba= 1.2 Mo= 0.8	26.5 \pm 9.3	1.3
IV.	Pioneer dry/ humid heath (burnt)	60.5	Ba=39.5 Cv=32.7 Mc=14.5 Et= 4.8 As= 2.5 Um= 1.0	3.5 \pm 3.2	0.4

Table 5.24 : Vegetation types and their species composition, mean heights and biomass (kg/m²) as defined for the comparative habitat use experiment at Site Four. Measurements are means of ten 0.25m² quadrats (five height measurements in each) except for biomass, where four 0.25 m² quadrats were sampled. Measurements were made in May 1986 except * where measurements were made in August 1986.

KEY

Ba: Bare ground, Et: Erica tetralix, Cv: Calluna vulgaris, Mo: Moss spp., Li: Lichen spp., Mc: Molinia caerulea, Ju: Juncus sp., Lh: Heather litter, Pi: Pinus sp., Pa: Pteridium aquilinum, Lp: Bracken litter, Gr: Grass sp., As: Agrostis setacea, Um: Ulex minor.

Site number	Vegetation type	% cover (%)	Species composition (%)	Typical height range (cm)
IX.	Pioneer humid heath	90.0	Cv=45.0 Et=20.0 Mc=15.0 Mo=10.0 Ba=10.0	0.0 to 15.0
IX.	Mature dry/humid heath	100.0	Cv=90.0 Mc= 5.0 Pa= 5.0	20.0 to 80.0
IX.	Wet bog	100.0	Ju=35.0 Mc=30.0 Mg=10.0 Et= 5.0 He= 5.0 Me= 5.0 Sp= 5.0 No= 5.0	10.0 to 50.0
IX.	Pine	100.0	Pi=30.0 Cv=25.0 Pa=25.0 Mc=10.0	Ground: 20.0 to 100.0 Trees: 200.0 to 400.0
IX.	Mature wet/humid heath	100.0	Mc=40.0 Et=35.0 Re=20.0 Cv=10.0	15.0 to 40.0
IX.	Bog	100.0	Mg=70.0 Mc=15.0 Ju=10.0 Cv= 3.0 Et= 2.0	20.0 to 80.0
IX.	Mature dry/humid heath	100.0	Cv=65.0 Et=20.0 Mc=10.0 Pa= 5.0	20.0 to 50.0

Table 5.25 : Vegetation types and their species composition (%) and typical range of heights (cm) as defined for the comparative habitat use experiment at Site Nine. Percentage cover was estimated by eye and 'typical' heights are representative of the minimum and maximum of the majority of vegetation cover. Estimates of the vegetation cover were made in August 1986.

KEY

Cv: Calluna vulgaris, Et: Erica tetralix, Mc: Molinia caerulea, Mo: Moss sp., Ba: Bare ground, Pa: Pteridium aquilinum, Ju: Juncus sp., Mg: Myrica gale, He: Hypericum elodes, Me: Menyanthes sp., Sp: Sphagnum sp., No: Narthecium ossifragum, Pi: Pinus sp., Re: Reed sp.,

Site number	Vegetation type	% cover (%)	Species composition (%)	Typical height range (cm)
X.	Mature dry heath	100.0	Cv=80.0 Mc=10.0 Ec= 5.0 Pa= 5.0	40.0 to 80.0
X.	Mature wet heath	97.0	Et=40.0 Cv=25.0 Mc=10.0 Ju=10.0 Mg= 5.0 Sp= 3.0 Ba= 3.0 Li= 2.0 Pi= 2.0	5.0 to 60.0
X.	Burnt dry heath	95.0	Pa=85.0 Lh=10.0 Ba= 5.0	10.0 to 40.0
X.	Cut dry/ humid heath	100.0	Pa=90.0 Cv= 8.0 Mc= 2.0	20.0 to 90.0
X.	Bracken	100.0	Pa=95.0 Gr= 5.0	70.0 to 180.0
X.	Pine/ wet heath	100.0	Mc=40.0 Cv=30.0 Et=18.0 Pi= 5.0 Ju= 5.0	Ground: 20.0 to 60.0 Trees: 300.0 to 500.0

Table 5.26 : Vegetation types and their species composition (%) and typical range of heights (cm) as defined for the comparative habitat use experiment at Site Ten. Percentage cover was estimated by eye and 'typical' heights are representative of the minimum and maximum height of the majority of vegetation cover. Estimates of vegetation cover were made in September 1986.

KEY

Cv: Calluna vulgaris, Mc: Molinia caerulea, Ec: Erica cinerea, Pa: Pteridium aquilinum, Et: Erica cinerea, Ju: Juncus sp., Mg: Myrica gale, Sp: Sphagnum sp., Ba: Bare ground, Li: Lichen spp., Pi: Pinus sp., Lh: Heather litter, Gr: Grass sp.

Vegetation type	<u>Coronella</u> <u>austriaca</u>	<u>Vipera</u> <u>berus</u>	<u>Natrix</u> <u>natrix</u>	<u>Lacerta</u> <u>vivipara</u>	<u>Anguis</u> <u>fragilis</u>
	<u>T.</u> <u>B.</u>	<u>T.</u> <u>B.</u>	<u>T.</u> <u>B.</u>	<u>T.</u> <u>B.</u>	<u>T.</u> <u>B.</u>
<u>Site Four</u>					
Pioneer humid heath (cut)	:	:	:	:	:
Building dry heath	:	:	:	:	:
Mature/ degenerate dry heath	1(f)	:	:	1	:
Mature wet/ humid heath	:	1(m)	:	:	:
Bracken	:	:	:	:	:
Burnt dry heath	:	:	:	:	:
Mature dry/ humid heath	:	:	:	1	:
Pioneer dry/ humid heath (burnt)	:	:	:	:	:

Table 5.27 : Number of observations of each reptile species in the eight defined vegetation types at Site Four on or below tin sheeting (T.) and on transects between tin sheeting (B.). The sex of specimens of C. austriaca observed are given (m= male, f= female). Data were collected between 15th April and 9th October 1986 inclusive from a total of 28 visits to the site. Four tins were placed in each vegetation type until 24th May, five tins until 31st July and thereafter six tins were placed in each vegetation type.

Vegetation type	<u>Coronella</u>		<u>Vipera</u>		<u>Natrix</u>		<u>Lacerta</u>		<u>Anquis</u>	
	<u>austriaca</u>		<u>berus</u>		<u>natrix</u>		<u>vivipara</u>		<u>fragilis</u>	
	<u>T.</u>	<u>B.</u>	<u>T.</u>	<u>B.</u>	<u>T.</u>	<u>B.</u>	<u>T.</u>	<u>B.</u>	<u>T.</u>	<u>B.</u>

Site Nine

Pioneer humid heath	:	:	:	:	:	:	:	:	:	:
Mature dry/ humid heath	:	:	:	:	:	:	:	:	:	:
Wet bog	:	:	:	:	:	3	:	:	:	:
Fine	:	:	:	:	:	:	:	1	:	:
Mature wet/ humid heath	:	:	:	:	:	3	:	5	:	:
Bog	:	:	:	:	:	:	3	1	:	:
Mature dry/ humid heath	:	:	:	:	:	:	:	:	:	:

Table 5.28 : Number of observations of each reptile species in the seven defined vegetation types at Site Nine. on or below tin sheeting (T.) and transects between tin sheeting (B.). Data were collected between 25th April and 2nd October 1986 inclusive in a total of nine visits to the site. Six tins were placed in each vegetation type throughout the sampling period.

Vegetation type	<u>Coronella</u>		<u>Vipera</u>		<u>Natrix</u>		<u>Lacerta</u>		<u>Anquis</u>	
	<u>austriaca</u>		<u>berus</u>		<u>natrix</u>		<u>vivipara</u>		<u>fragilis</u>	
	<u>T.</u>	<u>B.</u>	<u>T.</u>	<u>B.</u>	<u>T.</u>	<u>B.</u>	<u>T.</u>	<u>B.</u>	<u>T.</u>	<u>B.</u>

Site Ten

Mature dry heath	:	:	:	:	:	2	:	1	:	:
Mature wet heath	:	:	:	:	:	2	:	:	:	:
Burnt dry heath	:	:	:	:	:	:	:	:	:	:
Cut dry/ humid heath	:	:	:	:	:	:	:	:	:	:
Bracken	:	:	:	:	:	:	:	:	:	:
Pine/ wet heath	:	:	:	:	:	1	1	1	:	:
.	:	:	:	:	:	:	:	:	:	:

Table 5.29 : Number of observations of each reptile species in the six defined vegetation types at Site Ten on or below tin sheeting (T.) and on transects between tin sheeting (B.). Data were collected between 25th April and 9th September 1986 inclusive from a total of eight visits to the site. Six tins were placed in each vegetation type until 18th July and thereafter seven tin were placed in each vegetation type.

with two sightings in each of mature dry heath, mature wet heath and pine/ wet heath. A. fragilis was recorded in mature dry heath and pine/ wet heath (with a single sighting in each) at Site Ten.

The number of observations of C. austriaca or either of the lizard species in the different vegetation categories at any of the sites was deemed too small for statistical analysis.

e. Vegetation use demonstrated by selection of 'vegetation type' in laboratory video recording experiment

The proportion of time spent by specimens of C. austriaca in each of the two defined 'vegetation' types and below cover in the artificial arena during six 4-hourly period and over the whole day (as revealed by video recording) is presented in Fig 5.19. Significantly more time was spent in 'vegetation' than in the 'open' during each of the six periods (0100-0459 hr: $z = 4.79$, $n_1 = 32$, $n_2 = 32$, $p < 0.0001$; 0500-0859 hr: $z = 4.92$, $n_1 = 32$, $n_2 = 32$, $p < 0.0001$; 0900-1259 hr: $z = 6.72$, $n_1 = 28$, $n_2 = 28$, $p < 0.0001$; 0130-1659 hr: $z = 5.40$, $n_1 = 32$, $n_2 = 32$, $p < 0.0001$; 1700-2059 hr: $z = 6.18$, $n_1 = 32$, $n_2 = 32$, $p < 0.0001$; 2100-0059 hr: $z = 4.57$, $n_1 = 32$, $n_2 = 32$, $p < 0.0001$) and over the whole day (whole day: $z = 13.04$, $n_1 = 188$, $n_2 = 188$, $p < 0.0001$).

Significant variations in the use of each vegetation type were observed with time. 'Open' areas were used most during the morning, particularly between 0500-0859 hrs (Kruskal-Wallis chi-squared = 55.91, $n = 188$, $p < 0.0001$). Use of 'vegetation' increased throughout the morning with the greatest proportion of time being spent in this category between 0900-1259 hrs. Use of 'vegetation' decreased progressively throughout the afternoon and evening and was at a minimum between 2100-0059 hrs (Kruskal-Wallis chi-squared = 14.92, $n = 188$, $p < 0.02$). The proportion of time spent below 'cover' was greater during the night than during the day, with a maximum level being observed at 2100-0059 hrs (Kruskal-Wallis chi-squared = 55.91, $n = 188$,

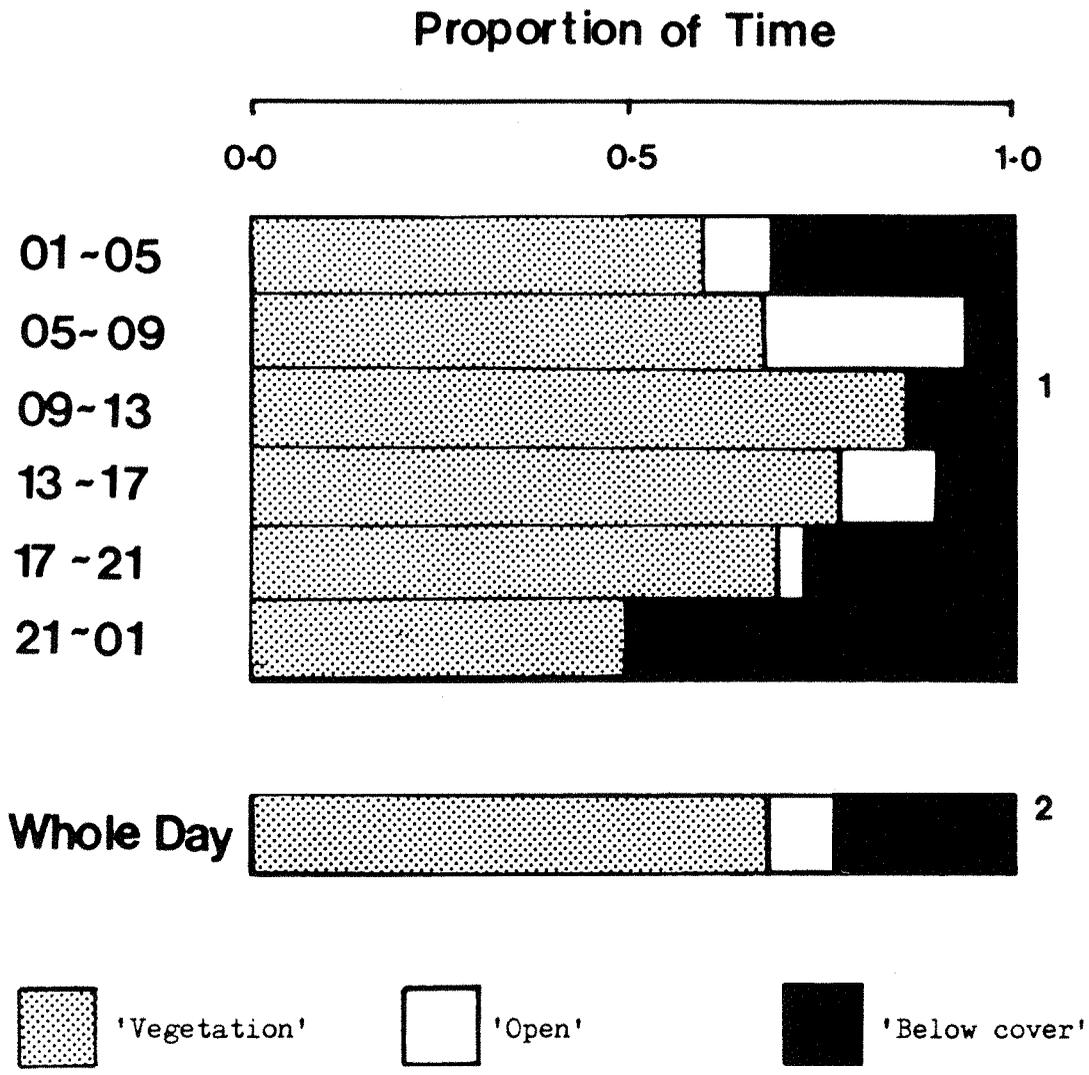


Fig 5.19 : Proportion of time spent in each defined 'vegetation' type and below cover during video observations of C. austriaca for six 4-hour time periods and over the whole day. Two animals were used, each for two days, during July 1986. Each period represents 32 hours of observation except 1 which represents 28 hours of observation and 2 which represents 188 hours of observation.

$p < 0.0001$). The smallest proportion of time spent below 'cover' was in the 0500-0859 hr period.

5.3.3. Distribution of potential prey, predator and competitor species

a. Reptilian and amphibian species

i. General observations

When searching for specimens of C. austriaca, between March 1984 and October 1986, other species of reptiles and amphibians were observed and the locations of these at Sites One and Two were recorded. Such data allowed the relative abundance of each species to be assessed and permitted distribution maps of each species to be plotted. At both Sites One and Two, three species of snake (Coronella austriaca, Vipera berus and Natrix natrix), two species of lizard (Lacerta vivipara and Anguis fragilis) and two species of amphibian (Bufo bufo and Rana temporaria) were observed. No specimens of Lacerta agilis or of any of the newt species were recorded at either site One or Two.

The snakes N. natrix and V. berus were widely distributed over both Site One and Site Two. Of the lizard species, L. vivipara was both common and widespread on both sites. Whilst A. fragilis was found in smaller numbers, it too showed a wide distribution at both study sites, and the lower frequency of sightings probably resulted in part from its secretive behaviour. One specimen of each of R. temporaria and B. bufo were recorded at both Site One and Site Two.

ii. Distribution of reptile species relative to each other (species distribution mapping)

The distribution of each of the reptile species was assessed at each site by recording the presence or absence of each species in 10 m x 10 m grid squares throughout the defined study areas at each site, using observations made

throughout all seasons during all three years of the study period. A total of 3377 such grid squares were incorporated within the study area at Site One and 2169 grid squares formed the study area at Site Two.

Smooth snakes were found in 110 grid squares at Site One and in 186 squares at Site Two. Four other species of reptile were found at each site and the distribution throughout each site and the occurrence of each in relation to squares occupied by C. austriaca is illustrated in Fig. 5.20 and Fig. 5.21 for Sites One and Two respectively. At Site One Vipera berus was recorded in a total of 68 grid squares, in 21 of which C. austriaca had also been recorded. Natrix natrix were recorded in 16 grid squares at Site One of which eight were common with those in which smooth snakes had been observed. One hundred squares at Site One had records of Lacerta vivipara and 29 had records of Anguis fragilis; of these 28 and nine squares respectively also contained sightings of C. austriaca.

At Site Two 17 squares contained records of V. berus and 14 of N. natrix, with smooth snakes occurring in 11 and 10 of these respectively. The lizards L. vivipara and A. fragilis were recorded in 134 and 19 grid squares at Site Two. Of these squares L. vivipara and C. austriaca both observed in 49 and A. fragilis and C. austriaca were both observed in nine.

The total numbers of squares in which both species, the first but not the second species, the second but not the first species and neither species were recorded are presented as 2 x 2 contingency tables for each pair of species at Site One (Table 5.30) and Site Two (Table 5.31). Significant positive associations were observed between C. austriaca and each of the other reptile species at both study sites when all grid squares at each site were included in analysis (at Site One: with V. berus, $G=66.724$; with N. natrix, $G=34.322$; with L. vivipara, $G=83.682$; with A. fragilis, $G=28.482$; at Site Two: with V. berus, $G=32.988$; with N. natrix, $G=33.565$; with L.

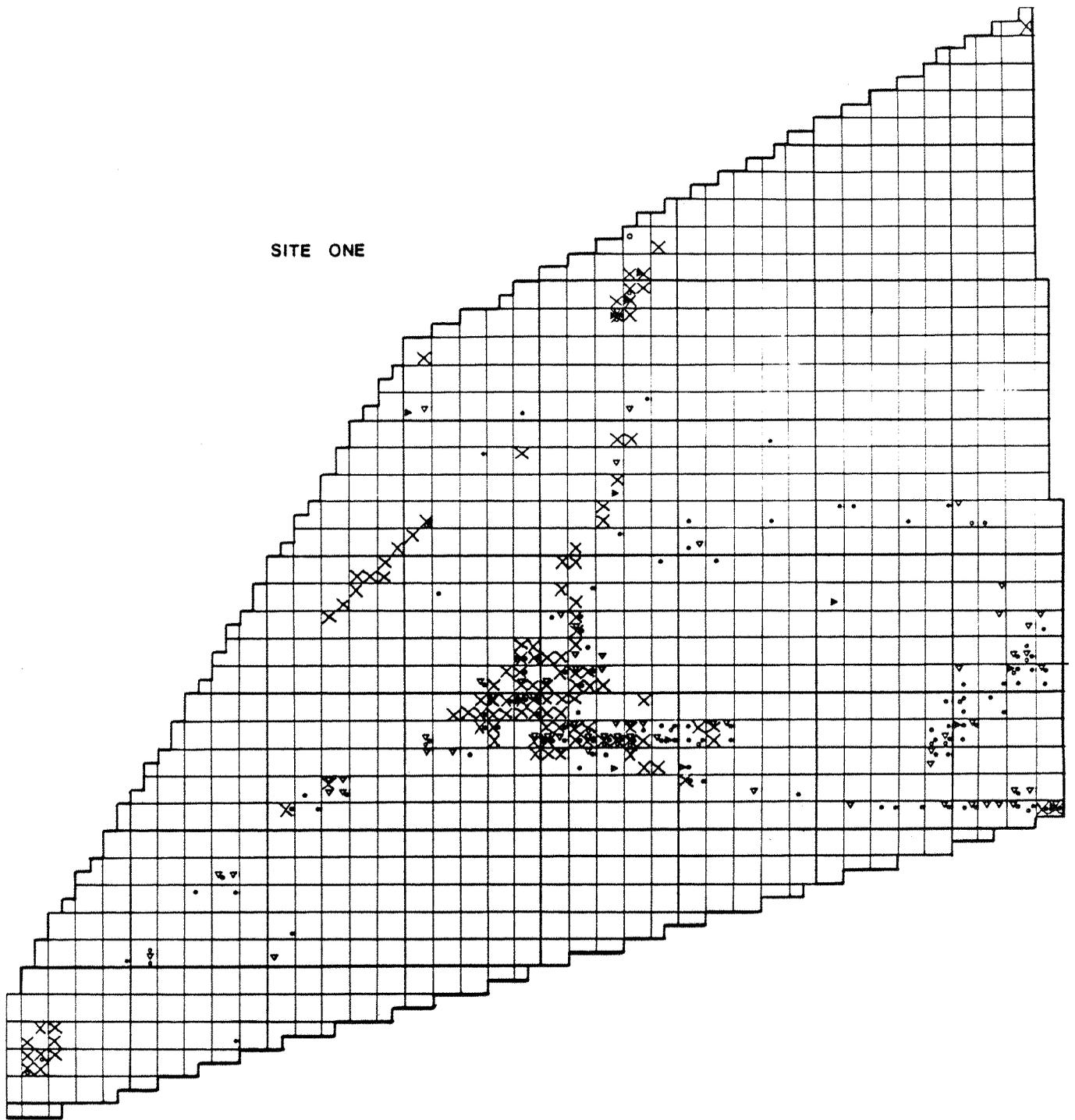
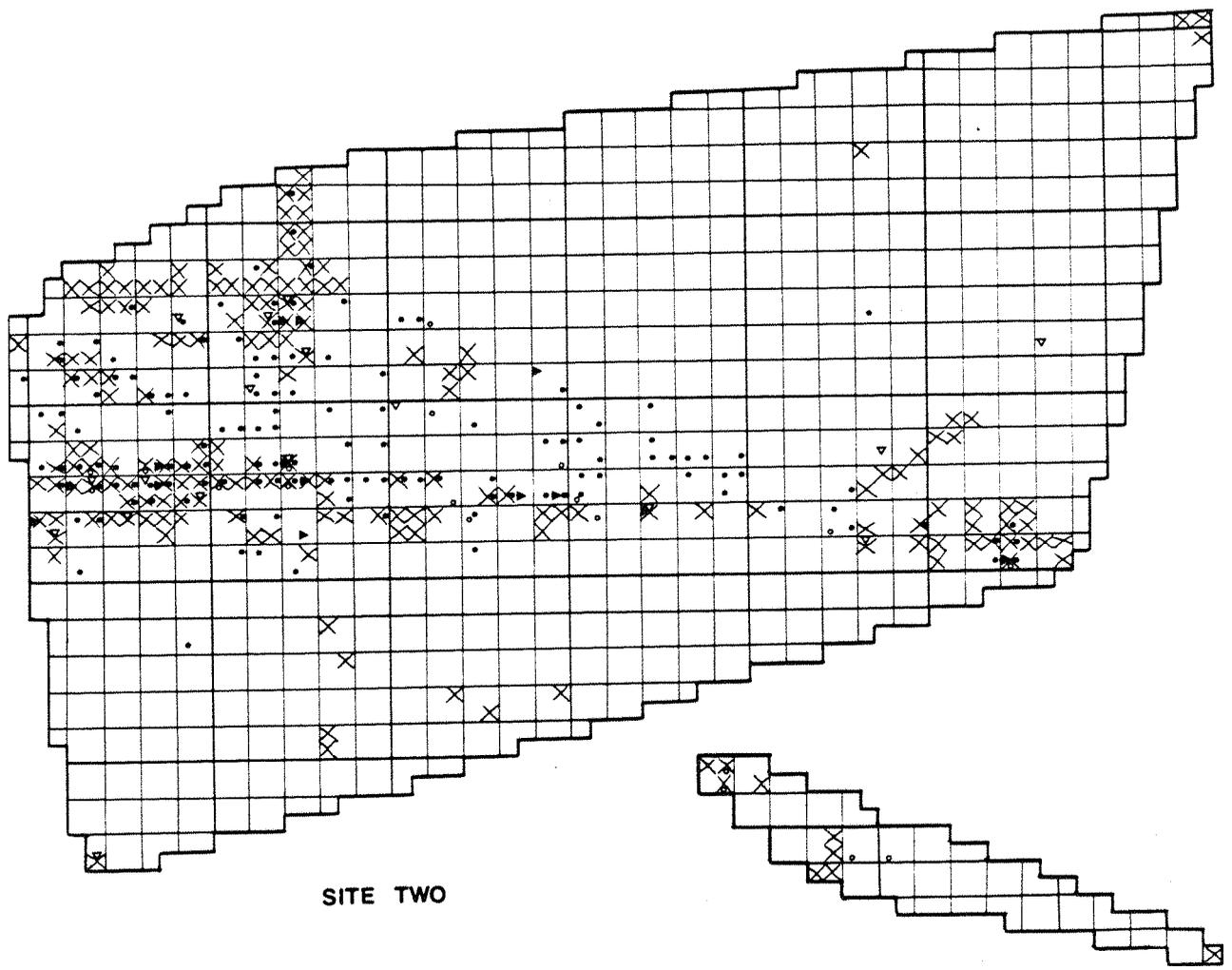


Fig. 5.20 : Distribution of C. austriaca and other reptile species at Site One as recorded on a presence or absence basis using 10 x 10 m grid squares, between March 1984 and October 1986 inclusive. 20 m grid lines (and darker 100 m grid lines) only have been drawn for clarity. One or more sightings of each species in each 10 x 10 m grid square are recorded as follows:

- × (centre of square) : Coronella austriaca
- ▽ (in top quadrant) : Vipera berus
- ▶ (in left quadrant) : Natrix natrix
- (in bottom quadrant) : Anguis fragilis
- (in right quadrant) : Lacerta vivipara



SITE TWO

Fig . 5.21 : Distribution of C. austriaca and other reptile species at Site Two as recorded on a presence or absence basis using 10 x 10 m grid squares, between March 1984 and October 1986 inclusive. 20 m grid lines (and darker 100 m grid lines) only have been drawn for clarity. One or more sightings of each species in each 10 x 10 m grid square are recorded as follows:

- | | |
|------------------------|------------------------------|
| × (centre of square) | : <u>Coronella austriaca</u> |
| ∇ (in top quadrant) | : <u>Vipera berus</u> |
| ▶ (in left quadrant) | : <u>Natrix natrix</u> |
| ◦ (in bottom quadrant) | : <u>Anguis fragilis</u> |
| • (in right quadrant) | : <u>Lacerta vivipara</u> |

SITE ONE - all 10 x 10 m grid squares in site

A. Coronella austriaca and Vipera berus

		<u>C. austriaca</u>		
		+	-	total
	+	21	47	68
<u>V. berus</u>		(2.2)	(65.8)	
	-	89	3220	3309
		(107.8)	(3201.2)	
	total:	110	3267	3377

B. Coronella austriaca and Natrix natrix

		<u>C. austriaca</u>		
		+	-	total
	+	8	8	16
<u>N. natrix</u>		(0.5)	(15.5)	
	-	102	3259	3361
		(109.5)	(3251.5)	
	total:	110	3267	3377

C. Coronella austriaca and Lacerta vivipara

		<u>C. austriaca</u>		
		+	-	total
	+	28	72	100
<u>L. vivipara</u>		(3.3)	(96.7)	
	-	82	3195	3277
		(106.7)	(3170.3)	
	total:	110	3267	3377

D. Coronella austriaca and Anguis fragilis

		<u>C. austriaca</u>		
		+	-	total
	+	9	20	29
<u>A. fragilis</u>		(0.9)	(28.1)	
	-	101	3247	3348
		(109.1)	(3238.9)	
	total:	110	3267	3377

Table 5.30 : 2 x 2 contingency tables recording presence (+) or absence (-) of each or both of C. austriaca and another species of reptile using the total number of squares in the study site as the sample size for A. Vipera berus, B. Natrix natrix, C. Lacerta vivipara and D. Anguis fragilis at Site One. Expected frequencies are given in parentheses.

SITE TWO - all 10 x 10 m grid squares in site

A. Coronella austriaca and Vipera berus

		<u>C. austriaca</u>		
		+	-	total
	:			:
	:			:
<u>V. berus</u>	+	11	6	17
	:	(1.5)	(15.5)	:
	-	175	1977	2152
	:	(184.5)	(1967.5)	:
total:		186	1983	2169

B. Coronella austriaca and Natrix natrix

		<u>C. austriaca</u>		
		+	-	total
	:			:
	:			:
<u>N. natrix</u>	+	10	4	14
	:	(1.2)	(12.8)	:
	-	176	1979	2155
	:	(184.8)	(1970.2)	:
total:		186	1983	2169

C. Coronella austriaca and Lacerta vivipara

		<u>C. austriaca</u>		
		+	-	total
	:			:
	:			:
<u>L. vivipara</u>	+	49	72	134
	:	(11.5)	(122.5)	:
	-	137	1898	2035
	:	(174.5)	(1860.5)	:
total:		186	1983	2169

D. Coronella austriaca and Anguis fragilis

		<u>C. austriaca</u>		
		+	-	total
	:			:
	:			:
<u>A. fragilis</u>	+	9	10	19
	:	(1.6)	(17.4)	:
	-	177	1973	2150
	:	(184.4)	(1965.6)	:
total:		186	1983	2169

Table 5.31 : 2 x 2 contingency tables recording presence (+) or absence (-) of each or both of C. austriaca and another species of reptile using the total number of squares in the study site as the sample size for A. Vipera berus, B. Natrix natrix, C. Lacerta vivipara and D. Anguis fragilis at Site Two. Expected frequencies are given in parentheses.

vivipara, $G = 89.378$; with A. fragilis, $G = 20.341$; with 1 d.f., $p < 0.001$ in each case). Smooth snakes, therefore, occurred in the same areas within the study areas as a whole at Sites One and Two as the other species of reptile, with observations of C. austriaca and each of the other species being observed in the same grid squares more often than expected by chance.

As many of the squares were not occupied by either of the species in a pair, further analysis was performed to assess whether any association was apparent between the pairs of species using a sample area produced from the sum of the total number of squares occupied by each of the two species (i.e. the maximum possible number of squares that could have been occupied by the species, based on field records, if the two species always occurred separately). The results of this analysis are presented as 2 x 2 contingency tables in Tables 5.32 and 5.33 for Sites One and Two respectively. In all cases, at both sites, a negative association was observed between smooth snakes and the other reptile species in each pair (at Site One: with V. berus, $G = 45.334$; with N. natrix, $G = 16.640$; with L. vivipara, $G = 47.326$; with A. fragilis, $G = 43.786$; at Site Two: with V. berus, $G = 11.414$; with N. natrix, $G = 6.506^*$; with L. vivipara, $G = 44.688$; with A. fragilis, $G = 27.771$; with 1 d.f., $p < 0.001$ in each case except * where $p < 0.01$). This indicates that C. austriaca occurred within the same square as the other species in each pair less often than would have been expected for the total number of squares that were occupied by the two species.

b. Mammalian and avian species

i. General observations

Small numbers of mammalian and avian species that were potentially either predatory upon or prey species for C. austriaca were observed at Sites One and Two during the three study seasons. The potential prey species observed were mostly small mammals, and several live and dead

SITE ONE - hypothetical maximum number of 10 x 10 m grid squares that could be occupied

A. Coronella austriaca and Vipera berus

		<u>C. austriaca</u>		
		+	-	total
	+ :	21	47	68
<u>V. berus</u>	:	(42.0)	(26.0)	:
	- :	89	21	110
	:	(68.0)	(42.0)	:
	total:	110	68	178

B. Coronella austriaca and Natrix natrix

		<u>C. austriaca</u>		
		+	-	total
	+ :	8	8	16
<u>N. natrix</u>	:	(14.0)	(2.0)	:
	- :	102	8	110
	:	(96.0)	(14.0)	:
	total:	110	16	126

C. Coronella austriaca and Lacerta vivipara

		<u>C. austriaca</u>		
		+	-	total
	+ :	28	72	100
<u>L. vivipara</u>	:	(52.4)	(47.6)	:
	- :	82	28	110
	:	(57.6)	(52.4)	:
	total:	110	100	210

D. Coronella austriaca and Anguis fragilis

		<u>C. austriaca</u>		
		+	-	total
	+ :	9	20	29
<u>A. fragilis</u>	:	(22.9)	(6.1)	:
	- :	101	9	110
	:	(87.1)	(22.9)	:
	total:	110	29	139

Table 5.32 : 2 x 2 contingency tables recording presence (+) or absence (-) of each or both of C. austriaca and another species of reptile using a hypothetical maximum number of squares as the sample size for A. Vipera berus, B. Natrix natrix, C. Lacerta vivipara and Anguis fragilis at Site One. Expected frequencies are given in parentheses.

SITE TWO - hypothetical maximum number of 10 x 10 m grid squares that could be occupied

A. Coronella austriaca and Vipera berus

		<u>C. austriaca</u>		
		+	-	total
	.	:	:	:
	+	:	:	:
<u>V. berus</u>	:	11	6	17
	:	(15.6)	(1.4)	:
	-	:	:	:
	:	175	11	186
	:	(170.4)	(15.6)	:
	total:	186	17	203

B. Coronella austriaca and Natrix natrix

		<u>C. austriaca</u>		
		+	-	total
	.	:	:	:
	+	:	:	:
<u>N. natrix</u>	:	10	4	14
	:	(13.0)	(1.0)	:
	-	:	:	:
	:	176	10	186
	:	(173.0)	(13.0)	:
	total:	186	14	200

C. Coronella austriaca and Lacerta vivipara

		<u>C. austriaca</u>		
		+	-	total
	.	:	:	:
	+	:	:	:
<u>L. vivipara</u>	:	49	85	134
	:	(77.9)	(56.1)	:
	-	:	:	:
	:	137	49	186
	:	(108.1)	(77.9)	:
	total:	186	134	320

D. Coronella austriaca and Anguis fragilis

		<u>C. austriaca</u>		
		+	-	total
	.	:	:	:
	+	:	:	:
<u>A. fragilis</u>	:	9	10	19
	:	(17.2)	(1.8)	:
	-	:	:	:
	:	177	9	186
	:	(168.8)	(17.2)	:
	total:	186	19	205

Table 5.33 : 2 x 2 contingency tables recording presence (+) or absence (-) of each or both of C. austriaca and another species of reptile using a hypothetical maximum number of squares as the sample size for A. Vipera berus, B. Natrix natrix, C. Lacerta vivipara and Anguis fragilis at Site Two. Expected frequencies are given in parentheses.

specimens of shrews (Sorex sp.; probably S. araneus in all cases) were recorded at each site. One wood mouse (Apodemus sylvaticus) was observed at Site One and a small vole (probably Microtus agrestis) was recorded at the edge of Site Two. Fledglings of ground nesting birds may be included in the diet of snakes, and meadow pipits (Anthus pratensis) and skylarks (Alauda arvensis) were observed nesting at Site Two.

Predatory animals, that may take smooth snakes, were observed at both sites. Foxes (Vulpes vulpes) were widespread throughout the New Forest and were observed at both Sites One and Two. Several earths were found at Site One and the presence of foxes throughout the area was additionally indicated by many fox scats. Superficial analysis of these scats, however, indicated that the foxes at Site One were primarily feeding on rabbits. Badgers (Meles meles) were known to be in the general locality of the two sites although their presence was only revealed by the remains of an animal killed on the road just north of Site Two. Absence of records of live specimens of M. meles indicated that this species was unlikely to be a major predator of reptiles on the study sites, this resulting either through their activity occurring when reptiles were inactive (i.e. at night) or through absence from the area altogether. One small mustelid (probably Mustela erminea) was observed at Site Two. This was observed in an area of bog close to a river where mink (Mustela vison) had previously been trapped (P.R. Eccles, pers. comm.). Hedgehogs (Erinaceus europaeus) will eat snakes occasionally (Morris 1983) although such occurrences will be rare as hedgehogs are primarily nocturnal. Hedgehogs were observed near to both study sites but never actually on either.

Two species of likely avian predator were recorded, these being observed at both Site One and Site Two. Kestrels (Falco tinniculus) were often seen at Site Two and less frequently at Site One. Buzzards (Buteo buteo) were recorded occasionally at both Sites One and Two. Buzzards

have been known to take snakes and kestrels frequently feed on lizards, particularly in late Spring (Davis 1975, Gensbol 1984, G.J.M. Hirons, pers. comm.). A further two species of falcon were recorded, namely hobby (Falco subbuteo), at Sites One and Two, and red footed falcon (Falco vespertinus) at Site Two; both these latter species occasionally take reptiles (Gensbol 1984). Herons (Ardea cinerea) were observed occasionally in the wetter habitats at Site Two; these large birds generally feed upon amphibians, fish and small mammals (Hewson and Hancox 1979) but could easily take snakes if the opportunity arose. Corvids are opportunists and will eat a variety of small animals, carrion and plant material. As such magpies (Pica pica), jays (Garrulus glandarius) and carrion crows (Corvus corone), all of which were common at Sites One and Two, may have represented potential threats to C. austriaca, especially immature specimens.

ii. Small mammal trapping

Small mammal trapping was undertaken over a total of 8.5 days, i.e. 1275 trap days (number of days x number of traps), between 14th and 17th May 1984 and between 20th and 25th August 1984. This yielded low capture rates on each of the three habitat types sampled. A total of nine animals (six Apodemus sylvaticus and three Clethrionomys glareolus) were captured on ten occasions, a rate of 0.0078 captures per trap day. As such small samples were obtained the totals from the two trapping periods are pooled and the data summarised in Table 5.34. Sample sizes were considered too small to permit statistical analysis or for estimation of population sizes based on recapture indices. Dry heathland yielded the greatest number of captures with a total of five animals being caught (on six occasions), the pine plantation was the next most productive, with three captures, and wet heathland had the lowest capture rate with only one animal being caught during the trapping period.

The mean weight of C. glareolus was 21.1 g \pm 2.7 (n= 4) and

Vegetation type	Bank vole <u>C. glareolus</u>	Wood mouse <u>A. sylvaticus</u>	Total
Dry heathland	2 (3)	3	5 (6)
Wet heathland	1	0	1
Pure pine stand	0	3	3
Total	3 (4)	6	9 (10)

Table 5.34 : Small mammal trapping records totalled for two trapping periods in May and August 1984 at Site One. Data are total number of individuals, numbers in parentheses are total number of captures (i.e. including recapture data).

that of A. sylvaticus, $20.4 \text{ g} \pm 2.5$ ($n= 5$).

5.4. Discussion

5.4.1. Home range size and shape

a. Effect of methodology and sampling procedure

During the present study, 'home range' is defined as the total area occupied by an animal (as Rose 1982) and the calculation of home range area described the area of a convex polygon that encompassed all sightings. Estimates for home ranges of C. austriaca from the present study varied between 34 m^2 (0.003 ha) and 17215 m^2 (1.722 ha) and yielded a median value of 688 m^2 (0.069 ha), although the methodology employed in locating the snakes, the time period over which observations were made and the number of observations in each home range estimate affected these area estimates.

The number of observations included in any home range estimate effected the size of the area estimate for some, but not all, methods of location (see Fig. 5.8). When all data were pooled (for males separately, females separately and males and females combined) and where radio-tracking and visual location data (for males and females combined only) were employed increasing numbers of sightings yielded increased range area estimates, although no such relationships were observed with range areas calculated from visual searching data alone. These observations may reflect differences inherent in the methodology, for example visually observed data may have been biased toward basking sites (and consequently subsequent sightings represented repeated locations within the same general area) whereas radio-tracking allowed repeated locations of dispersing snakes. However, even within methods, there was considerable deviation from the proposed relationships; for example, one range produced from only six (visual) observations yielded a range of over 10000 m^2 (1.0 ha) whilst another with 63 (radio- and visual) locations had an

area of 143 m² (0.014 ha). It was likely that much of this variation could have been a result of differences in the period over which these snakes were observed (see below).

Due to the great variability in these range size estimates, no clear relationships were observed that suggested a minimum number of sightings which could be used for 'reliable' range area estimation for any of the methods of location. Rose (1982) reported that increasing numbers of sightings of the lizard Sceloporus virgatus yielded increasing home range area estimates, up to a value of 18 sightings. This number of observations described approximately 80% of the home range area and only a slow rate of increase was observed with an increase in the number of sightings thereafter.

The relationship between range area and observation period was also affected by methodology (see Fig. 5.10), with a positive correlation being observed only for snakes observed by all methods combined (for both sexes and female snakes only) and for those snakes located by radio-tracking alone combined with those observed by both radio-tracking and visual location (for both sexes and for female snakes only). As with the relationships observed between range area and the number of observations, data here were highly variable. Notable deviations from the 'expected' relationship were apparent; some ranges, for example, were quite large despite only short periods of observation.

A comparison of Figs. 5.8 and 5.10 showed that fairly large ranges which were associated with short periods of observation were often also associated with quite large numbers of sightings. Conversely, small ranges with many sightings were often recorded over only a short period of time (e.g. by radio-tracking). Home range area estimates, therefore, seemed to be influenced by a combination of both the number of observations and the period over which observations were made. Thus, as the value of both of these variables increases, then the likelihood of representative range area estimates will also increase. The nature of this

relationship will vary between methods, as radio-tracking allows many more sightings to be made in a short period of time than can be made by visual location. Due to the complex interaction between range size estimation, the number of observations and observation period and the differences resulting from the different methodologies, the influence of each of these factors alone upon range size estimation could not be accurately assessed during the present study.

Rose (1982) recommended the use of many sightings, separated by a short distance in time, for accurate range area determination. In the present study, short intervals between locations were achieved through the use of radio-telemetry. There are, however, problems associated with using this method. Due to the variation in the interval between visual locations of snakes (and frequently quite small samples being obtained) and the comparatively large number of regularly-spaced observations obtained from radio-tracking data (usually collected over very short periods of time), the results from the two methods cannot be directly compared with each other. The short sampling interval associated with radio-tracking data means that successive observations are unlikely to be independent of each other and, as such, the use of statistical methods of range area calculation would be precluded.

The possible interactions between the number of sightings and range area and that between the period of observation and range area may in part explain the highly positively skewed distribution of home range areas observed during this study. Many home ranges were based upon small sample sizes (19 had ten or less sightings) and/ or were recorded over short periods of time (22 were observed over a period of less than two months). However, all observations over 0.5 ha were associated with either a large number of sightings (30 or more) or long observation periods or both. These observations may indicate that home ranges of C. austriaca are, in fact, larger than is suggested by the median value obtained from this study. Methods of location

that allow both numerous and prolonged observations of snakes (such as the combination of both radio-tracking and visual location data) will give the most representative estimates of 'typical' home range areas. Using only data from radio-tagged snakes and those located by both visual location and radio-tracking (i.e. omitting those data for snakes that were only located visually) yielded a median home range size of 1611 m² (0.161 ha) (range= 53 to 17215 m² (0.005 to 1.722 ha)). This latter median range value may, therefore, be more representative of smooth snake home range areas than the median value obtained from all range area estimates together.

However, home range sizes may consistently increase over time; an observation that would be expected for animals that do not limit their movement within rigidly defined home ranges. In such cases maximum home range estimates may provide a more representative estimate of range area; thus ranges of C. austriaca may typically be in the region of 10479 to 17215 m² (1.048 to 1.722 ha), based upon the five largest range size estimates.

Shapes of home ranges were notably variable (see Figs. 5.1 and 5.2) both within and between the sexes. A possible interpretation of such variability in range shape is that spatial behaviour is highly variable between individuals and that no single home range shape is typical for the species. However, it is likely that the ranges so described represent only a small proportion of the animals' lifetime ranges and would therefore reflect the shape of only part of the range. The use of convex polygons may distort any inherent patterns or range shapes since these are determined only by the peripheral locations. As such, other methods for describing home ranges (e.g. probability methods) may more accurately describe home range shapes for C. austriaca.

Often range shape was determined by vegetational or topographical features, for example long and narrow ranges often followed the length of embankments or described the

movement of snakes living adjacent to roads or conifer plantations. Therefore range shape would be expected to be variable where the habitat was markedly heterogeneous or where the snakes' ranges were bordered by unsuitable habitat.

b. Intra-specific comparisons

Other estimates for smooth snake home range areas have been published; Goddard's (1981) study of snakes in the New Forest, Hampshire yielded home range sizes between 0.005 and 10.30 ha, with a mean of 2.96 ha \pm 0.84 (standard error) (n= 17), at his Site One and 0.006 to 8.69 ha, with a mean of 0.69 ha \pm 0.28 (standard error) (n= 16), at his Site Two. Wheeler (in NCC 1983) produced home range estimates for four smooth snakes captured beneath tin sheeting on open heathland at Purbeck, Dorset ranging between 0.42 and 3.40 ha, with a mean value of 1.57 ha \pm 0.68 (standard error).

The results of the present study (see section 5.4.1 a.) suggest smaller home range areas than have previously been reported. However, when making these comparisons, several methodological considerations should be borne in mind. The periods over which Wheeler produced his area estimates are not known, nor are the number of observations which make up each. The four snakes selected for Wheeler's area estimates were probably animals for which home range areas were believed to be representative and, in practice, are likely to have been those for which much data was available or that were observed over a relatively long period of time. Those cases with fewer observations or where smaller (and probably less representative) estimates of ranges area were obtained may have been discarded. If this were so, then the calculated mean area estimate would be high. Goddard used Jennrich and Turner's (1969) correction factor to adjust areas in the light of sample sizes, and consequently area estimates so produced were greater than actual areas measured in the field (these resulted in increases of area of between 2.02 and 23.26 times from the polygon actually

recorded in the field). In addition, both workers report mean areas. During the present study highly positively skewed distributions of range area estimates were observed, and in these cases mean values tend to be greatly influenced by the larger values and, hence, are not representative of the sample as a whole. For this reason median values were used during the present study.

For the purpose of comparison, however, it is instructive to calculate a mean value for range area observed during the current study. Using all data (from all methods of location and from both sexes) a mean home range area of $2379 \text{ m}^2 \pm 501.6$ (standard error) ($0.238 \text{ ha} \pm 0.050$) was obtained. Using Goddard's unadjusted home range area estimates, mean areas of $0.909 \text{ ha} \pm 0.305$ (standard error) (range= 0.0014 to 4.3089 ha) and $0.159 \text{ ha} \pm 0.073$ (standard error) (range= 0.0010 to 1.0712 ha) were obtained for his Sites One and Two respectively and $0.545 \text{ ha} \pm 0.172$ (range= 0.0010 to 4.3089 ha) was obtained by pooling data from both his sites. Median values for Goddard's unadjusted data were 0.3242 ha, 0.0249 ha and 0.1046 ha for Site One, Two and both sites together. Thus observed range sizes during the present study were, in fact, comparable to those obtained by Goddard (1981).

Neither Breeds (1973) nor Spellerberg and Phelps (1977) gave estimates of range areas, although these authors reported upon distances between captures. Maximum distances between captures can be used to give an indication of ranging behaviour, and hence may be suggestive of likely home range areas. Breeds reported upon one snake which was located 180 m apart between two successive captures (between to consecutive afternoons) and on two other occasions was located 100 m away from previous locations (in 300 minutes and 130 minutes respectively). Another animal was observed to move 100 m (in 165 minutes). The longest single movement record reported by Breeds for C. austriaca was 400 m. At their Site Two, Spellerberg and Phelps reported movements of up to 130 m for males and up to 100 m for females, with distances between captures were

'often in the range of 70-80 m'. At their Site Three these authors described movement behaviour of female snakes that suggested this sex remained within fairly well defined areas whereas male snake movement yielded no such pattern and distances between recaptures were as great as 210 m.

No differences were observed in home range areas between the sexes during this study, an observation also made by Goddard (1981). Spellerberg and Phelps (1977), however, suggested a difference in the spatial behaviour between the sexes (at their Site Three) where females occupied smaller home ranges. This apparent discrepancy may be as a result of the period of observation used in the different studies. The behaviour described by these latter authors may reflect a short term period of relative inactivity (lasting up to one or two months) whereas the ranges described by the Goddard and in the present study describe behaviour often in more than one season. The repeated locations of female snakes at certain bask sites was observed during the present study. These sites typically included south and west facing embankments and sheltered road side verges. This behaviour was usually shown by pregnant animals. As pregnant snakes often do not feed (Shine 1980), habitat selection may primarily be governed by thermoregulatory considerations. As such, these snakes may be able to limit their movement to remain within favoured basking areas and consequently show only a limited dispersion throughout the summer months. Gravid reptiles are also likely to be more vulnerable to predation (Shine 1980). Decreased movement may help reduce the likelihood of predation (Viitanen 1967), especially in a species that uses crypsis as its primary defence, and familiarity with the location of burrows, etc., may also enhance an animal's survival (Stickel and Cope 1947).

Differences have been reported in home range areas between the sexes in many species of lizard (e.g. Lacerta agilis (Dent 1986) Sceloporous virgatus (Rose 1982)). In these species, males' home range areas are usually larger than those of females. Such differences usually result from the

species showing a degree of territoriality and each individual occupying well defined home range areas with only small overlap of adjacent ranges. Male lizards often extend their ranges during the breeding season to incorporate the ranges of several females. In general, snakes do not show territorial behaviour, although Andren (1981) reported that male Vipera berus showed agonistic behaviour towards other males (including territory marking displays) in the immediate locality of a sexually receptive female. Indeed, C. austriaca showed a marked overlap in home range area both between and within sexes. As ranges were poorly defined and not rigidly protected, such differences in home range area between the sexes would not be expected in the long term.

No correlation was observed between home range area and body size of C. austriaca by Goddard (1981) or during the present study, despite such a relationship being recorded in several species of lizard (Turner et al 1969). Range areas may be related to the distribution and abundance of food and, on energetic grounds, it would seem reasonable that larger animals would require a larger intake of food and hence require a larger home range. Nonetheless, this hypothesis would only be true if food were regularly spaced and food intake were proportional to movement behaviour. For C. austriaca, which takes a variety of prey species (some of which may be regularly spaced, e.g. lizards, whereas other are likely to clumped in distribution, e.g. nestling mammals) and that uses a variety of foraging techniques (e.g. 'sit and wait' and 'active searching' (sensu Pianka 1977), see Chapter 4, section 4.4.5 b.)), such conditions may not hold true. Consequently range area need not necessarily relate to either food intake or body size.

c. Limited movement areas in snakes

Home range area estimates have been produced for a variety of reptile species. Their comparability, though, is limited through the use of different methods for calculating areas,

different methods for collecting field data and through varying definition of the term home range (see Introduction, section 5.1.1.). Indeed, the application of the term home range to ecological studies of reptiles is itself somewhat controversial as the degree to which reptiles (and in particular snakes) restrict their movements to defined home areas is questionable. Differing interpretations of field data have been offered although, in a review of the literature, Brown and Parker (1976) concluded that, on balance, the majority of studies showed that snakes tended to limit their movements to within restricted home range areas rather than showing a series of random wanderings.

Prior to investigating whether limited dispersal was suggested for C. austriaca, it is worth discussing the reasons for, and any possible advantages conferred upon an animal through, the maintenance of a limited movement area. The home range of a snake will need to incorporate all components required for the life of that snake. Thus the observed area occupied will consist of a feeding range, a breeding range, a thermoregulatory range and shelter (overnight shelter, protection against predators and a hibernation site). These areas may be separate areas within the range or may all be served by a single area. The nature and size of the home range of the snake will be determined by the combination of these factors and variations within each of these factors will influence the total range area occupied.

The nature and distribution of food in the habitat will affect range size. Regularly spaced food items (particularly where these are small and can quickly become locally depleted) will promote the formation of ranges that are fairly static with regard to area and location. Insect prey may be expected to show such a distribution and therefore insectivorous lizards would tend to occupy fairly well defined home ranges. Indeed, this pattern of food distribution may well encourage the development of territorial behaviour (Stamps 1977). These lizards, in

turn, will become a regularly distributed food resource for lizard eating snakes. Herbivorous and generalist carnivorous animals tend to have clumped or erratically distributed food. In these species home ranges are less well defined and feeding territories generally are not maintained and (particularly for carnivores) may occupy large areas (Stamps 1977). Feeding ranges, in turn, influence breeding ranges since male home ranges have to overlap female ranges to allow mating. In insectivorous lizards, males tend to have large breeding territories covering the home ranges of several females. In herbivorous lizards smaller areas are defended, which are usually considerably smaller than the feeding range (Stamps 1977). Carnivores will not defend their entire feeding range, but may show territorial behaviour in the region of a receptive mate (Andren 1981).

A site that offers a variety of thermal habitats will permit behavioural thermoregulation in an ectotherm. Certain structural and vegetational characteristics, however, may favour body temperature regulation, for example embankments or open ground within the ground flora. Selection of some areas for their apparent suitability for basking was observed during the present study, even though these areas seemed not to offer much in the way of food, mates or shelter (e.g. grass verges, stoney embankments). Shelter, to avoid predation and extremes of temperature, must also be available within the home range. Over night refuges tended to be below ground or in the base of thick vegetation. Over wintering sites for C. austriaca were apparently located within, or close to, the summer ranges; in many temperate snake species (e.g. Vipera berus (Prestt 1971), Thamnophis sirtalis parietalis (Aleksiuk 1976), Crotalis viridis viridis (Duval et al 1985), see Chapter 3, section 3.3.1 a.) the home range areas are increased dramatically through migration between a summer range and a geographically distinct hibernaculum.

The degree to which a snake remains within a localised area will therefore depend upon the availability of all of the

above factors. There are advantages in limiting movement where possible. Familiarity with an area can affect survival through the benefits of knowing the location of burrows or patches of vegetation which can offer protection from predators (Stickel and Cope 1947), give shelter from inclement weather or provide over night refuges. Thermoregulation has been shown to benefit from site familiarity. Tortoises Testudo hermanni that are familiar with their environment are able to achieve their maximum body temperatures more rapidly than animals that are translocated to similar sites (Chelazzi and Calzolari 1986).

The repeated use of certain areas within a range may also provide knowledge of the prey availability throughout the range and permit most efficient exploitation of the prey in the environment. Mating too may occur earlier where snakes habitually return to certain areas. As mate location is probably effected through olfaction, the close proximity of the sexes initially may enhance the likelihood of encountering a pheromone trail and subsequently a mate. In addition unnecessary movement is energetically inefficient and consequently a snake may be expected to minimise its movement during its every day activity. The benefits of maintaining a LMA have been cited as possible reasons behind the homing ability reported for some snakes (e.g. Natrix sipedon sipedon (Fraker 1970)), although this phenomenon is by no means universal in the Ophidia.

d. Is the movement of C. austriaca confined to a LMA ?

Goddard (1981) suggested that C. austriaca showed a limited dispersal as successive observations of snakes showed frequent crossing of tracks and repeated use of certain areas. In the present study no consistent pattern of range use could be determined; whereas some snakes remained within small areas over long periods of time, others were found only on few occasions over a short period of time and were not seen again thereafter. For example, one female at Site One (FM13) was observed regularly during all three study seasons always within a relatively small part of the

study site (yielding a total range of 2136 m² from 106 radio- and visual observations). At the same site, however, another female was visually observed and radio-tracked for just over one month in a single year and in that period a range of 3257 m² was measured (from 31 observations).

In some snakes re-use of certain parts of the range was suggested during the present study. At Site One, a male snake (MM16) was observed to move from one area on the study site to a second some distance (approximately 300 m) away and then subsequently return to the first. A female at Site Two (FH03) was first observed early in each of the three seasons at a particular area of bog vegetation by a bank and subsequently recorded by a particular bramble (Rubus fruticosus) bush, approximately 200 m away, in two seasons. This movement was recorded by radio-tracking during one year, and the majority of distance was covered in under four hours (during which time the snake appeared to be homing towards its destination). Many subsequent locations of the snake showed that it remained within a very small area throughout most of the remainder of that year and a very similar pattern of behaviour was observed in the following year.

Short term movement behaviour (see Chapter 4, sections 4.3.8. and 4.4.6.) also suggested no consistent dispersal pattern by C. austriaca, in that radio-tagged specimens showed both dispersion and 'home site maintenance' behaviours to an equal extent. Thus, although the repeated use of certain areas within the home range and the frequent crossing of tracks were observed during the present study, the data were such that Goddard's observation of 'limited movement' could not be substantiated, at least not as a general rule. A certain limitation to the area occupied may be expected in the light of the small movement rates shown by C. austriaca (see Chapter 4). Recapture rates and the frequency of observation of each specimen of C. austriaca are presented in Chapter 3, section 3.5. The predominance of snakes captured only once or over a short period suggested that many snakes wandered widely and did not

restrict their movement.

The ranging behaviour of C. austriaca would appear to be described by a series of periods of relative inactivity of varying lengths of time interrupted by short to long movements. Daily activity is not centred around a single home site or burrow and no evidence could be gained suggest any possible seasonal activity based around a particular hibernation area. Short term data neither supported nor refuted the existence of LMAs for C. austriaca, although the variability of data do indicate that any measured home range areas are almost certainly underestimates of life time ranges.

It would appear, however, that dispersion by C. austriaca is not inherently limited and that in the long term large areas are traversed. Movement will however be limited to a degree; this limitation being determined by mate searching behaviour, foraging behaviour (both which will cause the crossing of the animal's own tracks), basking behaviour (which will result in periods of short movements and inactivity) and physical limitation imposed by the habitat (e.g. through barriers to dispersal). In addition, even a randomly moving snake would, upon occasion, return to certain areas within its home range. Movement is unlikely to be random, however, and shall be determined largely by the habitat that the snake encounters. It is likely that certain areas are deliberately re-used and that smooth snakes retain a knowledge of at least some parts of their home range. Whether homing behaviour is shown by C. austriaca was not specifically investigated during this study (e.g. through translocation experiments), nor was this type of behaviour conclusively demonstrated in the observations made in the field.

5.4.2. Vegetation use and habitat selection

Smooth snakes were recorded in association with a variety of different plant species of all heights, from bare ground to those well in excess of 2 m. In total, a large number of

vegetation communities were occupied (31 vegetation communities were used on one or more occasions by C. austriaca out of a total of 32 which were described at the two sites combined) indicating that the species is catholic in its use of habitat. Nonetheless, certain plant communities, dominated by a smaller subset of plant species, were used more frequently than others and these observations indicated that certain habitats are more suitable for the species.

The observations made during the present study largely reiterate the findings reported by many previous workers. In Britain, C. austriaca is primarily regarded as a heathland species, typically being found in dry heathland dominated by Calluna vulgaris and Erica cinerea, although references to the use of bog and woodland and various intermediate habitats have been made (Smith 1973, Breeds 1973, NCC 1983). Corbett (1980), however, suggested that dry heathland is the optimal habitat for C. austriaca, and that observations in other vegetation types represent only occasional use of marginal habitats.

During this study, Calluna vulgaris and Erica cinerera dominated dry heathland were the most commonly used habitat types at Site One, a site that was predominantly covered by coniferous trees. In addition Ulex europaeus bushes were often used. At the more open Site Two, C. vulgaris and E. cinerea heathland was commonly occupied but in addition humid heathland (dominated by E. tetralix and Molinia caerulea) and bog and wet heathland were also often used. These latter habitats were abundant at Site Two, but humid heath was not common and bog and wet heathland were not found in the study area at Site One. Vegetation heights were typically between 0 and 70 cm although a large number of sightings were also associated with vegetation of 2m and over.

The methodology used in the field affected the apparent vegetation use. At both Sites One and Two the use of fine grass (e.g. Agrostis spp.) and open vegetation was over

represented in the visually located sample compared to the sample of radio-located specimens. Visual location was biased towards shorter vegetation with significantly more observations in vegetation with median heights between 0 and 15 cm (at both sites). It is likely that this reflects the relative ease of location of snakes in these habitats. Conversely, radio-tagged snakes were found more often in association with bracken and deciduous woodland at Site One and bog and coarse grass (e.g. Molinia caerulea) at Site Two. Radio-location produced significantly more observations between 30 and 50 cm (and over 200 cm) at Site One and between 20 and 100 cm at Site Two than did visual observation.

Visual location suffered additional biases. Searching for snakes tended to be concentrated towards known 'snake areas' and particularly along verges, boundaries between vegetation types, embankments and in more open areas and tended to avoid, or be unsuccessful in, vegetation such as bog. The notably greater use of bracken at Site One and bog and coarse grasses at Site Two by radio-tagged snakes (cf. visually located snakes) may reflect the relative difficulty associated with location smooth snakes by eye in these habitat categories. The use of tin sheeting/ tiles was also notably variable between the methods of location. This technique increased the sample size of visually located snakes although the relative non-use of tin by radio-tagged animals (on only one occasion was a snake observed to move under a tile by radio-tracking) may indicate that snakes only use these objects infrequently. Consequently population estimates based upon recaptures under tin sheeting/ tiles may be under-estimates. Attempts to assess home ranges and movement behaviour from observations of snakes below such objects may also suffer similar limitations.

Previous studies that have relied upon visual location alone will have been restricted in both the range of habitats investigated and in the ability to located animals within these habitats. As such, data from radio-tagged

snakes was regarded as providing a more representative picture of habitat use. However, successive radio-locations as recorded in this study will suffer some degree of bias. The short interval of time between successive locations will mean that they are not independent of each other and consequently these results may over represent some habitats used only in the short term. Although the use of small quadrats will have reduced the effect of repeated sampling within an area, a more representative pattern of habitat use may be gleaned from sub-sampling to effectively increase the interval between locations (Kenward 1987).

Although many habitat types were used, this observation is not indicative of habitat selection. Such observations need to be discussed in the light of the abundance of each habitat type. At both sites, both sexes used dry heath more than would be expected from its abundance in the field suggesting that this vegetation category is used preferentially. Both sexes at Site One and males at Site Two also occupied humid heath more frequently than would have been expected (females at Site Two, however, used this habitat less than would have been expected for its abundance). Males at Site One also appeared to select scrub (Ulex and Rubus spp.) and Pteridium aquilinum and the latter species was also selected by females at Site Two. Vegetation heights between 30 and 50 cm were used disproportionately often at all sites, although the range of 'preferred' heights between sexes and between site (ranging between 5 and 150 cm). The apparent selection of bracken was not expected. Bracken is generally regarded as being unsuitable for heathland reptiles .

At all sites open ground and deciduous wood were used on fewer occasions than would have been expected and at Site One coniferous trees were generally not used. Thus shorter vegetation, between 0 and 5 cm was used relatively infrequently and at Site One vegetation over 200 cm was also generally not occupied.

Although the experiment to assess the relative

abundance of C. austriaca in different vegetation communities (section 5.3.2 d.) yielded only two sightings of smooth snakes, these were in mature stands of dry heath and wet/ humid heath. These observations complimented the general findings at Sites One and Two. Sightings of lizards indicated that a variety of mature habitats (including dry, humid and wet heath and bog) were used by reptiles although recently burnt/ cut and pioneer stage (sensu Gimingham 1972) heathland was apparently unsuitable. Although C. austriaca was observed in a variety of fairly open habitats through out the study, the species was not observed in recently burnt or early pioneer stage heath. Burning heathland removes not only the vegetation but also the invertebrate communities and the subsequent chain of small vertebrates upon which C. austriaca feed. In the short term the removal of cover is of primary importance to C. austriaca and even pioneer stage heath does not seem to offer adequate ground cover. Vegetation regrowth, dependent upon local conditions, may take over seven years before the structure of the vegetation provides adequate cover for frequent use by snakes. The use of video analysis in the laboratory also indicated a preference by snakes to occupy ground which was structurally varied.

Corbett (1980) advocated the maintenance of mature stands of dry heathland for the conservation of reptiles (and all elements of the heathland community). In such stands the heather will persist through a natural cycle of death and regeneration. However, such systems do become vulnerable to invasion by birch and pine trees, damage from trampling and unmanaged fires. Controlled heath burning does ensure long term persistence of the heather, provided that bracken does not invade (good heathland management can reduce the likelihood of 'undesireable' species invading and increase the likelihood of heather regeneration (e.g. Hazel 1983)), and in the New Forest such management is required for grazing of commoners' stock. The burning of large areas of heathland have been blamed for the decline of reptiles (and probable extinction of Lacerta agilis) in the New Forest. Where management by controlled burning is required, burning

smaller patches in a mosaic to provide the required area may be more beneficial to all ground living species, by providing cover in close proximity to the burn site and facilitating re-occupation of the pioneer community once it has matured sufficiently.

Differences in habitat use were suggested between the sexes. However, there was a lack of consistency between sites that prevented general conclusions being drawn. At both sites females were observed more than males in dry heath (e.g. Erica cinerea) and in fine grass (e.g. Agrostis setacea). At Site Two females also were observed in open vegetation and bracken more often than males. The observations at this site suggested that females selected generally shorter (0 to 10 cm and 15 to 20 cm, although vegetation between 60 and 100 cm was also used more often by females) and drier habitats than males; males were more frequently found in humid heath, bog and coarse grass (which was most frequently Molinia and typically associated with wetter habitats) and used intermediate height vegetation, between 20 and 50 cm, more than females. However such a pattern was not clearly indicated at Site One. Males at Site One were found more frequently in bracken, scrub (Ulex and Rubus spp.) and both deciduous and coniferous wood than females. This was associated with a greater use of vegetation in excess of 100 cm in height, whereas females (that also occurred more often in coarse grass) were found more often in shorter vegetation (5 to 20 cm and 30 to 40 cm).

Such inter-sexual differences can be brought about either by the selection of a habitat type by one sex or through its avoidance by the other, or both. For example, at Site One scrub and bracken were used more by males than by females and these habitats were also used preferentially by males (whilst females used them only in proportion to their availability in the environment). Thus it would appear that these were selected by males. However, deciduous and coniferous woods, which were also used more frequently by males than females were generally not used by males. This

inter-sexual difference therefore resulted from a more pronounced avoidance of woodland by females. Similarly the apparent preference of coarse grass by females related to avoidance by males at Site One whilst females there did not select it but used it only in relation to its abundance. As dry heath was selected by both sexes, the greater use of this habitat type by females represented a particular selection by this sex at both sites. Fine grasses were used more by females than males; this difference resulted from the selection of this habitat by females at Site Two, but at Site One was due to the avoidance of this habitat type by males. The apparent selection of bog and coarse grass by males and of open ground by females at Site Two also seems likely to be explained by non-use by the opposite sex. A combination of habitat selection by one sex and non-use by the other sex resulted in the predominance of males in humid heath and of females in bracken at Site Two.

Notwithstanding the lack of any consistent pattern of habitat selection between the sexes, it is worth speculating upon the possible causes of such behaviour. Female behaviour throughout much of the year will be largely influenced by the proportion of gravid snakes in that population, and may therefore reflect behaviour associated with enhancing the development of ova. This would primarily involve basking behaviours and, as such, habitat selection would reflect sites that are suitable for protracted basking (i.e. open ground, short vegetation and heathland). Males would not be confined by such considerations and might therefore exploit a wider variety of habitat types. Non-breeding females are likely to show a different behaviour to breeding females and consequently any patterns of inter-sexual variation may become less clearly defined.

The foraging behaviour of the two sexes may vary. Gravid females may reduce their food (Shine 1980) intake and hence may not need to forage away from their bask sites. Males may extend their range to reduce (or avoid) competition for food in the vicinity of gravid females. Indeed this may even be reflected in differences in prey species selected

by each sex (although no evidence was found to substantiate this hypothesis), resulting in the use of separate foraging areas. The use of different habitats, where habitat preference was not indicated, may reflect a greater tolerance of these 'marginal' habitats by one of the sexes. The use of these sub-optimal areas may be brought about through avoidance of intra-specific competition.

Regardless of reason, any implied difference between habitat selection by the sexes demonstrates the importance of including both sexes in any analysis of habitat usage.

Seasonal variation in habitat use was suggested for each of the sexes at the two sites, however these data lacked consistency and were restricted through small sample sizes. Seasonal variation may be caused in part by changes in the habitat that make areas more or less suitable, through variation in temperatures/ humidity that favour habitat change or through movement of prey species, etc.

A notable seasonal variation was that use of bog vegetation was only recorded in the Summer. These occurrences are likely to relate to foraging behaviour where snakes would probably be hunting lizards. Bog vegetation may only be dry enough and warm enough to allow snakes to use them during the Summer. However this may also reflect seasonal variation in prey behaviour, lizards may only use these habitats when invertebrate populations increase within them. These latter changes are likely to be related to season. Use of damper and more humid habitats may also be favoured during hot Summers; these perhaps reducing the risk of dehydration.

Bracken is notably variable during the year. Rapid growth occurs during the Summer causing the ground below to become shaded. This may be detrimental to snakes during cooler weather, but the cooler and more humid environment below a canopy of bracken may become favourable during particularly warm periods. No clear patterns were indicated during the present study to suggest whether bracken was used

preferentially during any one season, although most observations occurred in Summer and Autumn when some degree of shade would be provided.

No clear patterns of seasonal habitat use could be determined. This suggests that C. austriaca do not show predictable changes between habitats as has been suggested for Natrix natrix and Vipera berus (Phelps 1978). The suggestion that some variation does occur demonstrates the importance of collecting data throughout the entire activity season to assess vegetation usage for the species.

Habitat use during the night represents a subset of that shown during the day. Consequently it appears that C. austriaca do not occupy different habitats at night and that their overnight refuges are simply burrows below ground or in the base of vegetation selected shortly before nightfall. Such behaviour is also suggested by the apparent absence of particular 'home areas' around which activity would be based.

The identification of the most commonly used (and, by inference, 'optimum') habitats is obviously of great importance for the conservation of C. austriaca. With increasing pressures on land use and the declining areas of heathland it is also important to determine the range of habitat types that can be used as refuges and corridors for, and those that act as barriers against, dispersion. Of particular interest is the use of forest habitats by smooth snakes. Spellerberg and Phelps (1977) suggested the importance of young forests to C. austriaca as these provided a variety of thermal habitats and an abundance of prey species, and consequently allowed high densities of snakes. These authors also stated that these habitats eventually deteriorate as the canopy closes. In the present study even mature conifer stands were occupied, although, with the exception of one individual that travelled through a block of Corsican Pine, these observations were mostly limited to animals living in heather at the edge of the compartments. Thus, although such vegetation does not

represent a total barrier to dispersion, the majority of observations indicate that movement is generally restricted by pine plantations.

No sightings of C. austriaca were made in association with coniferous trees other than pines, although various spruces (Picea spp), firs (e.g. Pseudotsuga sp.) and cypresses (f. Cupressaceae) were common at the site.. Stands of deciduous trees were also occupied by C. austriaca, particularly where heather persisted below them. However in all cases only small blocks of deciduous trees were occupied and it appeared unlikely that smooth snakes would have occupied larger or denser stands of mature deciduous trees.

The present study has concentrated upon the habitat occupied by a snake and has not commented upon the role of surrounding vegetation. In her study of Lacerta agilis, Dent (1986) investigated the role of shading by trees adjacent to ride verges. The height and distance of adjacent compartments affected the sunlight reaching each site and these in turn affected lizard populations. Dent concluded that sites receiving over 30 seasonal sun-shine hours (a figure based on summation of one days sunshine for each month in the activity season and yielding a theoretical maximum of 52 seasonal s-s. hrs.) were suitable for the persistence of sand lizards. Although ride width also influenced the role of shading, Dent recommended that ride verges of at least 5 m width should be retained for the prolonged survival of lizards in forests. Such management would also be beneficial to smooth snakes, and no populations of C. austriaca were observed on ride verges of less than this width. Adders, grass snakes, common lizards and slow worms were all encountered in such areas, however.

These observations indicate that C. austriaca is less tolerant of shading than the commoner species of reptile. Indeed, in the centre of Site One an area previously used by Spellerberg and Phelps (1977) as their medium density population, revealed only a few smooth snakes during

Goddard's (1981) study and none were observed there during this study (despite numerous visits and the location of each of the other four species of reptile).

Short grassland was often inhabited by *C. austriaca* and radio-tracking revealed that snakes could conceal themselves in short (but dense) grass only a few centimetres deep. Smooth snakes were often found along grass covered road side verges. Although these were unlikely to reflect 'optimum' habitat, their regular use indicated that they were useful for at least short term occupancy. As such these areas may be particularly useful for providing corridors for dispersal. Sensitive management of immediate road side verges (e.g. timing and height of mowing) may enhance their usefulness and the encouragement of heathland vegetation on road embankments will be of considerable benefit by providing areas which are rarely visited by people and are not suited to other land uses (e.g. forestry, agriculture, recreation).

Roads themselves seem to restrict movement and on the two occasions where a snake was found to have changed sides of a major road were explained by passage below it (once under a bridge and once through an underpass). On one occasion a snake was found dead on a major road indicating that, whilst the road surface may not act as a barrier, heavy traffic will prevent dispersal over such structures. Consequently roads may represent a major cause of habitat fragmentation and have detrimental effect on populations of snakes, including restricting gene flow between animals on either side of these structures. Similar restrictions to movement have been reported in mice and carabid beetles (Mader 1984). Forest rides, even when gravelled and several metres wide, did not prevent movement across them. However movement was influenced by such structures and tended to be concentrated along side them.

5.4.3. Distribution of potential prey, predator and competitor species

At both sites there was a similarity in the general areas occupied by C. austriaca and the four other species of reptiles. At Site One these areas represented ride verges and patches of heathland or grassland that had not been planted with conifers and generally were away from the short grass associated with the grazing strip around the outside of the inclosure. At Site Two the areas occupied by reptiles were generally along the length of an embankment and in the dry and humid heath and the drier bog behind. Areas of very wet bog and thick vegetation along a small stream were not frequently sampled and as such may well have been occupied by some species. At the south of Site Two, a gentle north facing hill that had been burnt some years previously yielded relatively few observations of any species of reptile.

Within these general areas, however, smooth snakes did not occupy the same areas as other reptile species and a negative association was detected between C. austriaca and the other four species. However at both sites all species overlapped to some degree.

Both Natrix natrix and Vipera berus reportedly use separate Summer and Winter ranges, often re-using the same hibernaculum in successive years (Prestt 1971, Phelps 1978, Madsen 1984). As such, the degree of overlap in habitat use between C. austriaca and the other snake species may be further reduced through seasonal variation in habitat use. Vipera berus was observed throughout both study sites and occupied similar habitat types to C. austriaca. Phelps (1978) suggested that, due to the similarity of habitat used and prey taken by the adder and the smooth snake, competition could exist between the two species. However, with the fairly small numbers of both species observed at the two study sites and the apparent abundance of food such competition may be avoided. At Site One adders were often

seen basking along ride verges, often with only narrow bands of vegetation between the ride and the trees. At Site Two adders were most frequently observed close to Ulex europaeus bushes or in bog vegetation.

The principle foods of Natrix natrix are amphibians and small mammals (Smith 1973) and these are commonly found in wet habitats. Consequently grass snakes are generally regarded as wet heathland, bog or grassland animals. This association with wet habitat was not clearly demonstrated during this study. Grass snakes were frequently observed in dry heath at both sites and in 'dry' habitat beside rides at Site One. This, however, may result from observer bias, with searching being concentrated on these areas and through the large vagility of this species allowing to use many habitats in fairly short periods of time (Madsen 1984).

The two lizard species observed at both sites are both potential food for C. austriaca. Both species were widespread throughout each of the sites. At Site One Lacerta vivipara was observed in most types of ride verge habitat including grass, heath and bog and were particularly common at Site Two in association with humid to wet heath. Areas where bracken was invading tended to be occupied by lizards less often. Anguis fragilis was also abundant and widespread although less frequently seen than L. vivipara due to its fossorial habit. The variety of habitats occupied by A. fragilis were similar to those used by L. vivipara and varied from open (sometimes stoney) ground, to grassland, dry and humid heath and bog. The comparative habitat use experiment (see section 5.3.2 d.) indicated that both lizard species were most abundant in humid to wet heath and bog, but also common in mature dry heath.

Small mammal populations in the New Forest are generally low, particularly on heathland (Hill 1985). This has been attributed to grazing by large herbivores and management practices (e.g. burning). Although mammal trapping during

the present study was carried out in an inclosure (and hence cattle and ponies were mostly excluded) only small numbers of small mammals were captured. The very small trap captures meant that statistical analyses and population size estimates (e.g. by Lincoln Indices) were not undertaken. The results, very tentatively, suggest that populations of small mammals on dry heathland were larger than in pine or wet heath. Pure pine (Pinus nigra) yielded the next largest capture rates with wet heathland apparently sustaining the smallest populations of small mammals. Caution must be exercised in interpreting these observations due to the very small numbers of captures and the absence of replicates over similar areas.

Thus the range of prey species taken by C. austriaca is encountered in a wide variety of habitat types and within the study areas it would appear unlikely that food availability restricts the range of adult snakes. The apparently small overlap in areas occupied by C. austriaca and habitats favoured by the lizard prey species may indicate that smooth snakes would need to increase their home range area to incorporate feeding ranges. However as smooth snakes probably feed only infrequently, and capture both reptilian and mammalian prey species, such behavioural changes may be unnecessary. Goddard (1981) suggested an innate feeding preference in newborn C. austriaca for lizard prey and St. Girons (1980) reported that vipers (V. berus and V. aspis) cease eating lizard prey and concentrate upon mammalian prey as they mature from juvenile to adults. This change in feeding behaviour may have evolved to reduce competition between different age classes. Thus juvenile C. austriaca may be dependent upon reptilian prey species and as such their distribution may be affected by prey distribution. Consequently, although adult smooth snakes may be very catholic in their tastes and that prey species distribution may have little influence on these animals (cf. Beebee 1978), the distribution of smooth snakes may be restricted in part through the dependence of young upon reptilian prey.

5.5. Summary

5.5.1. Home range size and shape

- i. Home range areas were estimated using the convex polygon method. Areas of convex polygons for all specimens of C. austriaca varied between 34 m² and 17215 m², with a median value of 688 m² (n= 55).
- ii. Range shape was highly variable and considerable overlap was observed between ranges both within and between the sexes at the two study sites.
- iii. The method of observation influenced range area estimates: data collected by 'Visual location only' yielded different area estimates from 'Radio-tracking data only' and from data collected using both 'Radio-tracking and visual location' together. The latter two categories yielded similar range area estimates to each other and hence were combined in subsequent analysis.
- iv. Home range area estimates correlated with the number of observations used in each range area estimate when all data collected by all methods were pooled (both sexes), when data from all methods were pooled but analysed separately for each sex and when all data collected by 'Radio-tracking' and 'Visual location and radio-tracking' were combined (both sexes).
- v. Home range area estimates correlated with the period of observation used in each range estimate when all data collected by all methods were pooled (both sexes), when data collected for females by all methods were pooled and when data collected by 'Radio-tracking' and 'Visual location and radio-tracking' were combined for both sexes and for females.
- vi. The median range area obtained by 'Visual location only' was 182 m² (range= 34 to 10479 m², n= 18) and that for both 'Radio-tracking only' and 'Visual location and radio-tracking' combined was 1611 m² (range= 53 to 17215 m², n= 37). The latter of these estimates was deemed most

representative of range areas of C. austriaca.

vii. No differences in home range size were detected between the two study sites.

viii. No differences in home range size were detected between the sexes.

ix. Home range area was not correlated with snake body length.

x. Range use consisted of movements between short term basking and foraging sites to which the snakes showed only short term site fidelity (the time spent in each area may have been determined by physiological condition).

xi. Evidence as to whether C. austriaca maintained a limited movement area or displayed wandering movement was equivocal from the present study. It was suggested that the species remain within a fairly large, and not rigidly maintained, area in the long term with ranging behaviour being restricted through the re-use of basking sites, foraging areas or hibernacula (to which the snake shows only limited site fidelity), through mate searching behaviour and through the physical constraints imposed by habitat.

xii. Home range areas measured during the present study were regarded as being gross underestimates of life time ranges of C. austriaca.

5.5.2. Vegetation use and habitat selection

i. Smooth snakes were located in many different habitat types although not all of these appeared to be 'optimal'.

ii. Methodology affected the results: visually located sightings were biased towards shorter and more open vegetation and sightings below tin and tile were over represented. Radio-tracking data were deemed to be independent of these biases.

iii. Dry heath (dominated by Calluna vulgaris and Erica cinerea) was used most frequently by male and female C. austriaca located by both methods at Site One. At Site Two humid heath was used most often by male smooth snakes whereas bracken was used most often by radio-tagged females and females were most frequently visually located in fine grass (Agrostis sp(p).)

iv. Dry heath vegetation (Calluna vulgaris and Erica cinerea) was selected by both sexes at both sites. Humid heath (Erica tetralix), scrub (Ulex and Rubus spp.) and bracken (Pteridium aquilinum) were also selected by one or more sexes at either or both of the sites. Median vegetation heights between 30 and 50 cm were selected at all sites.

v. Open ground and deciduous wood and coniferous wood were generally not selected and vegetation heights less than 5 cm (and over 200 cm at Site One) were used relatively infrequently.

vi. Heath burning creates habitat that is not suitable for reptiles for long periods of time thereafter.

vii. Different use of vegetation was suggested between the sexes. Females tended to use drier and shorter vegetation than males although the lack of consistency between sites precluded general conclusions being drawn.

viii. Seasonal variation in habitat use was indicated although small sample sizes and inconsistency of results between sites and sexes precluded general conclusions being drawn.

ix. Over night refuges are areas within the day time range and do not represent separate ranges or indicate use of specific 'home sites'.

x. Infrequently used habitats may be important in conservation as these may offer temporary refuges or

corridors for dispersion. Road side verges, agricultural boundaries and forestry rides may be particularly important and sensitive management of these should be encouraged.

xi. Although both roads and forest plantations can be traversed, these represent effective barriers for dispersal.

5.5.3. Distribution of potential prey, predator and competitor species

i. Similar areas of each study site were occupied by all five species of reptile.

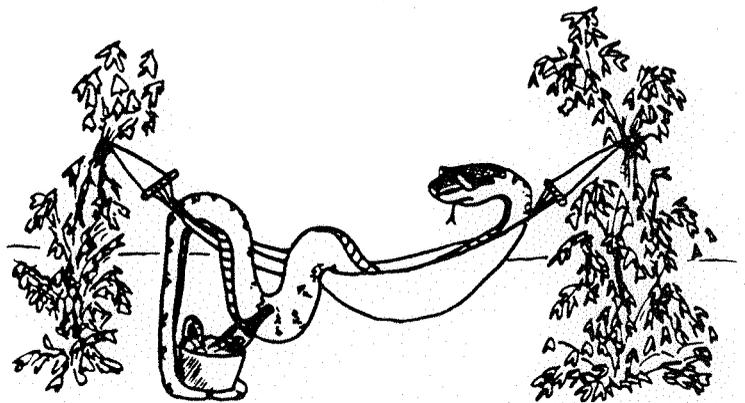
ii. Within these general areas smooth snakes occupied ^{geographically} different areas to each of the other four species of reptile.

iii. Lizard prey species inhabit a variety of habitats, similar to those occupied by C. austriaca. Use of humid heath and bog vegetation seemed particularly common.

iv. Small mammals were apparently more abundant on dry heath compared to pine plantations or wet heath.

v. Prey distribution and abundance were unlikely to limit the distribution of adult C. austriaca, although the species may be restricted through the apparent dependence of juveniles on lizard prey.

VI. Thermal Biology I: Field Data



CHAPTER SIX

THERMAL BIOLOGY I

FIELD DATA

6.1. Introduction

All reptiles are ectothermic, that is their body temperature results from the exchange of heat energy between their bodies and the environment. Little or no contribution to body heat is attributable to the animal's oxidative metabolism and thus maintenance of certain body temperature levels in reptiles is essentially a behavioural process. Certain physiological adaptations are also found in reptiles, including cardio-vascular mechanisms (such as the ability to alter the rate of blood flow), alteration of the reflectance of the integument and evaporative cooling (e.g. by panting), which enhance or retard the rate at which heat is exchanged with the environment (Spellerberg 1982).

Since the pioneering work by Cowles and Bogert (1944) into the thermal biology of desert reptiles, body temperature measurements have been a major element in the study of reptilian biology and an extensive literature has been produced (see reviews, e.g. Avery 1982, Huey 1982). With this literature has developed a complex (and sometimes inconsistent) vocabulary (Gans and Pough 1982) which reflects the diversity of aspects investigated, and the variety of physiological and behavioural strategies found within the Reptilia, which relate to thermal biology.

The term used to describe the behavioural maintenance of body temperature is thermoregulation. This term is used to distinguish the active regulation of body temperature via specific behaviours from the passive fluctuations in the body temperature of an ectotherm in response to changes in the ambient temperature; this latter condition is termed

thermoconformity (Huey and Slatkin 1976). The nature and precision of thermoregulation is highly variable between species of reptile. Some species achieve remarkably constant (and frequently quite high) body temperatures which can appear almost independent of prevailing weather conditions, whereas others demonstrate great fluctuations of body temperature or a dependence on ambient temperatures.

The terms heliothermy and thigmothermy are often employed to describe the nature of thermoregulatory behaviour. The former refers to animals which maintain their body temperature by seeking (or avoiding) direct sunshine (and the raising of the body temperature is largely effected via radiant heat energy). Thigmothermy refers to body temperature maintenance by the selection of suitable thermal microclimates in the environment; here the animals would achieve their body temperatures through heat exchange with the surrounding substratum by conduction. The majority of species, however, will demonstrate body temperatures that are a product of both methods of thermoregulation; however this dichotomy provides a useful classification for describing the behavioural regulation of body temperature.

The degree to which body temperature varies will have important consequences for the metabolism of an animal and may reflect aspects of the physiology of the species or, indeed, of the environment that it occupies. For example, animals that experience wide fluctuations in body temperature may indicate that the animal is not a 'precise' thermoregulator (sensu Gibson and Falls 1979) which may cause large variations in metabolic rate. Widely varying body temperatures could alternatively mean that an animal has a wide range of acceptable activity temperatures, i.e. is eurythermal (sensu Pough and Gans 1982); such an animal would have a correspondingly 'flexible' physiology. Thermoconformity, however, need not necessarily indicate imprecise thermoregulation. Animals occupying constant thermal habitats, such as those experienced by many fossorial, nocturnal, aquatic and tropical species, e.g.

Uropeltis sp. (in Avery 1982), Acrochordus arafurae (Shine and Lambeck 1985), may not require the development of complex thermoregulatory behaviour to maintain their 'preferred' body temperatures (Huey 1982).

In this chapter, the body temperatures of C. austriaca recorded in the field are analysed. The range of body temperatures demonstrated can yield information about the thermal niche of the species. The degree to which body temperatures are dependent upon environmental temperatures and cloud cover can indicate the nature of thermoregulation of the species and may help explain observed relationships between behaviour and weather conditions. Certain aspects of thermoregulation were investigated further by laboratory experiments. This latter aspect is presented in Chapter Seven.

6.2. Methods and materials

6.2.1. Data collection

The body temperature (T_b) of each C. austriaca was taken immediately upon capture by inserting a quick acting 'Shultheis' type mercury thermometer into the snake's cloaca. The shaded air temperature (T_a) and bask site temperature (T_{bs}) were then recorded, as defined in Chapter 2 (section 2.2.2). All temperatures were recorded to the nearest tenth of one degree Celsius. Many further values of T_a and T_{bs} were collected whilst radio-tracking, but these values have no corresponding record for body temperature; this latter measurement not being taken so that disturbance to the animal was minimised during radio-tracking. Data from the 1984, 1985 and 1986 field seasons are presented here.

6.2.2. Analysis

The statistical tests used in each analysis are noted along with the significance values in the results. A summary of

the analyses undertaken in section 6.3 is given below.

a. Basic statistics

Mean body temperatures, along with the associated standard deviations and sample sizes, were calculated for all specimens and for each of the sexes separately. Comparisons between the mean values and the distributions of the body temperatures for the two sexes were made.

b. Environmental temperatures and body temperature

Pearson's correlation coefficients were calculated for the relationships between body temperatures and the shaded air temperature and the bask site temperature, for all specimens and the two sexes separately, and the regression equations calculated.

c. Cloud cover and body temperature

The influence of cloud cover on the body temperatures of male, female and all specimens of *C. austriaca* was investigated by calculating Spearman's rank correlation coefficients for the two variables in each case. The effect of varying cloud cover on the displacement of the regression lines for the Body Temperature - Environmental Temperature relationships (for each of shade air and bask site temperatures) was additionally investigated using both five categories and two categories of cloud cover in each case. Mean body temperatures in each of the cloud categories were compared.

d. Environmental temperatures, cloud cover and body temperature

The combined effect of cloud cover and environmental temperatures (shade air and bask site temperatures separately) on body temperatures were described using multiple regression equations.

e. Relationships between environmental variables

Regression equations describing the relationships between shade air and bask site temperatures and between each of these variables and the degree of cloud cover were calculated.

f. Seasonal variation in body temperature

The mean body temperatures for male, female and all specimens of C. austriaca were compared between three defined seasons within the activity period (via One way ANOVA) and between the sexes in each season (via Student's t-test).

g. Diurnal variation in body temperature

The variation in body temperature throughout the course of a day was investigated by comparing body temperatures recorded in discrete two-hourly time periods. Comparisons for male, female and all smooth snakes captured were undertaken for all seasons together and for Spring, Summer and Autumn separately (via One way ANOVA) and between the sexes in each time period (via Student's t-test).

h. The effect of individual condition on body temperature

Body temperatures of smooth snakes were subdivided and compared on the basis of individual condition relating to the slough, feeding and breeding conditions of the animals, (via One way ANOVA and Student's t-test as appropriate).

i. Behaviour and body temperature

The influence of seven defined behaviours on the body temperature of C. austriaca was investigated, performing the analysis on data for all specimens together and the two sexes separately. The analysis was repeated but omitting any 'non-basking' behaviours so that the role of posture on the body temperature of a basking animal could be observed. These analyses used the One way ANOVA.

* Differences in T_A and T_{BS} between the sexes were analysed via Student's t-test and between the time periods via One way ANOVA.

j. Environmental temperature records

The variation in environmental temperatures recorded whilst observing smooth snakes (i.e. T_A and T_{BS}) across the day was investigated by comparing successive discrete two-hourly time blocks*. Data from the three defined seasons were compared both together and separately. Additionally temperature records were collected at hourly intervals throughout the 24-hour cycle, at each of six different locations within the environment, using an automatic temperature recorder. Mean hourly temperatures at each of these points in the habitat are presented separately for each of six months during the final field season. Monthly maxima and minima at each location (and the time periods in which they were recorded) are presented.

6.3. Results

6.3.1. Body temperatures recorded in the field

The mean observed body temperature for male C. austriaca recorded in the field was $23.30^{\circ}\text{C} \pm 3.89$ (range= 13.1 to 31.6°C , $n = 152$) and that for females $23.63^{\circ}\text{C} \pm 4.01$ (range= 10.5 to 31.1°C , $n = 175$). The frequency distributions for these data are presented in Fig. 6.1, and these demonstrate an overall similarity in the observed occurrence of each body temperature between the sexes and that the majority of observations occurred within the range of 20 to 30°C . The F_{max} test indicated homogeneity of variances of body temperatures between male and female C. austriaca ($F = 1.06$, $p > 0.05$). A Student's t-test showed no significant difference between body temperatures in the two sexes ($t = 0.74$ with 325 d.f., $p > 0.05$), nor were the observed frequency distributions shown to differ when tested using the Kolmogorov-Smirnov two-tailed test ($D = 0.060$, $n_1 = 152$, $n_2 = 175$, $p > 0.05$). Thus the data for the the two sexes were pooled for further analysis. The mean body temperature for all specimens of C. austriaca recorded in the field throughout all three study seasons was $23.48^{\circ}\text{C} \pm 3.95$

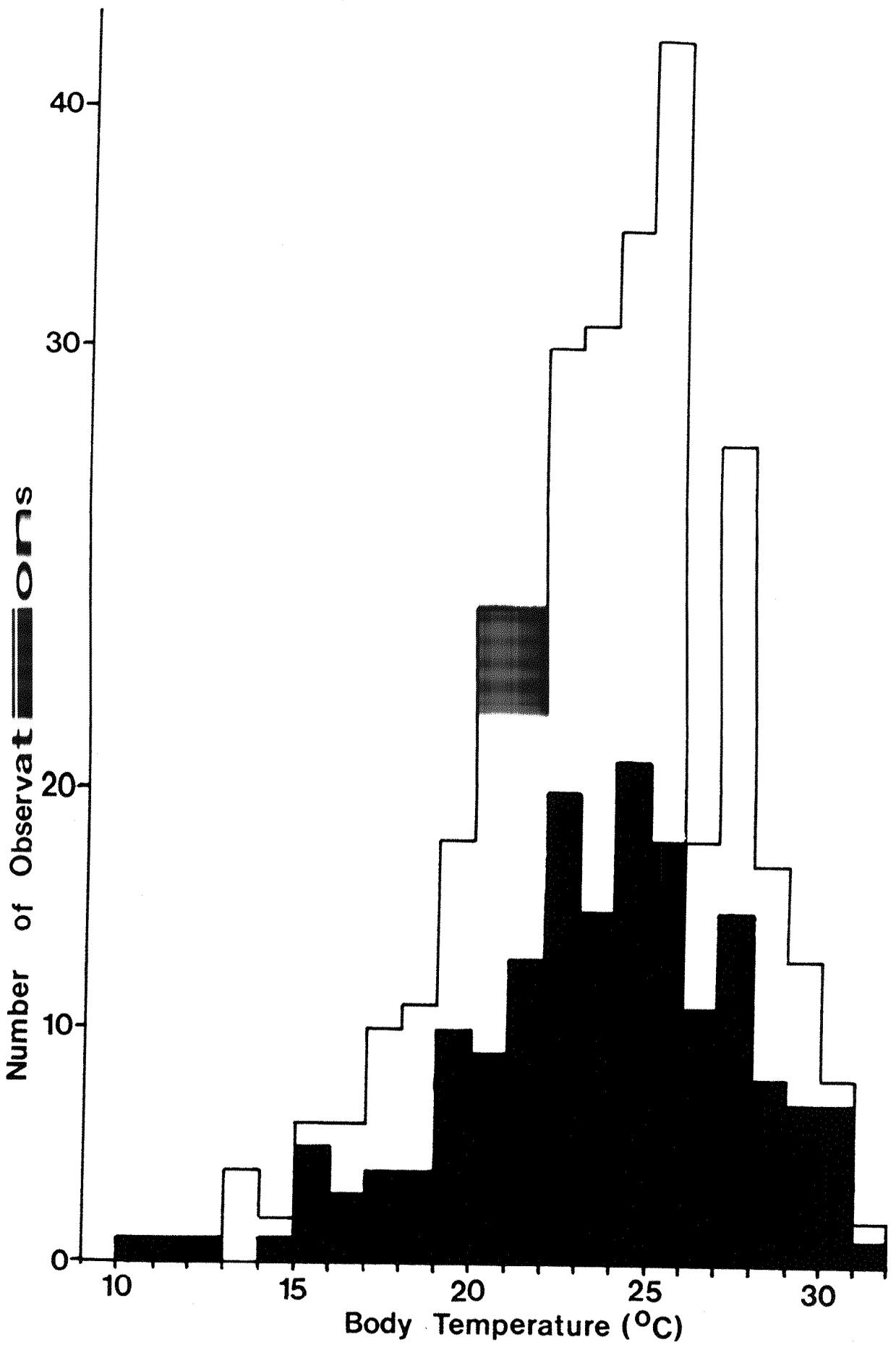


Fig. 6.1 : Frequency Distribution of Body Temperatures ($^{\circ}$ C) of *C. austriaca* observed in the field between April 1984 and October 1986 inclusive, showing those observed for males (unshaded, n=152) and females (dark shading, n=175).

(range= 10.5 to 31.6°C, n= 327).

6.3.2. Relationship between body temperature and environmental temperatures

Body temperature was directly related to shade air temperature (see Fig. 6.2) and showed a high degree of correlation ($r= 0.698$ with 325 d.f., $p<0.001$). In all but ten cases the observed body temperature was higher than the shade air temperature, and often considerably so. The regression equation calculated for this relationship was:

$$T_B = (0.916 \times T_A) + 6.42$$

The equation illustrates that the observed relationship was displaced to the left of the 'expected' relationship if the two variables were always equal. In addition, Fig. 6.2 shows the similarity of the relationship of T_B and T_A for each of the two sexes. This similarity was further demonstrated by the similarity of the regression equations derived from separate analysis of the data for each of the sexes. The regression equations obtained from these analyses were:

$$\text{Males: } T_B = (0.909 \times T_A) + 6.07$$

$$(r= 0.681 \text{ with } 150 \text{ d.f.}, p<0.001)$$

$$\text{Females: } T_B = (0.951 \times T_A) + 6.21$$

$$(r= 0.728 \text{ with } 173 \text{ d.f.}, p<0.001)$$

Both the slopes and the intersects of the regression lines for the two sexes showed a considerable degree of similarity.

Body temperatures showed a closer correlation with bask site temperatures ($r= 0.818$ with 325 d.f., $p<0.001$), (Fig. 6.3) than with shade air temperatures. The regression equation derived from the relationship between body

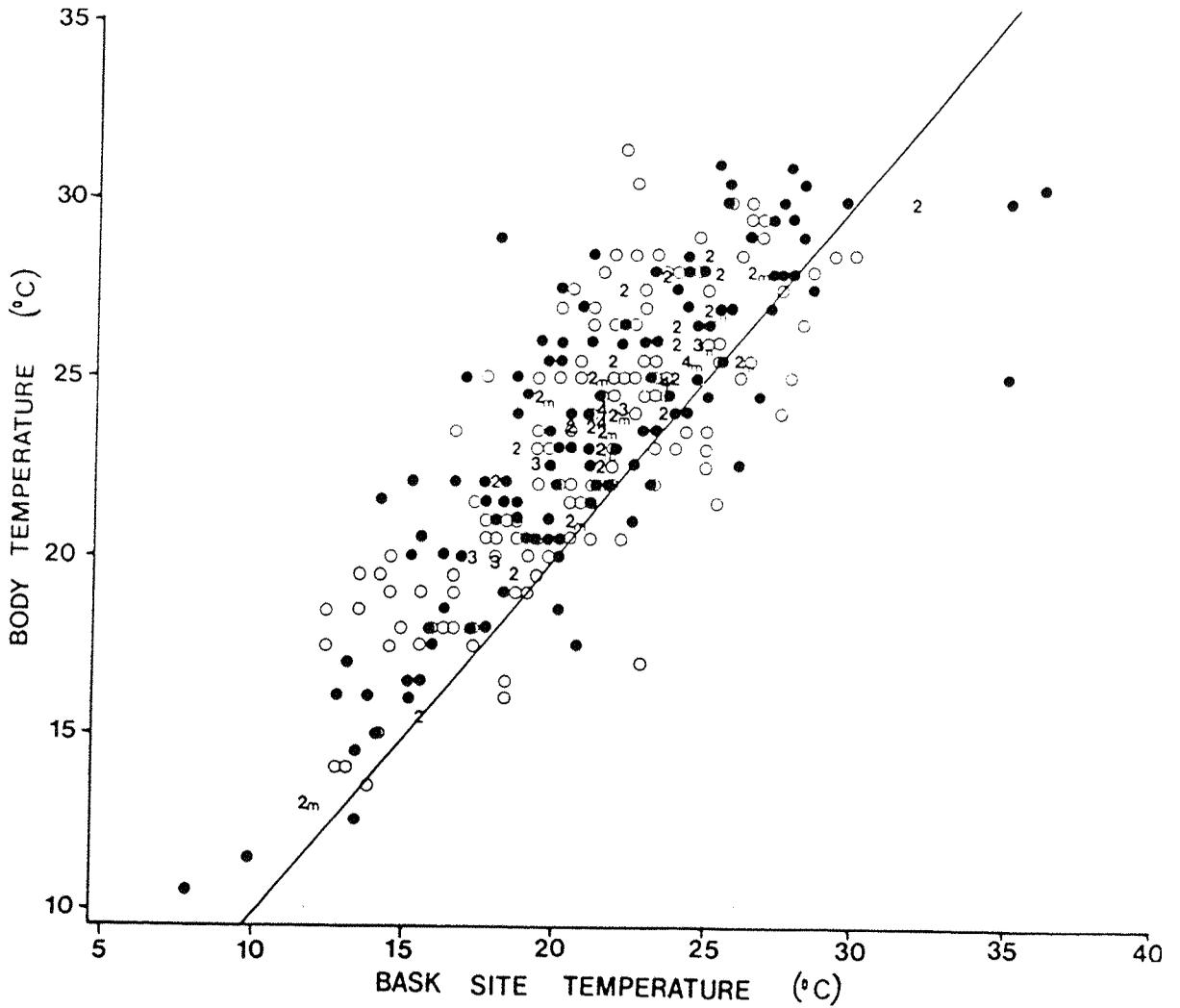


Fig. 6.3 : Relationship between Body Temperature ($^{\circ}\text{C}$) and Bask Site Temperature ($^{\circ}\text{C}$) for male (open circles, $n=152$) and female (closed circles, $n=175$) *C. austriaca* recorded in the field between April 1984 and October 1986 inclusive.

Solid line indicates Body temperature equalling Bask Site Temperature. Numbers indicate positions where more than one sighting occurred and are for female snakes unless accompanied by the subscript 'm' which indicates observations of male specimens.

temperature and the associated bask site temperature was:

$$T_B = (0.753 \times T_{BS}) + 7.16$$

Data for the two sexes showed a very similar relationship between body temperatures and bask site temperatures (T_{BS}) in each case (see Fig. 6.3.) and the respective regression equations, and associated correlation coefficients, further illustrated this. The regression equations and correlation coefficients obtained from the analysis of the data separately for each sex were as follows:

$$\text{Males: } T_B = (0.796 \times T_{BS}) + 6.46$$

$$(r = 0.804 \text{ with } 150 \text{ d.f.}, p < 0.001)$$

$$\text{Females: } T_B = (0.757 \times T_{BS}) + 7.43$$

$$(r = 0.829 \text{ with } 173 \text{ d.f.}, p < 0.001)$$

Visual comparison of the regression lines showed that body temperatures were more closely correlated with bask site temperatures than with shade air temperatures over the range of values recorded (Fig. 6.4) (see above for equations). The regression line describing the relationship between body and shade air temperatures had a gradient of 0.916 and lay almost parallel to the hypothetical line which describes where the two variables are equal. This regression line shows that body temperature was maintained at between approximately 4 and 6°C above the ambient temperature. Bask site temperature showed a less consistent relationship with body temperature. In this latter case the line had a less steep slope (with a gradient of 0.818). Hence, at lower temperatures (T_{BS} below 10°C) the value of T_B was almost 5°C above T_{BS} , but with increasing temperature the two variables became increasingly similar. Body temperature equalled the bask site temperature at about 30°C.

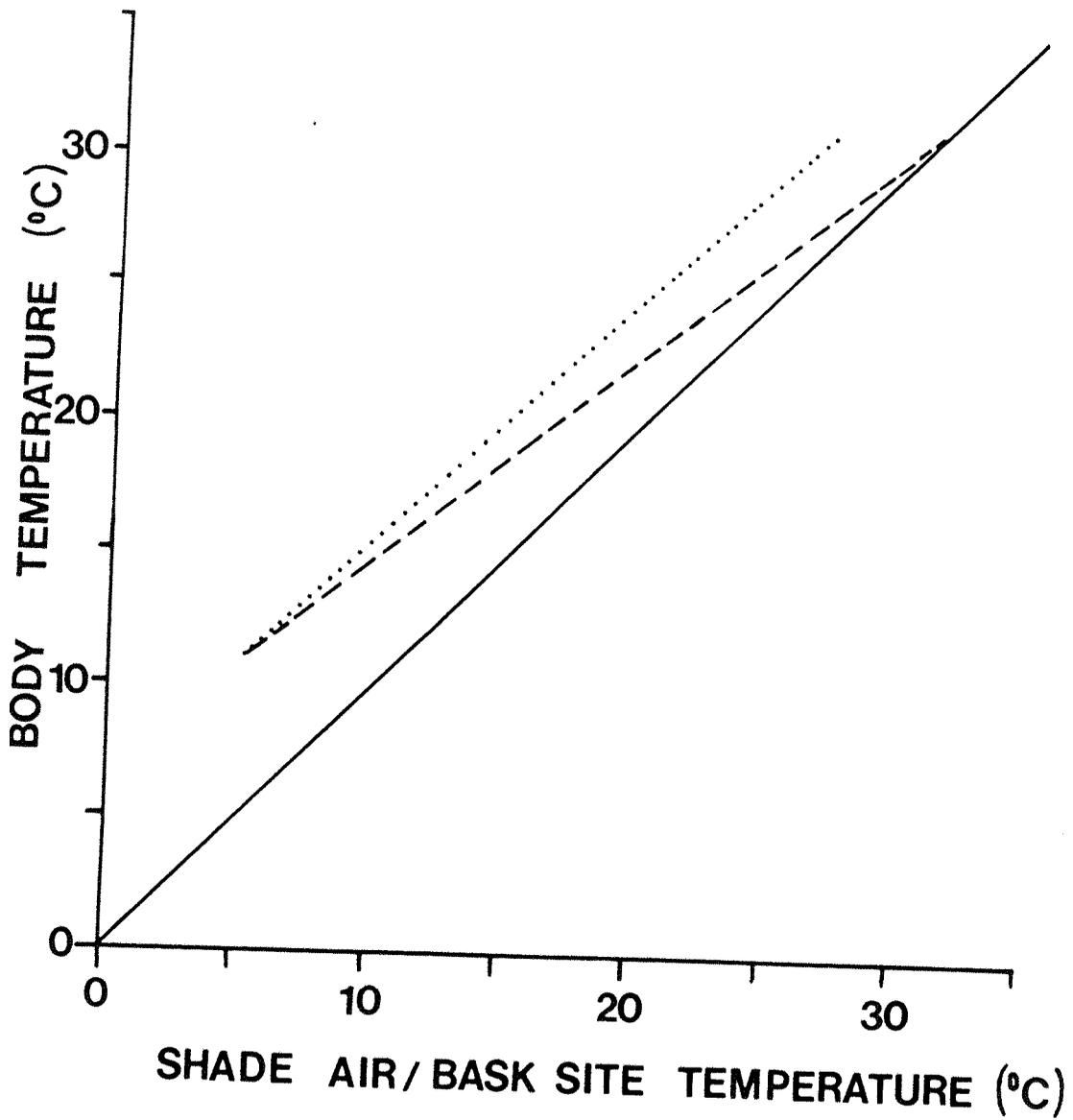


Fig. 6.4 : Regression lines showing the relationship between Body Temperature ($^{\circ}\text{C}$) and Shade Air Temperature ($^{\circ}\text{C}$) (dotted line) and between Body Temperature ($^{\circ}\text{C}$) and Bask Site Temperature ($^{\circ}\text{C}$) (dashed line) for male and female *C. austriaca* captured in the field between April 1984 and October 1986 inclusive. Solid line indicates Body Temperature equalling Shade Air / Bask Site Temperature.

6.3.3. Effect of cloud cover on body temperature

Although the amount of solar radiation reaching the ground varies both diurnally and seasonally, one of the major factors effecting insolation on a daily basis is cloud cover. The influence of solar radiation upon body temperature may help in the understanding of the nature of thermoregulation of a species. It was therefore considered instructive to investigate the effect of changing cloud cover on the body temperature of C. austriaca captured in the field.

Cloud cover was quantified using nine distinct categories (Cld) (0 to 8 inclusive) describing the fraction (in eighths) of the sky covered by cloud. Comparisons between these categories, therefore, necessitated the use of non-parametric statistics. A Spearman's rank correlation indicated that increasing cloud had a significantly depressing effect on the body temperatures of C. austriaca in the field ($r_s = -0.304$ $n = 325$, $p < 0.001$). The regression equation describing the relationship observed between body temperature and cloud cover was:

$$T_b = (-0.374 \times \text{Cld}) + 25.42$$

The regression line of body temperature against cloud cover is presented in Fig. 6.5 and illustrates the decreasing value of T_b observed with increasingly overcast skies.

The effect of cloud cover on body temperature was further investigated by observing the position of the regression lines which described the relationships between body temperature and shade air and bask site temperatures for different categories of cloud cover. Thus the influence of increasing cloud cover on the body temperatures of C. austriaca could be observed over the range of observed shade air and bask site temperatures. For an animal that is dependent on solar radiation for the maintenance of its body temperature, an increase in cloud cover could be

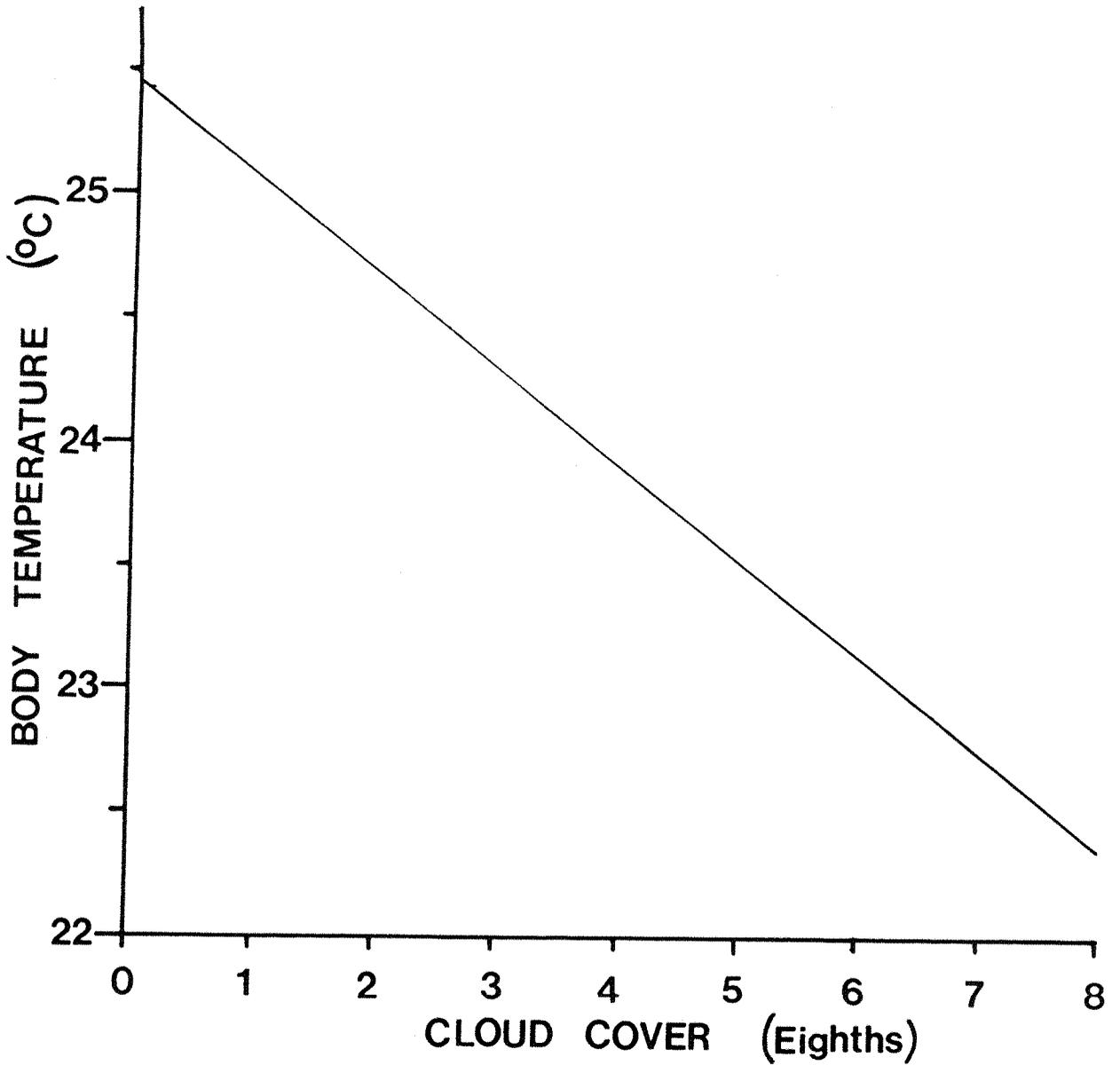


Fig. 6.5 : Regression line showing the relationship between Body Temperature (°C) and Cloud Cover (eighths) for specimens of *C. austriaca* captured in the field between April 1984 and October 1986 inclusive.

expected to result in a decreased body temperature at any given environmental temperature (T_A or T_{BES}), and hence displace the regression line of body temperature against environmental temperature to the right. The degree of displacement of these lines, however, will depend on the importance of solar radiation to the respective environmental temperatures relative to importance of this factor to body temperature.

Regression equations for the relationships between body temperature and shade air and bask site temperatures were calculated for each of five different categories of cloud cover namely: Cloudless (0 eighths), light cloud (1 to 2 eighths), medium cloud (3 to 5 eighths), mostly cloudy (6 to 7 eighths) and totally overcast (8 eighths); sample sizes were 23, 36, 76, 98 and 92 respectively.

The regression lines for body temperature against both shade air and bask site temperatures for each of the cloud cover categories are presented in Fig. 6.6. Increasing cloud cover generally resulted in the displacement of the regression lines towards the right for shade air temperatures of less than about 23°C. Above this value the regression lines merged, perhaps indicating less dependence on solar radiation when the ambient temperatures are higher. The exception to this trend is the regression line calculated from data obtained on cloudless days (0 eighths cloud cover). Here the regression line lies between those obtained for the two most overcast categories. It should also be noted that this line was calculated from data that included higher values of T_A than found in any other category of cloud cover. The equations describing these lines were as follows:

0 eighths:	$T_B = (0.96 \times T_A) + 5.10$
1 to 2 eighths:	$T_B = (0.54 \times T_A) + 15.0$
3 to 5 eighths:	$T_B = (0.82 \times T_A) + 8.67$
6 to 7 eighths:	$T_B = (0.83 \times T_A) + 8.34$
8 eighths:	$T_B = (1.16 \times T_A) + 0.77$

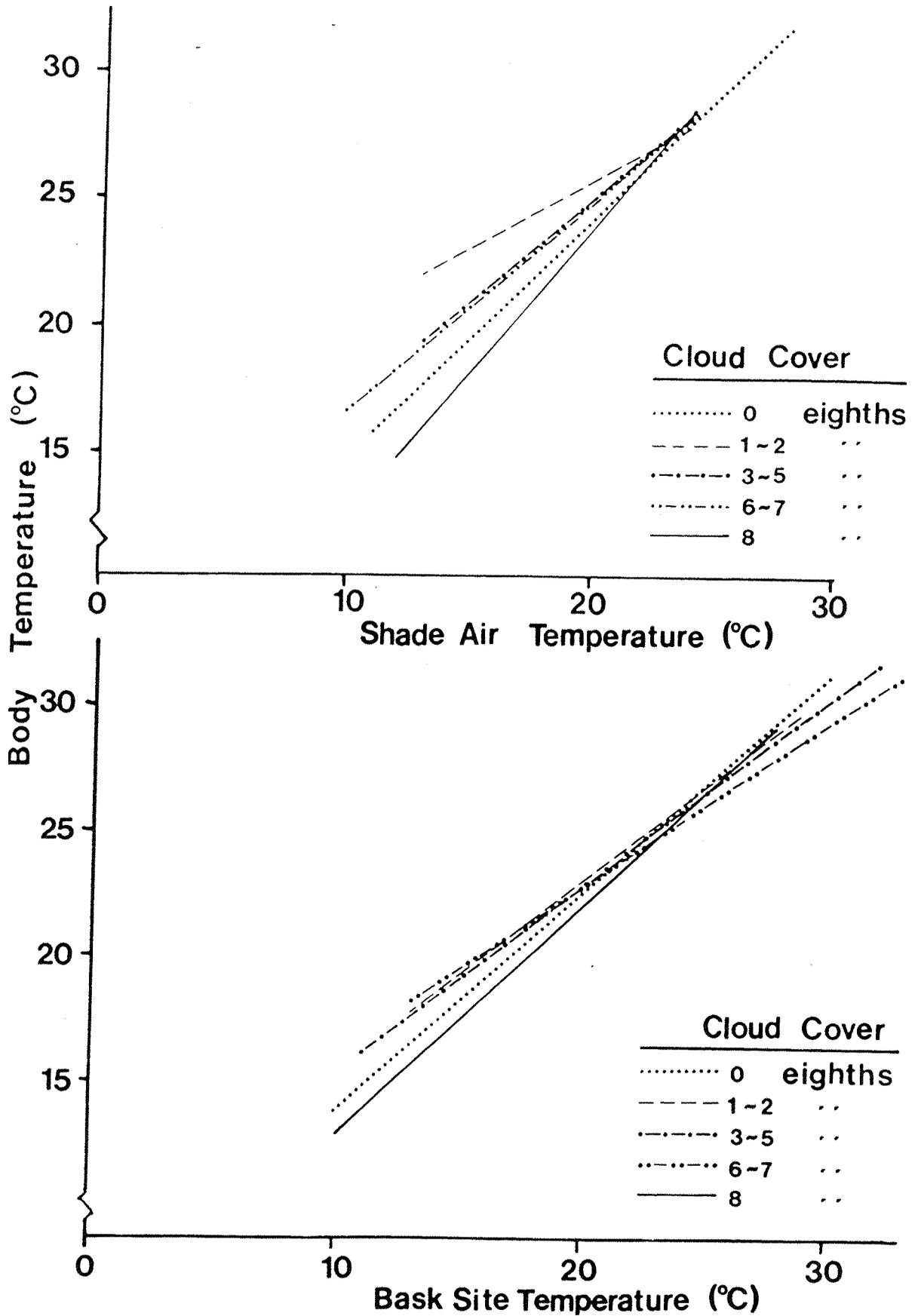


Fig. 6.6 : Regression lines showing the relationship between body temperature ($^{\circ}\text{C}$) and A. Shade Air temperature ($^{\circ}\text{C}$) and B. Bask Site temperature ($^{\circ}\text{C}$) for each of five different degrees of cloud cover (0, 1 to 2, 3 to 5, 6 to 7 and 8 eighths cover) for specimens of *C. austriaca* captured in the field between April 1984 and October 1986 inclusive.

The regression equations obtained from the five different cloud cover categories for the relationship between snake body temperature and the associated bask site temperatures yielded regression lines that were quite similar to each other with regard to both position and slope. At lower temperatures (i.e. below approximately 24°C) the regression lines obtained from data associated with three intermediate categories of cloud cover are displaced slightly more to the left than those associated with the two extremes. However at approximately 24°C the lines intersect and thereafter higher values of T_B are associated with cloudless and completely overcast skies, at any given bask site temperature, than for the intermediate categories of cloud cover. The regression equations that described these lines were as follows:

0 eighths:	$T_B = (0.87 \times T_{BS}) + 5.14$
1 to 2 eighths:	$T_B = (0.75 \times T_{BS}) + 8.00$
3 to 5 eighths:	$T_B = (0.74 \times T_{BS}) + 7.88$
6 to 7 eighths:	$T_B = (0.65 \times T_{BS}) + 9.74$
8 eighths:	$T_B = (0.91 \times T_{BS}) + 3.81$

A more simplistic approach to that used above for investigating the relationship of cloud cover with body temperature, and that used by Goddard (1981), is to observe two categories of cloud cover only. The most useful binary division was into 'clear skies' (0 to 7 eighths), where solar radiation could penetrate the cloud and hence potentially influence body temperature, and 'cloudy skies' (8 eighths cover), where total cloud cover was likely to prevent the sun from directly effecting the thermoregulation of the animal. The regression equations obtained from the relationship between body temperature and shade air temperature for the two cloud cover conditions were as follows:

Clear skies (0 to 7 eighths):	$T_B = (0.81 \times T_A) + 8.87$
Cloudy skies (8 eighths):	$T_B = (1.16 \times T_A) + 0.77$

for $n = 233$ and 92 observations respectively. These

equations describe two converging lines, which meet where the value for $T_B = 27.62$ and $T_A = 23.14$, with the former line (clear skies) being above the latter (cloudy skies) over the range of values below the intersect. Thus, for the majority of the temperatures observed in the field, a greater body temperature was recorded at any given shade air temperature when associated with clear rather than cloudy skies.

The relationships between body temperature and bask site temperature for each of the two cloud conditions yielded regression equations that also described converging lines, although the slopes of these two lines were more similar to each other than those observed for the relationships between body and shade air temperatures. Thus, over the range of temperatures recorded, body temperatures at any given bask site temperature were very similar for either of the two cloud conditions. The regression equations calculated for the two cloud conditions for the Body Temperature - Bask Site Temperature relationship were:

$$\begin{aligned} \text{Clear skies (0 to 7 eighths): } T_B &= (0.73 \times T_{BS}) + 8.26 \\ \text{Cloudy skies (8 eighths): } T_B &= (0.91 \times T_{BS}) + 3.82 \end{aligned}$$

for $n = 233$ and 92 observations respectively. The lines intersected at a value for $T_B = 26.27$ and $T_{BS} = 24.67$. At values below this point body temperatures at any given bask site temperature were higher when associated with cloudless skies (0 to 7 eighths) than with cloudy skies (8 eighths cloud cover). At higher bask site temperatures higher body temperatures were associated with cloudy skies than clear skies.

Mean values for body temperatures recorded in each of the five above mentioned cloud cover categories (0, 1 to 2, 3 to 5, 6 to 7 and 8 eighths) are presented in Table 6.1. Body temperatures recorded in each group were compared via a one way ANOVA. The variances for each group were homogeneous ($F = 1.28$, $p > 0.05$). A highly significant difference was detected between the body temperatures in

Cloud group	Cloud cover (eighths)	Mean Body Temp. (°C)	s.d.	Sample size (n)
1	0	24.1	4.90	23
2	1 to 2	25.4	3.52	36
3	3 to 5	24.2	3.98	76
4	6 to 7	23.3	3.52	98
5	8	22.0	3.74	92

Table 6.1 : Mean body temperature (°C), and associated standard deviation (s.d.) and sample size (n), of all specimens of C. austriaca captured in the field for each of five cloud cover categories, during April 1984 to October 1986 inclusive.

the different cloud cover groups ($F= 6.771$, with 4 and 320 d.f., $p<0.001$) indicating that cloud cover affected body temperature. With the exception of skies with 0 eighths cloud cover, where a mean value between that recorded for intermediate (3 to 5 eighths) and mostly cloudy skies (6 to 7 eighths) was observed, a trend of decreasing body temperature with increasing cloud cover was detected. A similar comparison, dividing the data into just two categories (namely 'clear skies' (0 to 7 eighths) and 'cloudy skies' (8 eighths)), was undertaken using a Student's t-test. The variances of the two groups were homogeneous ($F_{max} = 1.07$, $p>0.05$). The corresponding mean values for two cloud cover regimes were $24.0^{\circ}\text{C} \pm 3.87$ ($n=233$) and $22.0^{\circ}\text{C} \pm 3.74$ ($n =92$) for 'clear' and 'cloudy skies' respectively. These values were significantly different ($t= 4.35$ with 323 d.f., $p<0.001$).

6.3.4. Relationship between body temperatures and both environmental temperatures and cloud cover combined

Results from sections 6.3.2 and 6.3.3 demonstrated that the body temperatures of C. austriaca were a function of both environmental temperatures and the degree of cloud cover. Thus, regression equations to predict body temperature are likely to be more accurate if both environmental temperatures and cloud cover are incorporated. Correlation coefficients cannot, however, be calculated since these require all elements on the right hand side of the equation to be independent of each other. Environmental temperatures, and in particular the bask site temperature, were correlated with cloud cover (see section 6.3.5). The regression equations derived for the relationship between body temperature and shade air and bask site temperatures which additionally incorporated a measure of the degree of cloud cover were as follows:

$$T_B = (0.886 \times T_A) - (0.215 \times \text{Cld}) + 8.118$$

$$T_B = (0.768 \times T_{BS}) - (0.106 \times \text{Cld}) + 7.696$$

where T_B , T_A and T_{BS} are in degrees celsius and Cld is

cloud cover in eighths.

6.3.5. Relationship between environmental variables (shade air and bask site temperatures and cloud cover)

At anyone time different sites within the habitat will offer a variety of temperature regimes (see section 6.3.10). Thus a thermoregulating ectotherm may select sites on the basis of temperature and that these in turn would result in a body temperature as near to a 'preferred' value as possible. Comparison of observed bask site temperatures with some measurement of the corresponding 'weather conditions' that are independent of snake behaviour, i.e. the shade air temperature, enabled the degree of thermal site selection shown by C. austriaca to be investigated.

Bask site temperature was highly positively correlated with shade air temperature ($r = 0.806$ with 1753 d.f., $p < 0.001$) with an increase in shade air temperature being associated with an increase bask site temperature (see Fig. 6.7). The regression equation that describes this relationship was:

$$T_{bs} = (1.02 \times T_a) + 0.522$$

The regression line of bask site temperature against shade air temperature is presented in Fig. 6.7. The regression line and equation showed that the bask site temperature was consistently higher than the shade air temperature. The gradient of the slope was very close to 1 and hence, over the range of values measured, the bask site temperature was an approximately constant amount greater than the associated shade air temperature, i.e. by 0.522°C .

Spearman rank correlation coefficients demonstrated that cloud cover was negatively correlated with both shade air and bask site temperatures ($r_s = -0.311$, $n = 1755$, $p < 0.001$ and $r_s = -0.294$, $n = 1753$, $p < 0.001$ respectively), with

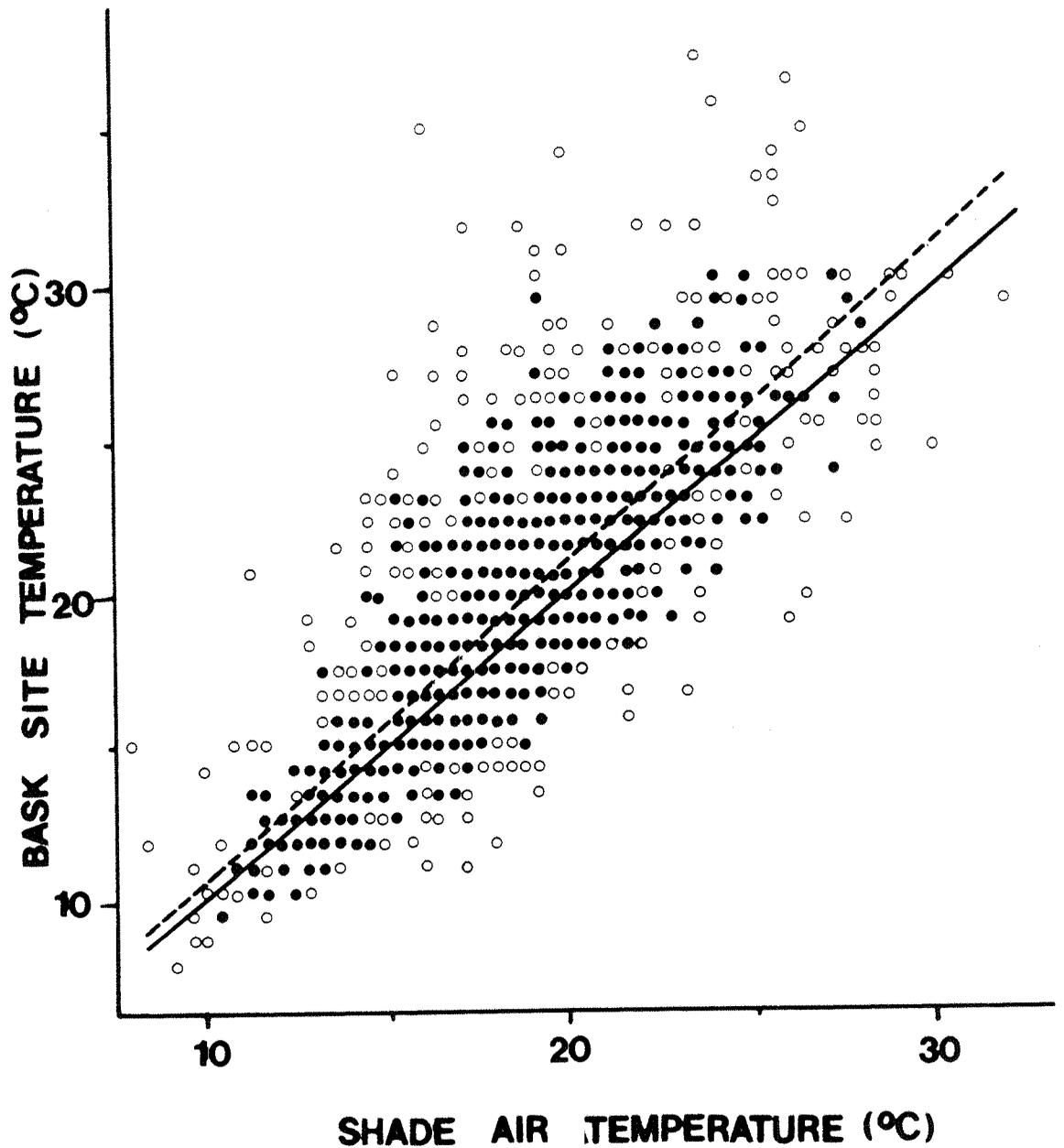


Fig. 6.7 : Relationship between Bask Site Temperature ($^{\circ}\text{C}$) and Shade Air Temperature ($^{\circ}\text{C}$) and the regression line of the relationship (dashed line) recorded whilst observing male and female *C. austriaca* in the field between April 1984 and October 1986 inclusive ($n=1755$). Open circles represent a single observation, closed circles represent more than one observation at any given pair of coordinates. The solid line indicates Bask Site Temperature equalling Shade Air Temperature.

increasing levels of cloud having a depressive effect on both temperature variables. Regression equations describing the relationship between the two temperature variables and cloud cover were:

$$T_A = (-0.375 \times \text{Cld}) + 20.58$$

$$T_{BB} = (-0.415 \times \text{Cld}) + 21.75$$

Regression lines illustrating the above relationships are presented in Fig. 6.8.

6.3.6. Seasonal variation of body temperature

With the aim of investigating seasonal variation in field body temperatures, the activity period was arbitrarily divided into three 'seasons', namely Spring (March to May), Summer (June to August) and Autumn (September to October). Body temperatures were separated by sex and comparisons made between seasons for each sex and between sexes within each season using one way analysis of variance and Student's t-tests respectively.

Mean body temperatures, and their respective standard deviations and sample sizes, for each sex in each season are presented in Table 6.2 and illustrated in Fig. 6.9. Heterogeneity of variances was indicated for body temperatures for both male and female smooth snakes between the seasons using the Bartlett-Box F test ($F=4.222$, $p<0.02$ and $F=6.276$, $p=0.02$ respectively) and hence the results of the analyses of variance must be treated with caution. Significant differences in body temperature were observed for each of the sexes between the seasons ($F=5.805$ with 2 and 148 d.f., $p<0.004$ for males and $F=5.995$ with 2 and 172 d.f., $p=0.003$ for females), with higher mean body temperatures being observed during the summer than during either Spring or Autumn in both cases. For both male and female C. austriaca body temperatures observed in Spring were slightly higher than those observed during Autumn although large variances were associated with these values and they were not

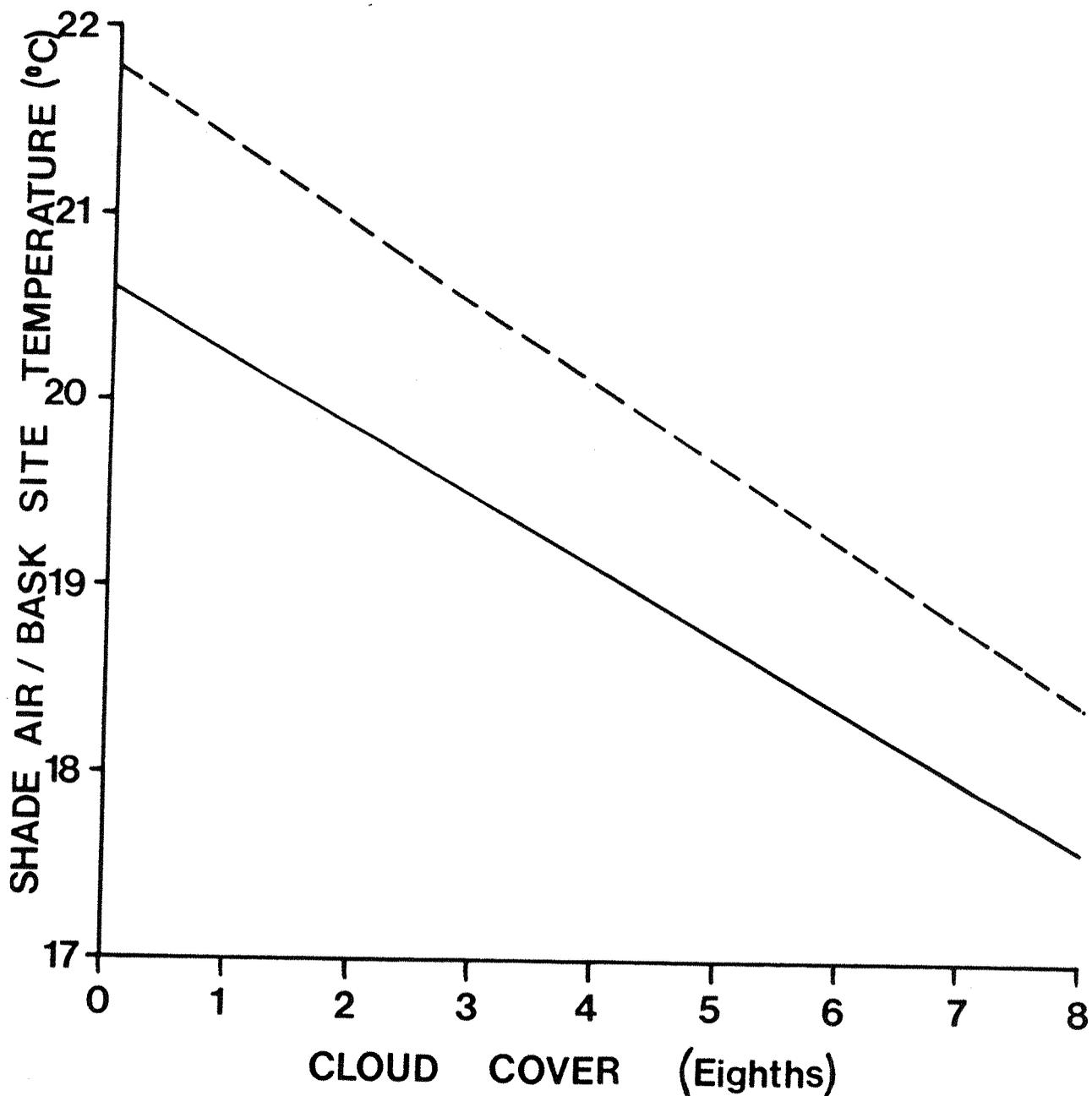


Fig. 6.8 : Regression lines showing the relationship between Shade Air Temperature (°C) and Cloud Cover (eighths) (solid line) and between Bask Site Temperature (°C) and Cloud Cover (eighths) (dashed line) recorded whilst observing *C. austriaca* in the field between April 1984 and October 1986 inclusive.

<u>Sex</u>	<u>Spring</u>			<u>Summer</u>			<u>Autumn</u>		
	Mean	s.d.	n	Mean	s.d.	n	Mean	s.d.	n
Male	22.38	4.63	36	24.18	3.20	87	21.74	4.29	28
Female	22.73	5.53	19	24.45	32.7	105	22.26	4.36	51
Male and Female	22.50	4.91	55	24.33	3.23	192	22.08	4.31	79

Table 6.2 : Mean body temperatures ($^{\circ}\text{C}$) of male, female and both male and female *C. austriaca* recorded in the field during Spring, Summer and Autumn throughout the study period between April 1984 and October 1986 inclusive, with associated standard deviations (s.d.) and sample sizes (n).

statistically significant when tested pairwise ($t = 0.566$ with 62 d.f., $p > 0.05$ and $t = 0.372$ with 68 d.f., $p > 0.05$, respectively).

No significant differences were detected between the two sexes within any one season ($t = 0.25$ with 53 d.f., $t = 0.57$ with 190 d.f. and $t = 0.51$ with 77 d.f., $p > 0.05$ in all cases, for Spring to Autumn respectively) nor were the variances observed to be heterogeneous in any case ($F_{\max} = 1.43, 1.04$ and 1.03 respectively, $p > 0.05$ in all cases).

The absence of any significant differences between the sexes within any season allowed data for male and female snakes to be pooled to enhance sample sizes for comparisons between the seasons. Mean body temperatures for each season for the two sexes combined are presented in Table 6.2. A Bartlett-Box F test indicated heterogeneity of variances between seasons ($F = 10.028$, $p < 0.001$) and, as such, the result of the analysis of variance must be interpreted with care. Significantly different body temperatures were recorded in the three different seasons ($F = 11.82$ with 2 and 323 d.f., $p < 0.001$) with the highest mean body temperature being observed in the Summer. The mean body temperature recorded during Spring was slightly higher (0.42°C) than that recorded during Autumn although these latter two values were not statistically different, when tested pairwise ($t = 0.711$ with 132 d.f., $p > 0.05$), due to the large variances associated with each.

6.3.7. Diurnal variation of body temperature

Diurnal variation in body temperature was investigated by comparison of body temperatures in two-hourly time blocks over the day using a one way ANOVA. Data for the two sexes and the three seasons were analysed by pooling body temperature measurements for each season and for each sex and by analysing the data separately for each sex, each season and each sex within each season.

Mean values for body temperatures of male, female and both male and female smooth snakes during two hour time periods over the day recorded in all three seasons during the study period are presented in Table 6.3. Mean body temperatures for the three seasons and the two sexes, both pooled and separately, are illustrated in Fig. 6.10.

Pooled data for male and female snakes throughout the entire activity period showed homogeneity of variances of body temperatures between the time groups ($F = 0.056$, $p > 0.05$) and indicated no variation in body temperature across the day ($F = 1.831$ with 6 and 320 d.f., $p > 0.05$). The overall mean value of body temperature for the two sexes over the whole season is $23.5^{\circ}\text{C} \pm 3.95$ (see Table 6.3). Mean values, and the associated standard deviations, for body temperatures during each two hour period are presented in Table 6.3. Mean body temperatures ranged from 17.4 to 24.6°C , however relatively large standard deviations were associated with each value.

Differences in mean body temperature between the two sexes at each time period were tested using a Student's t-test on data from all seasons combined. Variances of the body temperature data were homogeneous between the two sexes at each time category when tested using the F_{\max} test ($F_{\max} = 1.59, 1.06, 1.39, 1.71, 1.68$ and 1.41 for the time periods 0800-0959, 1000-1159, 1200-1359, 1400-1559, 1600-1759, 1800-1959 hrs respectively. $p > 0.05$ in all cases). No difference in body temperature was observed between male and female C. austriaca at any of the time periods ($t = 1.04$ with 21 d.f., 0.28 with 66 d.f., 1.39 with 68 d.f., 0.01 with 58 d.f., 1.61 with 69 d.f. and 1.51 with 32 d.f. for the six time categories from 0800-0959 to 1800-1959 hrs respectively. $p > 0.05$ respectively).

Although no heterogeneity was detected between the body temperatures of the different sexes in each time category, data for male and female snakes were separated to assess whether body temperatures varied across the day within each sex. Mean body temperatures for the two sexes during

Time (BST)	Male			Female			Male & Female		
	Mean	s.d.	n	Mean	s.d.	n	Mean	s.d.	n
08-0959	22.2	3.48	9	24.1	4.38	14	23.3	4.07	23
10-1159	22.7	3.88	26	23.0	3.99	42	22.9	3.92	68
12-1359	23.7	4.30	36	22.4	3.66	34	23.0	4.03	70
14-1559	23.6	3.34	28	23.6	4.37	32	23.6	3.89	60
16-1759	23.9	4.23	35	25.3	3.26	36	24.6	3.82	71
18-1959	22.4	3.49	18	24.4	4.15	16	23.3	3.89	34
20-2159	-	-	-	17.4	-	1	17.4	-	1
Overall	23.3	3.90	152	23.6	4.01	175	23.5	3.95	327

Table 6.3 : Mean Body Temperatures ($^{\circ}$ C) of male, female and both male and female C. austriaca captured in the field in different two-hour time blocks, April 1984 to October 1986 inclusive, and the associated standard deviations (s.d.) and sample sizes (n).

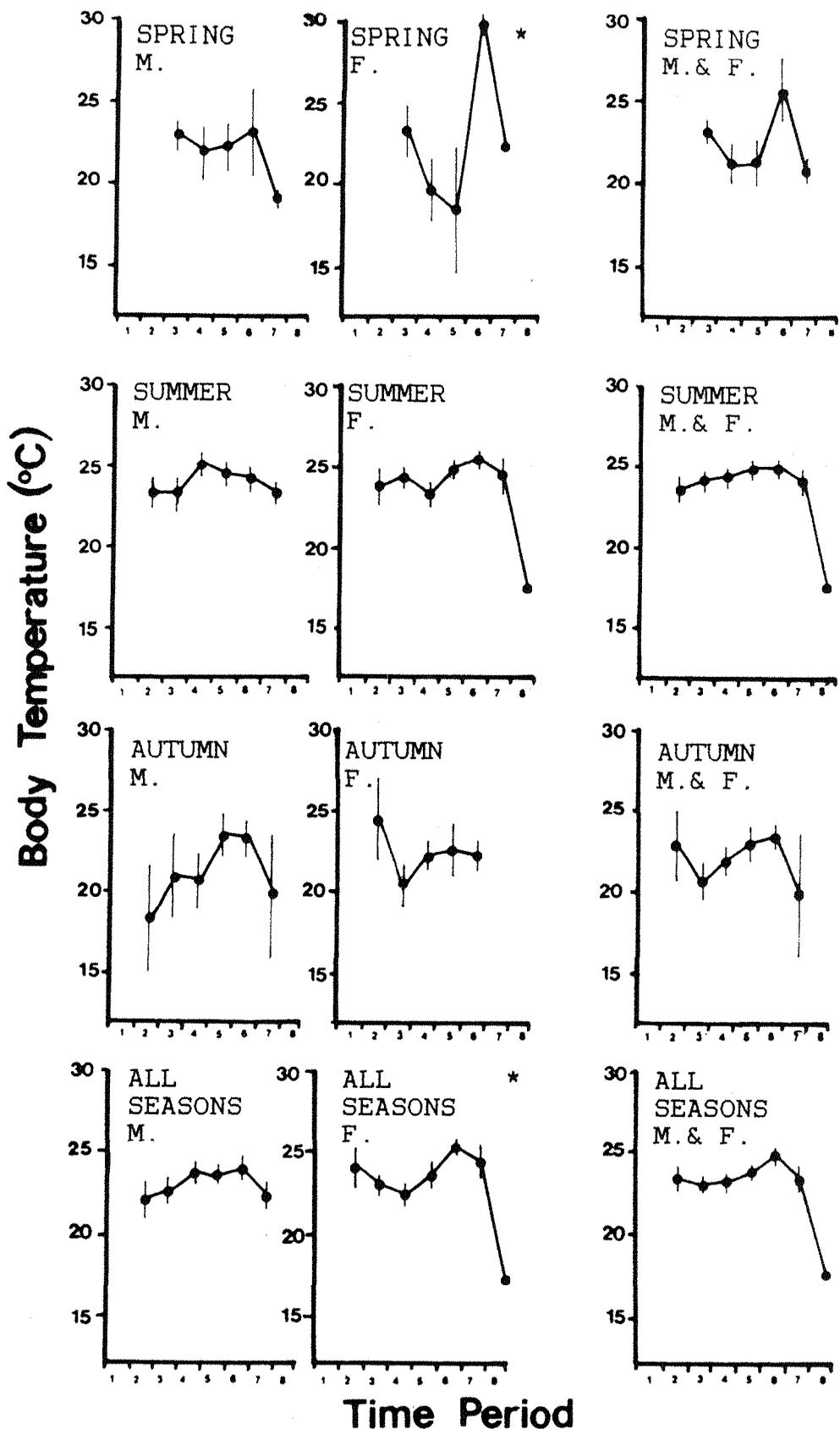


Fig. 6.10 : Diurnal variation in mean body temperature ($^{\circ}\text{C}$) (± 1 s.e.) for male (M.), female (F.) and male and female (M. & F.) *C. austriaca* captured in the field during Spring (March-May), Summer (June-August), Autumn (September-October) and All seasons combined during 1984 and 1986 inclusive. Time periods are in two hour time blocks as follows: 1= 06-0759, 2= 08-0959, 3= 10-1159, 4= 12-1359, 5= 14-1559, 6= 16-1759, 7= 18-1959 and 8= 20-2159 hrs BST. * denotes significant difference in mean body temperatures between time periods at 5% level.

each time period, and their associated standard deviations, are presented in Table 6.3 and Fig. 6.10. Body temperatures of male C. austriaca demonstrated no heterogeneity of variances ($F = 0.582$, $p > 0.05$) and a one way ANOVA indicated no differences in body temperature across the day ($F = 0.706$ with 5 and 146 d.f., $p > 0.05$). The data for female smooth snakes also showed homogeneity of the variances for the body temperatures between the seven time periods ($F = 0.608$, $p > 0.05$) although here a significant variation in the mean body temperature was detected throughout the day ($F = 2.475$ with 6 and 168 d.f., $p < 0.03$). A slight 'peak' in body temperature of female snakes was observed during the late afternoon (1600–1759 hrs) with the lowest values being recorded during the early afternoon (1200–1359 hrs).

Collective body temperature records were shown to vary at different times of year (see section 6.3.6) and therefore body temperature data were analysed for variation across the day during each of the three seasons separately. Analyses of variance were performed on data for the two sexes, both separately and pooled together. Mean body temperatures recorded during each time period for male and female C. austriaca and for all specimens captured within each season are presented in Table 6.4 for Spring, Table 6.5 for Summer and Table 6.6 for Autumn.

Pooling data for the two sexes and analysing data for each of the three seasons separately, via a one way ANOVA, showed that no significant variation in body temperature occurred between the time categories in any of the seasons ($F = 1.863$ with 4 and 50 d.f., $F = 1.294$ with 6 and 185 d.f. and $F = 1.080$ with 5 and 73 d.f. for Spring, Summer and Autumn respectively. $p > 0.05$ in all cases). The variances associated with the body temperatures in each time group were homogeneous in Spring, Summer and Autumn ($F = 1.992$, 0.637 and 1.080 respectively, $p > 0.05$ in all cases).

Male smooth snakes showed no variation of body temperature between the time periods during any of the three seasons

Spring

Time (BST)	Male			Female			All Specimens		
	Mean	s.d.	n	Mean	s.d.	n	Mean	s.d.	n
10-1159	22.9	3.22	10	23.1	3.97	6	23.0	3.39	16
12-1359	21.9	4.94	9	19.5	4.17	5	21.0	4.68	14
14-1559	22.2	4.16	8	18.3	6.78	3	21.1	4.95	11
16-1759	23.2	7.27	7	29.7	0.99	4	25.6	6.54	11
18-1959	19.9	0.64	2	22.1	-	1	20.6	1.37	3
Overall	22.4	4.63	36	22.7	5.53	19	22.5	4.91	55

Table 6.4 : Mean Body Temperatures ($^{\circ}$ C) during Spring (March to May) 1984 to 1986 inclusive of male, female and all specimens of C. austriaca captured in the field in different two-hour time blocks showing standard deviation (s.d.) and sample size (n). Time is indicated as '00hrs BST.

Summer

Time (BST)	Male			Female			All specimens		
	Mean	s.d.	n	Mean	s.d.	n	Mean	s.d.	n
08-0959	23.3	2.52	7	23.8	3.75	9	23.6	3.18	16
10-1159	23.3	3.59	11	24.4	2.92	23	24.1	3.15	34
12-1359	25.5	3.66	21	23.3	3.11	16	24.3	3.52	37
14-1559	24.5	2.65	13	24.9	2.70	19	24.8	2.65	32
16-1759	24.2	3.39	22	25.5	2.92	22	24.8	3.19	44
18-1959	23.4	2.50	13	24.5	4.25	15	24.0	3.53	28
20-2159	-	-	-	17.4	-	1	17.4	-	1
Overall	24.2	3.20	87	24.5	3.27	105	24.3	3.23	192

Table 6.5 : Mean Body Temperatures ($^{\circ}$ C) during Summer (June to August) 1984 to 1986 inclusive of male, female and all specimens of C. austriaca captured in the field in different two-hour time blocks, showing standard deviation (s.d.) and sample size (n). Time is indicated as '00hrs BST.

Autumn

Time (BST)	Male			Female			All specimens		
	Mean	s.d.	n	Mean	s.d.	n	Mean	s.d.	n
08-0959	18.4	4.53	2	24.5	5.82	5	22.8	5.91	7
10-1159	21.0	5.81	5	20.3	4.52	13	20.5	4.74	18
12-1359	20.7	5.81	5	22.3	3.76	13	21.9	3.80	18
14-1559	23.5	3.35	7	22.6	5.16	10	22.9	4.40	17
16-1759	23.3	2.93	6	23.3	2.84	10	23.3	2.77	16
18-1959	19.8	6.60	3	-	-	-	19.8	6.60	3
Overall	21.7	4.29	28	22.3	4.36	51	22.1	4.31	79

Table 6.6 : Mean Body Temperatures ($^{\circ}$ C) during Autumn (September to October) 1984 to 1986 inclusive of male, female and all specimens of C. austriaca captured in the field in different two-hour time blocks, showing standard deviation (s.d.) and sample size (n). Time is indicated as '00hrs BST.

($F= 0.239$ with 4 and 31 d.f., $F= 0.853$ with 5 and 81 d.f. and $F= 0.811$ with 5 and 22 d.f. for Spring, Summer and Autumn respectively. $p>0.05$ in all cases), with the variances for the time periods being homogeneous in each season ($F= 1.874$, 0.730 and 0.640 for Spring, Summer and Autumn respectively. $p>0.05$ in all cases).

With the exception of those recorded during the Spring, body temperatures of female *C. austriaca* were homogeneous across the day with no variation being observed between time periods using ANOVA ($F= 0.936$ with 6 and 98 d.f. and $F= 1.143$ with 4 and 46 d.f. in Summer and Autumn respectively. $p>0.05$ in both cases). The variances were homogeneous between time periods in both seasons ($F= 0.936$ and 1.056 respectively, $p>0.05$). Differences in the body temperatures of female smooth snakes between the two hourly time periods were detected during Spring ($F= 4.414$ with 4 and 14 d.f., $p<0.02$). Here the recorded mean body temperature decreased from morning to early afternoon, reaching a minimum value at 1400–1559 hrs. Between 1600–1759 hrs the value of the mean body temperature was at a maximum; it then decreased between 1800–1959 hrs. These data, however, were obtained from a small sample of observations and a single record constituted the 1800–1959 hrs category.

The body temperatures of male and female smooth snakes were compared within each time category in each season to determine whether body temperatures of the two sexes differed throughout the day in any of the seasons. Student's t-tests were employed in all cases where variances were shown to be homogeneous via the F_{max} test, which was in all but one of these comparisons. This latter case was at 1600–1759 hrs during the Spring where heterogeneity of variances between the two sexes was indicated ($F_{max} = 54.32$, $p<0.01$). Here the separate variance estimate method was used to produce a value of 't'. No significant variation was observed between the sexes at any time period during any of the three seasons ($t= 0.12$ with 14 d.f., 0.94 with 12 d.f., 1.16 with 9 d.f., 2.32 with 6.4

d.f and 2.89 with 1 d.f. for Spring between 1000-1159 and 1800-1959 hrs respectively; $t = 0.27$ with 14 d.f., 0.98 with 32 d.f., 1.65 with 35 d.f., 0.42 with 30 d.f., 1.26 with 42 d.f. and 0.86 with 26 d.f. for Summer between 0800-0959 and 1800-1959 hrs respectively; $t = 1.31$ with 5 d.f., 0.26 with 16 d.f., 0.81 with 16 d.f., 0.41 with 15 d.f. and 0.02 with 14 d.f. for Autumn between 0800-0959 and 1600-1759 hrs respectively, $p > 0.05$ in all cases).

6.3.8. Body temperature in relation to individual condition

a. Slough condition

Body temperatures of C. austriaca captured in the field were analysed to see if there were variations during the skin-molting cycle. This aspect was investigated in two ways. Firstly four categories of slough condition were compared, these being 'post-slough' (immediately after sloughing), 'mid-slough', 'pre-slough' (just prior to sloughing the skin) and whilst shedding the skin; (these categories are described in Chapter 2, section 2.2.2).

Secondly just two categories were used, these being combinations of the first four. In this latter case the slough status was divided into 'after sloughing' (post- and between sloughs) and 'before sloughing' (pre-slough and whilst shedding the skin). Differences in body temperature were investigated via a one way ANOVA and a t-test for the two methods respectively. No distinction was made between the snakes on grounds of sex, since no differences were detected here during earlier analysis.

The Bartlett-Box F-test indicated homogeneity of the variances of body temperatures between the four defined slough conditions ($F = 2.455$, $p > 0.05$), with the mean values of body temperature being $23.49^{\circ}\text{C} \pm 3.91$ ($n = 111$), $23.03^{\circ}\text{C} \pm 4.34$ ($n = 133$), $24.14^{\circ}\text{C} \pm 3.16$ ($n = 62$) and $24.33^{\circ}\text{C} \pm 3.48$ ($n = 3$) for post-slough, between sloughs, pre-slough and sloughing respectively. No significant difference was detected between these values ($F = 1.171$ with 3 and 305

d.f., $p > 0.05$).

Comparison between the latter two slough categories required the t-test employing separate variance estimates since the F_{max} test indicated that the variances of the body temperatures in the two groups were heterogeneous ($F_{max} = 1.74$, $p = 0.01$). The mean body temperatures associated with the 'before sloughing' and 'after sloughing' conditions were $24.1^{\circ}\text{C} \pm 3.15$ ($n = 65$) and $23.2^{\circ}\text{C} \pm 4.15$ ($n = 244$) respectively. These values were not significantly different ($t = 1.92$ with 129.7 d.f., $p > 0.05$).

b. Feeding condition

Body temperature records were divided into three groups depending on the feeding status of the animals when they were captured. These groups are described in Chapter 2 (section 2.2.2) and were termed 'recently fed', 'having a small item in the gut' and 'unfed' respectively. A one way ANOVA was performed on these data to assess whether significant variation was detected between the body temperatures associated with the observed feeding statuses.

The mean body temperature for *C. austriaca* deemed to have recently fed was $23.01^{\circ}\text{C} \pm 3.43$ ($n = 27$), that for snakes with only a small item of food detectable in the gut $22.30^{\circ}\text{C} \pm 4.16$ ($n = 44$) and that for unfed specimens $23.71^{\circ}\text{C} \pm 3.97$ ($n = 210$). Variances of body temperatures between the different feeding statuses were homogeneous ($F = 0.581$, $p > 0.05$) and no significant difference was detected between the body temperatures recorded within these categories ($F = 2.497$ with 2 and 278 d.f., $p > 0.05$).

The assignment of the above three categories was based upon subjective criteria and with the view to reducing the likelihood of overlap between the categories a further analysis was performed which omitted the intermediate feeding condition category. Pairwise comparisons were made between animals that had recently fed and those captured without any food in the gut. By looking only at the

extremes of feeding condition any variation associated with feeding condition may become more apparent. This analysis showed that the variances of the body temperatures associated with the two feeding conditions to be homogeneous ($F_{max} = 1.340$, $p > 0.05$) and that no difference was detectable between field recorded measurements of body temperature of unfed and recently fed animals ($t = 0.875$ with 235 d.f., $p > 0.05$).

c. Female breeding condition

The investigation into the influence of breeding condition on the observed body temperatures of C. austriaca in the field was restricted to female snakes since these undergo a marked and easily detectable changes associated with pregnancy. Variation of body temperature in male snakes was not investigated as the change in breeding condition in this sex was difficult to ascertain in the field.

Data from female snakes were divided into two categories, namely those that were pregnant and those that were not, and a pairwise comparison made between these. Comparisons between each of these categories with data from all male snakes was additionally undertaken to see whether differences could be detected between the sexes which could be associated with a change in breeding condition.

The F_{max} test indicated homogeneity of the variances of body temperature in the two breeding condition categories for female snakes ($F_{max} = 1.47$, $p > 0.05$) and hence a Student's t-test was employed to compare the values in each group. No significant difference in body temperature was detected between pregnant and non-pregnant specimens ($t = 1.75$ with 141 d.f., $p > 0.05$) with the mean values obtained being $23.86^{\circ}\text{C} \pm 3.84$ ($n = 108$) and $22.48^{\circ}\text{C} \pm 4.66$ ($n = 35$) respectively.

Mean body temperature for male smooth snakes recorded in the field was $23.30^{\circ}\text{C} \pm 3.89$ (see section 6.3.1). Homogeneity of variances was detected for body temperatures

of both pregnant and non-pregnant female snakes when separately compared with those recorded for male specimens ($F_{max} = 1.026$ and 1.435 respectively, $p > 0.05$ in both cases). No significant difference in body temperature was observed in the field between male C. austriaca and either pregnant ($t = 1.150$ with 258 d.f., $p > 0.05$) or non pregnant ($t = 1.082$ with 185 d.f., $p > 0.05$) female specimens.

6.3.9. Relationship between observed behaviour and body temperature (with special reference to basking posture)

With the view to investigating the possible relationship between body temperature and behaviour in C. austriaca the body temperatures associated with eight different behaviours, i.e. six different basking postures of increasing tightness of coil (illustrated in Fig. 2.1, Chapter 2), 'movement' and 'other behaviour' (e.g. feeding, mating, etc.), were compared. Body temperatures recorded from a ninth category, 'below cover', were omitted as these incorporated a variety of situations including being underground and below tin sheeting and would not take into account variations in the postures of the animals found below these objects. Additionally these data would yield little information about basking behaviour, since the animals would have been shaded from solar radiation.

Mean body temperatures for male, female and all specimens of C. austriaca recorded in the field for each observed behaviour are presented in Table 6.7 and illustrated in Fig. 6.11; body temperature records were obtained only from the six basking posture and the movement behaviour categories only, with no records being associated with 'other behaviour'. As such the analyses were limited to only seven behaviour categories. The variances of body temperatures between the behaviour groups were homogeneous ($F = 1.453$, $p > 0.05$) when pooling the data for all specimens. A significant difference was observed using one way ANOVA between body temperatures in the seven behaviour categories for all ($F = 3.716$ with 6 and 278 d.f., $p < 0.02$)

Behaviour	Males			Females			All Specimens		
	Mean	s.d.	n	Mean	s.d.	n	Mean	s.d.	n
Basking 1	-	-	-	15.7	6.17	3	15.7	6.17	3
Basking 2	23.2	4.32	12	21.3	3.86	10	22.4	4.13	22
Basking 3	23.2	2.91	10	22.3	4.01	14	22.7	3.56	24
Basking 4	23.7	3.68	14	24.3	4.30	27	24.1	4.06	41
Basking 5	24.1	4.52	22	24.1	4.05	51	24.1	4.17	73
Basking 6	23.6	3.16	46	24.2	3.18	47	23.9	3.17	93
Moving	21.9	4.26	16	23.1	3.58	13	22.4	3.95	29

Table 6.7 : Mean Body Temperature ($^{\circ}\text{C}$) associated with each of seven observed behaviours for male, female and all specimens of *C. austriaca* captured in the field during 1984 to 1986 inclusive, showing standard deviation (s.d.) and sample size (n). The behaviour categories observed were six bask postures, numbered in ascending order to indicate an increasingly tight coil, and movement. Data recorded from animals captured below cover were omitted from this analysis.

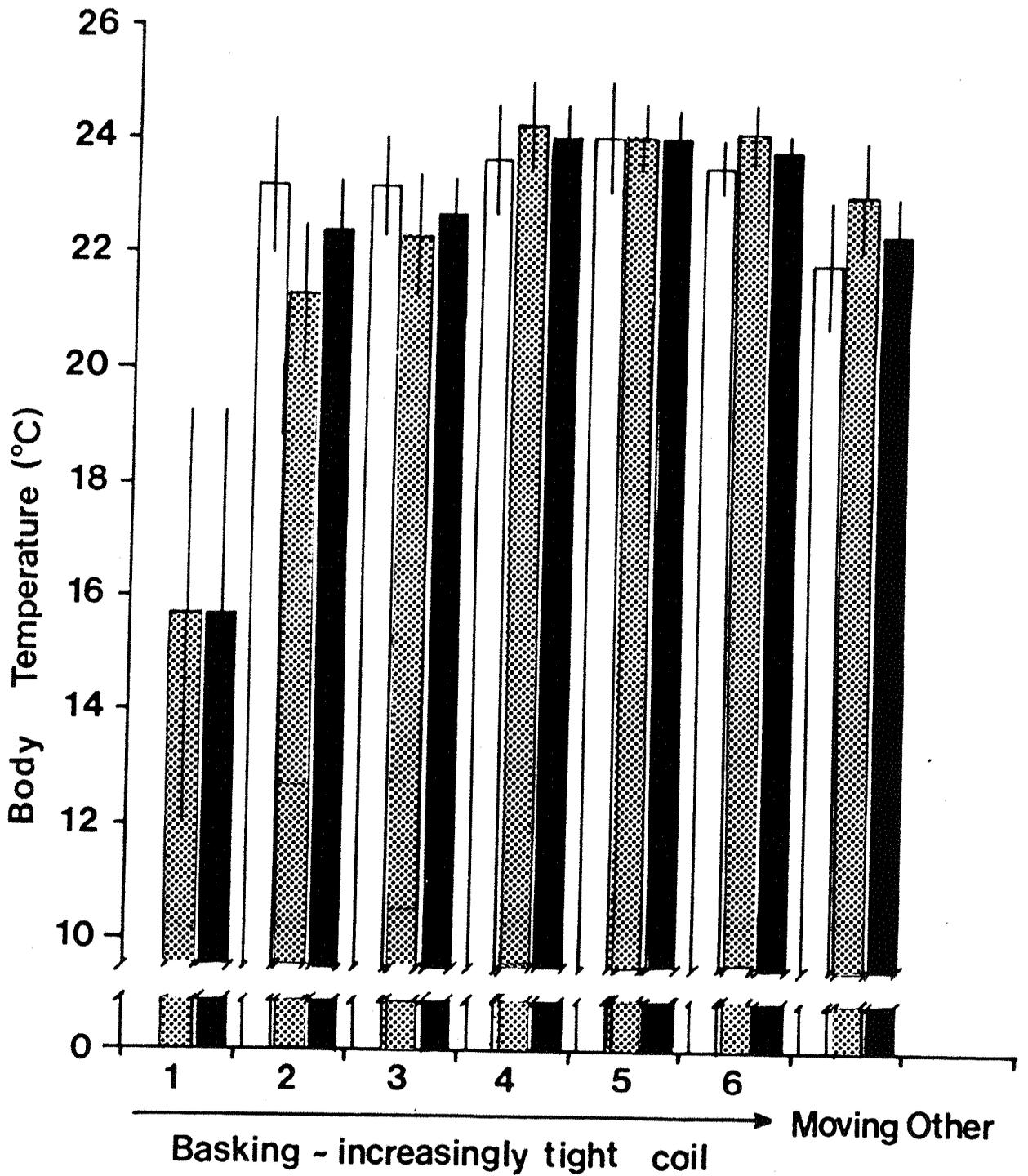


Fig. 6.11 : Mean body temperatures ($^{\circ}\text{C}$) (± 1 s.e.) associated with eight different defined behaviours (1 to 6= Basking with increasing tightness of coil, 7= Moving, 8= All other behaviours) for male (unshaded), female (light shading) and both male and female (dark shading) specimens of *C. austriaca* captured in the field between April 1984 and October 1986 inclusive.

C. austriaca. The highest mean body temperatures were those from snakes basking in postures 4 and 5, with values of $24.1^{\circ}\text{C} \pm 4.06$ and $24.1^{\circ}\text{C} \pm 4.17$ respectively. The third highest mean body temperature was $23.9^{\circ}\text{C} \pm 3.17$ and was obtained from animals that were basking in very tight coils (posture 6). Successively lower mean body temperatures were observed as the degree of tightness of coil decreased. Mean values of $22.7^{\circ}\text{C} \pm 3.56$, $22.4^{\circ}\text{C} \pm 4.13$ and $15.7^{\circ}\text{C} \pm 6.17$ were obtained for bask postures 3, 2 and 1 respectively. Sample sizes in these latter three categories were, however, notably smaller than those associated with the former three bask postures. Body temperatures associated with moving animals yielded a mean value of $22.4^{\circ}\text{C} \pm 3.95$.

Data for body temperatures in different behaviour categories were analysed separately for male and female specimens to ascertain whether the different body temperatures associated with behaviour varied between the sexes. Variances of the body temperatures in the six observed behaviour categories for male specimens were homogeneous ($F= 1.176$, $p>0.05$), with no data being available here for snakes in posture 1. Male C. austriaca demonstrated no significant variation between the body temperatures in these behaviour categories ($F= 0.739$ with 5 and 114 d.f., $p>0.05$). Body temperatures of 23.2 ± 4.32 , 23.2 ± 2.91 , 23.7 ± 3.68 , 24.1 ± 4.52 and $23.6^{\circ}\text{C} \pm 3.16$ were obtained for the bask postures 2 to 6 respectively. Movement behaviour in male smooth snakes was associated with a mean value for body temperature of $21.9^{\circ}\text{C} \pm 4.26$.

Female C. austriaca showed homogeneity of variances between the seven behaviour categories for which body temperature data were available ($F= 0.850$, $p>0.05$) and between these categories significant differences in body temperature were detected via one way ANOVA ($F= 3.518$ with 6 and 158 d.f., $p<0.003$). The highest mean body temperature for female specimens was associated with the intermediately tight coil bask posture, posture 4, where a value of $24.3^{\circ}\text{C} \pm 4.30$ was obtained. However, with values of 24.1 ± 4.05 and $24.2^{\circ}\text{C} \pm 3.18$ respectively, very similar body temperatures were

observed for bask postures 5 and 6. Body temperatures of 15.7 ± 6.17 , 21.3 ± 3.86 and $22.3^{\circ}\text{C} \pm 4.01$ were recorded for the basking behaviours 1,2 and 3 respectively and a value of $23.1^{\circ}\text{C} \pm 3.58$ was associated with records of female snakes captured whilst moving.

The use of posturing behaviour by C. austriaca for thermoregulation was investigated by comparing body temperatures in the six recognised basking postures, via a one way ANOVA, for data from all specimens together and from each sex separately.

A significant effect of posture was detected when data for all specimens were pooled ($F= 3.960$ with 5 and 250 d.f., $p<0.002$) with the variances between the different behaviour categories being homogeneous ($F= 1.715$, $p>0.05$). Thus the tighter coils seem to be associated with higher body temperatures. No such variation was detected for male specimens. Variances between the body temperature in the respective behaviour categories were homogeneous ($F= 1.316$, $p>0.05$) and the associated significance value obtained from the ANOVA was $F= 0.172$ with 4 and 99 d.f., ($p>0.05$). Homogeneity of variances between body temperatures in the different bask posture categories was also detected for female specimens ($F= 0.992$, $p>0.05$) and a significant effect of bask posture on body temperature was detected ($F= 4.128$ with 5 and 146 d.f., $p<0.002$).

6.3.10. Environmental temperature records

Mean values of shade air and bask site temperatures, recorded whilst making observations of C. austriaca in the field were studied to see how these vary over the day and between seasons. In addition mean hourly temperature records across the day for six different positions in the environment are presented for May to October 1986, to demonstrate the range of environmental temperatures that could be experienced by a smooth snake.

a. Shade air and bask site temperatures recorded whilst observing smooth snakes

Data were analysed by pooling shade air and bask site temperature records together within two-hourly time blocks, as was performed above for body temperature records. Using data collected from all seasons, the environmental temperatures associated with observations of male and female snakes were separated within each time block and tested via a Student's t-test (where homogeneous variances were observed) or a Separate variance estimate t-test (where variances were shown to heterogeneous via the F_{max} test) to see whether differences attributable to the sex of the study animals could be detected. Shade air and bask site temperatures recorded over the day for each of the sexes are presented in Table 6.8. No significant variation in shade air temperatures were observed between male and female C. austriaca in any of the eight time blocks. Differences in bask site temperature were, however, detected between the two sexes at 1600–1759 hrs ($t = 2.21$ with 279 d.f., $p < 0.03$) and 1800–1959 hrs ($t = 2.91$ with 210 d.f., $p < 0.005$).

Further division of the data by season revealed inter-sexual differences for both shade air and bask site temperatures only during Spring at 16–1759 hrs (mean values for T_a for males = $15.9^\circ\text{C} \pm 3.36$ ($n = 31$) and for females = $18.9^\circ\text{C} \pm 4.14$ ($n = 7$), $t = 2.04$ with 36 d.f., $p < 0.05$ and for T_{bs} for males = $16.1^\circ\text{C} \pm 4.57$ ($n = 31$) and for females = $23.7^\circ\text{C} \pm 6.34$ ($n = 7$), $t = 3.70$ with 36 d.f., $p = 0.001$) and for shade air alone at two time groups in the Summer (10–1159 hr mean T_a for males = $20.2^\circ\text{C} \pm 3.47$ ($n = 80$) and for females = $19.0^\circ\text{C} \pm 2.84$ ($n = 79$), $t = 2.29$ with 157 d.f., $p < 0.03$ and 14–1559 hr mean T_a for males = $21.7^\circ\text{C} \pm 3.51$ ($n = 87$) and for females = $20.6^\circ\text{C} \pm 3.40$ ($n = 77$), $t = 2.04$ with 162 d.f., $p < 0.05$). In the light of these few differences between the sexes, the data from the two sexes were regarded as being sufficiently homogeneous to allow them to be pooled during further analysis.

A. Shade Air Temperature

Time (BST)	Males			Females		
	Mean	s.d.	n	Mean	s.d.	n
06-0759	16.5	2.76	12	16.1	2.49	6
08-0959	17.4	2.63	107	17.5	2.73	81
10-1159	18.7	3.69	164	18.4	3.02	138
12-1359	19.6	3.75	172	19.7	3.62	141
14-1559	19.9	3.88	166	19.8	3.49	125
16-1759	19.3	3.67	158	19.5	3.39	124
18-1959	17.4	3.54	171	18.0	3.74	113
20-2159	17.1	3.05	45	17.2	2.41	26

B. Bask Site Temperature

Time (BST)	Males			Females		
	Mean	s.d.	n	Mean	s.d.	n
06-0759	14.9	2.72	12	16.9	3.10	6
08-0959	17.5	3.62	107	18.4	3.82	81
10-1159	19.8	4.54	164	20.2	4.17	138
12-1359	20.7	4.27	173	21.6	4.47	140
14-1559	20.8	4.60	165	21.7	4.37	125
16-1759 *	20.0	4.66	157	21.2	4.78	124
18-1959 *	17.1	3.95	172	18.7	4.70	113
20-2159	16.4	3.18	45	17.6	2.75	26

Table 6.8 : Mean Shade Air and Bask Site Temperatures (°C) recorded in the field in different two-hourly time blocks whilst observing male and female *C. austriaca* during April 1984 to October 1986 inclusive, and the associated standard deviations (s.d.) and sample sizes (n). * denotes a significant difference between the sexes.

Mean shade air and bask site temperatures during each time period, obtained from data collected whilst observing all animals throughout the duration of the study, are presented in Table 6.9. Variances associated with the shade air temperature were heterogeneous between the time groups ($F=5.18$, $p<0.001$) indicating that the result of the analysis of variance should be interpreted with caution. However, a large F-ratio was obtained such that it is reasonable to conclude that this value was representative and that a significant difference in shade air temperatures occurred over the day ($F=20.41$ with 7 and 1752 d.f., $p<0.0001$). Shade air temperatures demonstrated a gradual increase throughout the morning and reached their maximum (19.8°C) between 1400–1559 hrs before decreasing as the night time approached.

Bask site temperatures showed a similar trend. Significant heterogeneity of variances between the time periods ($F=4.50$, $p<0.001$) was detected and meant that the result obtained from the ANOVA should be treated with caution. However, a large F-ratio indicated that the highly significant result obtained was indeed representative ($F=30.80$ with 7 and 1750 d.f., $p<0.001$) and that bask site temperature fluctuated during the day. The mean bask site temperature increased more rapidly over the morning than the corresponding shade air temperature and attained a maximum value, of 21.2°C , at 1400–1559 hrs. The bask site then demonstrated a more rapid decrease in temperature than did the shaded air.

Combining environmental temperature data from three seasons together may be misleading because day length, and consequently day time temperatures, will increase from Spring to Summer and decrease as the Summer progresses via Autumn toward Winter. As such, three distinct seasons have arbitrarily been identified and the weather variables divided accordingly.

Mean shade air temperatures for each two-hourly time block

Time (BST)	Shade Air Temperature			Bask Site Temperature		
	Mean	s.d.	n	Mean	s.d.	n
06-0759	16.3	2.61	18	15.5	2.92	18
08-0959	17.4	2.67	190	17.9	3.70	190
10-1159	18.5	3.42	306	20.0	4.40	305
12-1359	19.6	3.69	315	21.1	4.37	315
14-1559	19.8	3.71	292	21.2	4.52	291
16-1759	19.4	3.53	284	20.5	4.73	283
18-1959	17.6	3.63	284	17.7	4.32	285
20-2159	17.1	2.82	71	16.8	3.07	71
Overall	18.7	3.61	1760	19.7	4.58	1758

Table 6.9 : Mean Shade Air and Bask Site Temperatures (°C) recorded in the field in different two-hourly time blocks whilst observing *C. austriaca* during April 1984 to October 1986 inclusive, and the associated standard deviations (s.d.) and sample sizes (n).

recorded during the three seasons are presented in Table 6.10. Shade air temperature demonstrated a consistently depressed level throughout the day during Spring when compared with the Summer and Autumn and attained its maximum value later in the day during the former month than during the latter two, with maxima being recorded at 1600-1769, 1400-1559 and 1400-1559 hrs respectively. Maximum mean shade air temperatures for the three seasons were 16.5, 21.2 and 19.1°C respectively. Significant variation in shade air temperature was demonstrated during the course of the day in each of the seasons via an ANOVA (Spring: $F=3.247$ with 6 and 199 d.f., $p<0.05$, Summer: $F=22.43$ with 7 and 1013 d.f., $p<0.001$, Autumn: $F=21.73$ with 6 and 525 d.f., $p<0.001$). Variances associated with temperatures in Spring and Autumn were homogeneous ($F=1.46$, $p>0.05$ and $F=0.499$, $p>0.05$ respectively) between time periods and those recorded in the Summer were heterogeneous over the day ($F=3.94$, $p<0.001$). In this latter case caution was exercised in interpreting the result of the ANOVA, however a large value for the F-ratio indicated that the significant result obtained was likely to be representative.

Heterogeneous variances were associated with the bask site temperatures between the different time periods in all three seasons ($F=3.55$, $p<0.002$, $F=3.20$, $p<0.002$ and $F=3.71$, $p<0.001$ for Spring, Summer and Autumn respectively) although large F-ratios calculated by one way analysis of variance showed that significant variation occurred across the day in all cases (Spring: $F=4.67$ with 6 and 198 d.f., $p<0.0002$, Summer: $F=30.70$ with 7 and 1015 d.f., $p<0.0001$ and Autumn: $F=24.39$ with 6 and 522 d.f., $p<0.0001$). Mean bask site temperatures recorded during each time period are presented for each season in Table 6.11. Maximum bask site temperature was recorded at 1000-1159 hrs in Spring where a value of $18.1^{\circ}\text{C} \pm 5.70$ was obtained. During both Summer and Autumn the mean maximum mean temperatures were recorded at 1400-1559 hrs and were $22.7^{\circ}\text{C} \pm 4.19$ and $20.1^{\circ}\text{C} \pm 3.50$ respectively, with temperatures in both cases rising quickly over the morning period and decreasing again towards nightfall.

Time (BST)	Spring			Summer			Autumn		
	Mean	s.d.	n	Mean	s.d.	n	Mean	s.d.	n
06-0759	-	-	-	16.3	2.61	18	-	-	-
08-0959	15.2	2.67	8	18.1	2.56	124	16.1	2.28	58
10-1159	15.8	3.64	47	19.6	3.22	159	17.8	2.75	100
12-1359	15.9	2.84	42	21.1	3.59	173	18.8	2.67	99
14-1559	15.8	3.19	42	21.2	3.49	164	19.1	2.52	86
16-1759	16.5	3.65	38	20.7	3.34	158	18.3	2.65	88
18-1959	13.5	2.76	27	19.4	3.22	161	15.8	2.53	96
20-2159	10.5	0.28	2	17.6	2.44	64	14.0	2.72	5
Overall	15.6	3.35	206	19.9	3.46	1021	17.7	2.88	532

Table 6.10 : Mean Shade Air Temperature ($^{\circ}$ C) recorded during two-hourly time categories ('00hrs BST) whilst observing *C. austriaca* in the field in Spring, Summer and Autumn during 1984 to 1986 inclusive, showing standard deviation (s.d.) and sample size (n).

Time (BST)	Spring			Summer			Autumn		
	Mean	s.d.	n	Mean	s.d.	n	Mean	s.d.	n
06-0759	-	-	-	15.5	2.92	18	-	-	-
08-0959	14.5	4.47	8	18.7	3.46	124	16.6	3.51	58
10-1159	18.1	5.70	47	21.2	3.86	160	18.8	3.88	98
12-1359	17.8	4.09	42	22.5	4.11	173	20.0	3.93	99
14-1559	17.2	4.79	41	22.7	4.19	164	20.1	3.50	86
16-1759	17.5	5.69	38	22.1	4.24	158	18.9	3.85	87
18-1959	13.1	2.70	27	20.0	3.87	162	15.1	2.54	96
20-2159	10.2	0.64	2	17.3	2.77	64	13.9	2.86	5
Overall	16.9	5.09	205	21.0	4.28	1023	18.3	4.01	529

Table 6.11 : Mean Bask Site Temperature ($^{\circ}$ C) recorded during two- hourly time categories ('00hrs BST) whilst observing *C. austriaca* in the field in Spring, Summer and Autumn during 1984 to 1986 inclusive, showing standard deviation (s.d.) and sample size (n).

b. Continually recorded temperatures at six locations in the environment

With a view to observing temperature variation during the day within the habitat potentially occupied by C. austriaca, (and hence observing the potential thermal habitat of the species) temperatures were automatically recorded (details of equipment are presented in Chapter 2, section 2.2.6) at hourly intervals at six different locations. These were i. shade air, ii. open ground, iii. below short, loose heather, iv. below thick heather, v. 10 cm below ground and vi. under tin sheeting. Temperature records were made for between 5 and 8 days during each of six consecutive months (May to October) during 1986 so that the variation in temperatures across the season to be observed. Mean temperatures were calculated for each location at each hour. No measure of variation around these means were calculated, these being deemed unnecessary as the exercise was simply to illustrate variation in typical temperatures in each month with no intention of statistical comparisons. Further as the intention was to illustrate these variations graphically, superimposing all data onto a single figure for each month, drawing error bars would be both complicated and would make interpretation less clear. Mean temperatures recorded each hour at each location are presented separately for each month in Fig. 6.12 and maximum and minimum mean temperatures recorded at each position in the environment are presented for each month, together with the time periods in which they were recorded, in Table 6.12.

Environmental temperature of this nature can be usefully employed in two ways, firstly it allows comparisons of temperatures recorded between months in any season to be made and secondly it allows variation in temperatures across the day to be observed between habitat types.

Monthly variation in temperature is illustrated in Fig. 6.12 and can also be described by looking at the values of

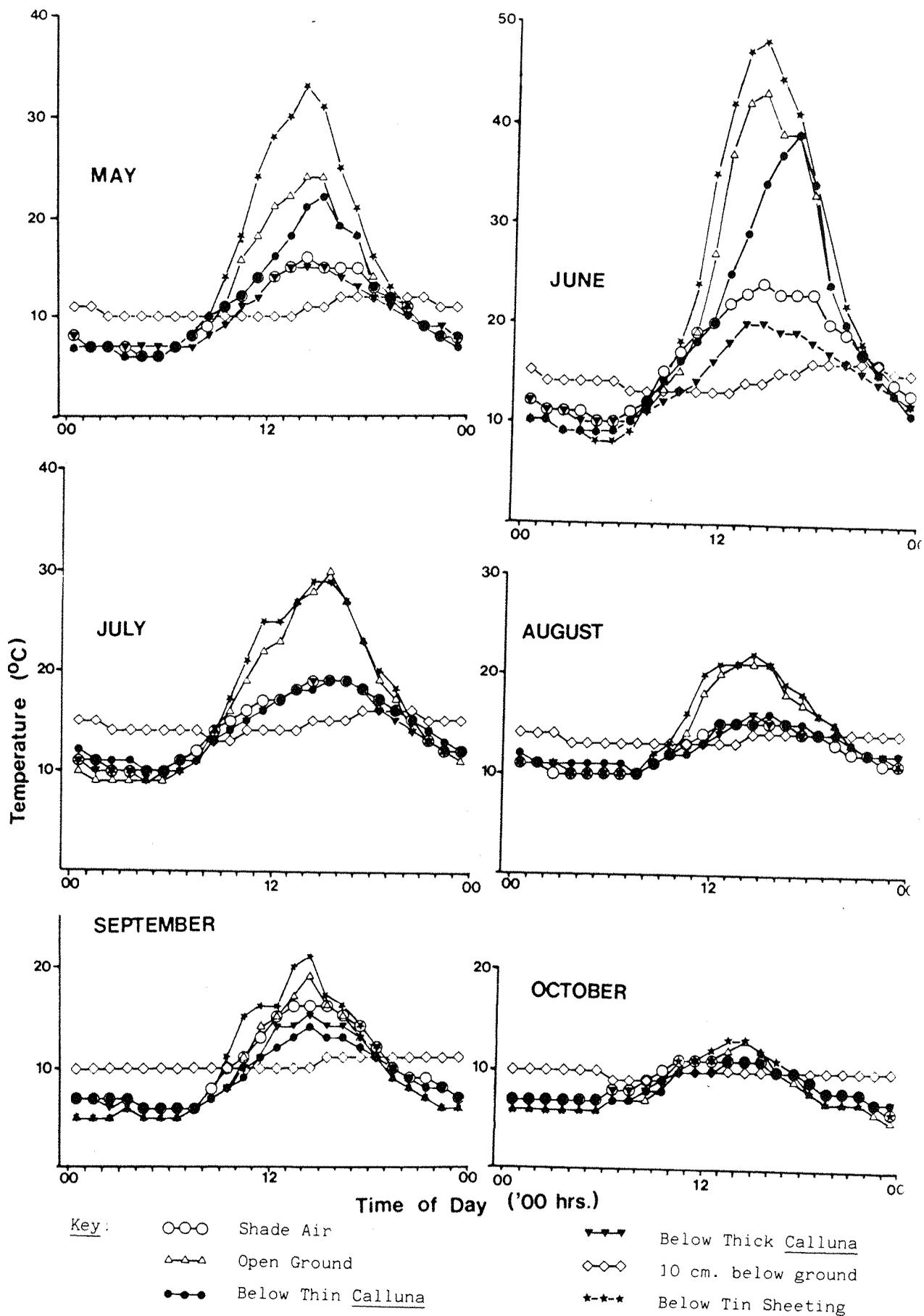


Fig. 6.12 : Mean Temperatures at Six Different Locations in the Environment (see key) recorded at Hourly Intervals during sampling periods (of between five and eight days) during May to October 1986 inclusive.

		MAY	JUNE	JULY	AUGUST	SEPTEMB.	OCTOBER
		<u>Time</u> °C					
Shade air	Max:	14-15 16	14-15 24	14-17 19	12-17 15	13-16 16	10-16 11
	Min:	04-06 6	04-06 10	02-06 10	02-08 10	04-08 6	23-00 6
Open ground	Max:	14-16 24	14-15 43	15-16 30	13-16 21	14-15 19	14-15 13
	Min:	03-06 6	02-06 9	02-06 9	03-08 10	00-07 5	23-00 5
Loose veg.	Max:	15-16 22	16-17 39	15-17 19	15-16 16	14-15 14	13-16 11
	Min:	03-06 6	02-06 9	04-06 10	07-08 10	04-08 6	22-08 7
Thick veg.	Max:	13-16 15	13-15 20	14-17 19	14-15 16	14-15 15	11-16 11
	Min:	01-08 7	03-07 10	01-07 10	03-08 10	02-08 6	22-06 7
Below ground	Max:	16-22 12	17-22 16	17-21 16	14-03 14	15-00 11	10-06 10
	Min:	02-14 10	06-13 13	08-10 13	03-14 13	00-15 10	06-10 9
Below tin	Max:	14-15 33	14-15 48	14-16 29	14-15 22	14-15 21	13-15 13
	Min:	04-06 6	04-06 8	04-05 9	03-08 10	00-07 5	23-06 6

Table 6.12 : Maximum and Minimum temperatures (°C), and time period ('00hrs BST) during which they were recorded, for Shade air, Open ground, Loose vegetation, Thick vegetation, 10 cm Below ground and Below tin sheeting for May to October 1986, inclusive.

maximum and minimum temperatures recorded at each position in the environment during each month (see Table 6.12). Monthly maximum temperatures were greatest during the month of June at all positions where temperature was recorded in the habitat during the 1986 field season. Maximum values were lower during the preceding month (May) and during the subsequent months a gradual decrease in maximum temperature was detected at all locations as the year progressed (from July, through August and September, to October).

Monthly minima, however, were greatest during August, although these values were equalled in four of the six cases by the corresponding values in July and in three of these by the minima recorded in June. Thus, although the month with the highest temperatures was June, the increased minimum temperatures during July and August may be interpreted as a general warming of the environment as the Summer progressed. These latter months, and in particular August, were unusually cold and overcast (HMSO 1987) and consequently demonstrated diminished monthly maxima compared with temperatures usually experienced during that time. The range of temperatures experienced were likely to be much condensed as a result of the cloud during these months, with reduced maxima resulting from a decrease in the amount of incoming solar radiation received by the earth and additionally raised minima through the cloud insulating the earth from excessive heat loss during the night. Thus although the data recorded during July and August were believed to be representative of the temperatures occurring during these months, these temperatures were unlikely to be characteristic for these months if compared between years.

The temperatures observed during September and October were regarded as being characteristic for these months, with moderate temperatures being recorded during the day, which decrease further during the latter month, and fairly cold temperatures during the night. The temperature recorded 10 cm below ground demonstrated a fairly consistent pattern over the day and hence is of interest for comparison between seasons. A gradual warming of the soil temperature

was recorded during May to July, where the daily median temperature of the mean hourly values increased from 10.5°C, through 14.0°C, to 14.5°C. During the latter months of the field season the below ground temperature decreased, with typical values (again illustrated by the median of the hourly mean temperatures over the day) decreasing from 14°C in August to 10°C during the September and October.

During the course of a day similar patterns of temperature variation were observed at each of the locations in the environment within each of the different months, although the extent of the diurnal fluctuations in temperature in each case varied considerably between months. As such general diurnal trends of temperature variation for each of the six positions in the environment are described. With the exception of the below ground temperature which remained at an almost constant level throughout the day, all environmental temperatures increased during the early morning typically between 0500-0759 hrs BST. The rate and extent of temperature increase, however, varied considerably between the different locations. Shade air temperature increased during the morning, reached a maximum value typically at 1300-1459 hrs, and then decreased during the night to a minimum, usually at 0400-0559 hrs. Unshaded ground temperature increased markedly during the morning, attaining high temperatures rapidly. The rate and extent of this heating was further enhanced by a piece of tin sheeting which caused a more notable increase in temperature through its greater ability to absorb radiant energy than the surrounding open ground. The rate of cooling was also most marked in these latter two cases, with rapid cooling being effected by the emission of radiant energy from the uninsulated ground. This cooling was also enhanced by tin sheeting, often resulting in the temperature below the tin sheeting being reduced to below that of the surrounding ground or shade air temperatures.

As the depth of the vegetation increased the thermal environment became more stable; with fluctuations in

temperature being both smaller and less rapid. Soil further offers protection from temperature variation and at a depth of 10 cm only small fluctuations of between 1 and 3°C were detected over a day. The below ground temperature maintained its maximum value later in the day than the other recorded variables, with the heating and cooling here being delayed relative to the other measured environmental temperatures.

6.4. Discussion

6.4.1. Body temperatures, thermoregulation and the environment

The use of cloacal temperatures to represent body temperature has been criticised by some workers. The elongate shape of a snake's body means that points along the body are likely to vary in temperature (through rapid heat gain and loss through the integument due to the relative narrow body) and that temperatures at the cloaca may not reflect a true 'body temperature' (Bartholomew 1982, Avery 1982). This variation may also be significant when comparing results from studies using cloacal temperatures with those using other measurements, e.g. stomach temperatures from ingested radio-transmitters (e.g. Bont et al 1986). Reptilian body temperatures may also be affected by handling (through the transfer of heat between the reptile and the experimenter's hand). These methodological considerations should be borne in mind throughout the remainder of this discussion.

Smooth snakes are poikilothermic (sensu Spellerberg 1976) and body temperatures recorded in the field varied between 10.5° and 31.6°C. The majority of observations (over 80%), however, were confined within the range 19° to 29°C. A mean body temperature of 23.48°C was obtained during the present study which is comparable to results published by other workers. Spellerberg and Phelps (1975) reported a mean value 25.8°C from 88 field measurements of body temperature and Goddard (1981) presented mean values of

24.24° and 23.96°C for C. austriaca captured in the open and under-cover respectively. Bont et al (1986), in a radio-telemetric study of free ranging smooth snakes, indicated that body temperatures were maintained at between 29° and 33°C. These latter values, however were based upon the observation of typical temperatures attained during the day and did not include the lower temperatures that were recorded; combination of all their records would have been likely to yield a mean value comparable to that obtained during the present study.

Body temperatures were directly related to both shade air and bask site temperatures and were affected by the degree of cloud cover. The strong correlation between environmental conditions and body temperatures could suggest a tendency towards thermoconformity (sensu Huey and Slatkin 1976). Observation of the regression lines associated with these relationships showed that body temperatures were typically about 6°C higher than shaded air temperatures and were elevated above bask site temperatures (typically upto 6°C) at lower values and approximated bask site temperatures at higher values over the ranges measured in the field. Shaded air temperatures provide a useful indication of general weather conditions and will be independent of snake behaviour. 'Bask site temperature', on the other hand, will measure the temperature of the sites occupied by snakes and will therefore be dependent to a degree upon the behaviour of the snakes. The relationship between shaded air and body temperatures was indicative of a passive interaction between the two variables and suggested that (over the range of temperatures recorded in the field) there was little, if any, thermoregulatory compensation to varying environmental temperatures. Thus body temperature seemed to vary in direct relation to air temperatures (i.e. suggesting thermoconformity). However, body temperatures increased relatively less quickly than bask site temperatures; and this relationship suggested some degree of regulation of body temperature. That the increases in body and bask site temperatures were not directly

proportional to each other suggests that the mechanism of body temperature regulation is not directly attributable to bask site selection.

Observation of regression lines alone may prove misleading, since the interaction between the variables may not be consistent at different portions of the line. For example, both sets of data in Figs. 6.2 and 6.3 suggested a more rapid increase in body temperatures at lower environmental temperatures than at the higher temperatures. In addition the highest body temperatures (i.e. above 29°C) were observed at a variety of medium to high environmental temperatures (T_A between 17° and 28°C and $T_{B\pm}$ between 22° and 36°C). Although environmental temperatures occurred that could have permitted higher body temperatures to be attained (see Fig. 6.12), no snakes were captured with body temperatures higher than 31.6°C.

These observations may be indicative of the 'preferred' body temperature of C. austriaca. It would therefore appear that C. austriaca are able to increase body temperatures above ambient over much of the range encountered in the field and where possible maintain them at around 30°C. This is in agreement with the observations made by Bont et al (1986) (29° to 33°C) and with the maximum values obtained from field studies by Spellerberg and Phelps (1975) (31°C), Goddard (1981) (31°C) and the present study (31.6°C). Evidence from laboratory selected temperatures (see Chapter 7) further support this hypothesis (mean= 29.6°C). The 'preferred' temperature is therefore much greater than the mean body temperatures recorded (Spellerberg and Phelps 1975, Goddard 1981, present study), and many body temperatures were observed below this value.

It is possible that C. austriaca are unable to maintain optimum body temperatures in England (where it is at the north-western limit of its range). Relatively cool and wet Summers (compared to other parts of the range) would restrict the potential to achieve high body temperatures. However, this alone would not explain the low mean value

observed. It is likely that other behavioural requirements (see below) will affect the precision of body temperature maintenance and that smooth snakes may therefore not be able to exploit the potential heat sources with maximum efficiency. These will compound the effect of the cooler English climate. It is tempting to suggest that C. austriaca is adapted for warmer climates. Whether higher body temperatures are obtained from snakes in other regions (as may be suggested from the study by Bont et al (1986)) needs to be ascertained. However, it is also worth considering that reptiles from different climatic regions may also show a different (laboratory determined) selected body temperature (e.g. Al-Sadoon and Spellerberg 1985a) and that differences in field body temperatures may not simply reflect differences in weather conditions in the short term.

Body temperatures exhibited at any one time will be the product of varying (and sometimes conflicting) factors and consequently the 'preferred' body temperature might not be maintained in nature. These factors will include climatic, behavioural and physiological considerations. For example mate selection, foraging or anti-predator behaviour may prevent 'precise' thermoregulation, different physiological states may invoke differing thermal requirements (and perhaps different 'preferred' temperatures) and weather conditions may preclude achievement or maintenance of a specific body temperature. This is discussed further in Chapter 7 (section 7.4.2.). The role of various biotic and abiotic factors affecting body temperature regulation and maintenance are reviewed by Huey (1982). In addition, many of the observations were of snakes that were basking and consequently may have been warming up and consequently captured prior to attaining their 'desired' body temperature.

Cloud cover was observed to affect body temperatures yielding lower values and generally depressing the relationship between body temperature and the shade air and bask site temperatures. Goddard (1981) and Bont et al

(1986) also demonstrated a similar effect due to cloud cover. In the latter study cloud affected the variability of the data and the clear diurnal variation of warming up, 'plateau' phase and cooling down became disrupted. Goddard (1981) reported a similar variation in the pattern of body temperatures resulting from cloud cover.

Spellerberg (1976) described smooth snakes as thigmotherms/shuttling heliotherms. In the absence of a clear correlation with bask site temperatures, it would appear that body temperatures of C. austriaca are not principally determined by thigmothermic behaviour. The depression and the increased variability of body temperature with increasing cloud cover indicates that body temperatures are greatly influenced by the degree of insolation and therefore would suggest that this species is primarily heliothermic. Nonetheless, C. austriaca do spend much time below ground and in thick vegetation (e.g. whilst foraging). The lack of sunlight may mean that body temperatures will be determined by the surrounding substratum temperatures, since it would be unlikely that 'shuttling' behaviour could be exhibited in these circumstances. Thigmothermy is most likely to be observed where snakes are exhibiting behaviours that are not primarily associated with body temperature regulation. At these times snakes are likely to show less precise thermoregulation and may tend towards thermoconformity.

Bont et al (1986) observed the rapid increase in body temperature during the early morning of a snake that they believed was inactive (at a rate almost comparable to basking animals). They cautioned their classification as 'inactive' on the grounds that the snake may have been emerged but below thick vegetation such that it could not be seen. Basking by snakes that were obscured to varying degrees by vegetation, etc., was observed during the present study. Several factors may account for this behaviour. Partial shading may provide an optimal thermal habitat whereas basking in direct sunlight may have caused the animal's body temperature to go beyond normal levels

(it is also likely that most shaded sites would also be more humid, thereby also reducing the possibility of dehydration). Selecting a partially shaded site may, therefore, preclude the need to 'shuttle' between warm and cool areas in the environment, a behaviour that may become energetically demanding over prolonged periods of time (Huey 1982); this type of behaviour has been called 'mosaic basking' (Avery 1982). For a species whose primary anti-predator mechanism is crypsis inactivity is also beneficial. Indeed basking below vegetation would greatly reduce the visibility of the snake and such behaviour may take precedence over 'precise' thermoregulation. The term 'cryptic heliothermy' (S. Hedges, pers. comm.) would describe this activity which is produced as a compromise between two potentially conflicting requirements.

A change in the body temperature of an ectotherm, may be expected to affect the animal's behaviour. This may operate in either of two ways. An animal may respond to a particular temperature by exhibiting certain behaviours, for example movement may be favoured at certain body temperatures (see Chapter 4). Conversely, the animal may alter its behaviour in order to effect a change in its body temperature in response to an unfavourable change in body temperature. Examples of the latter are short movements between exposed ground and shade ('shuttling heliothermy') and 'posturing heliothermy' where animals adopt certain postures to enhance or reduce the rate of warming of the body by the sun.

Posturing and orientation behaviour has been described for several snake species in which it appears to relate to thermoregulation. These behaviours are, however, less highly developed in snakes than for certain lizard species (e.g. the iguanid Holbrookia maculata (Axtell 1960) and the agamid Amphibolurus fordi (Cogger 1974)). Lillywhite (1980) described thermoregulation in five species of Elapid snakes and suggested that posturing may be used to regulate body temperature. Different bask postures have been described for Crotalus spp. (Norris 1967), Vipera berus (Prestt 1971)

and Notechis scutatus (Heatwole 1976) and these, particularly where body flattening occurs (which is achieved through the spreading of the ribs), may be related to thermoregulation. Spellerberg and Phelps (1977) suggested that there was a relationship between weather variables and the body posture of C. austriaca. Based on field observations, Goddard (1981) tentatively suggested that C. austriaca may display some form of posturing heliothermy, with a tendency for outstretched and loosely coiled postures to relate to low body temperatures and tight coils to relate to higher body temperatures. During the present study, significant variation was observed between the body temperatures of snakes in different bask postures. Tighter coils related to warmer temperatures, in agreement with the observations made by Goddard (1981). Tighter coils would reduce the surface area exposed to the sun and thus slow down the rate of warming. However, whether the different coiling behaviours were the cause of (i.e. loose coils to enhance warming) or were in response to (i.e. tight coils being favoured once the snake had warmed sufficiently) the different body temperatures cannot be ascertained from these observations.

6.4.2. Diurnal and seasonal variation

The diurnal variation in mean body temperature and shade air and bask site temperatures for all seasons and within each season separately are collectively presented in Fig. 6.13. No significant variation in body temperatures were observed during the day during the present study (during any season or all seasons combined) although both shade air and bask site temperatures showed marked diurnal variation throughout each of the seasons and for all seasons combined (a difference was detected in the body temperatures of female snakes during Spring, however, although this was based on only a small sample size). This difference in the degree to which body and environmental temperatures varied may in part be explained by the different periods over which the two sets of temperatures were recorded. Body temperatures were only recorded from active animals

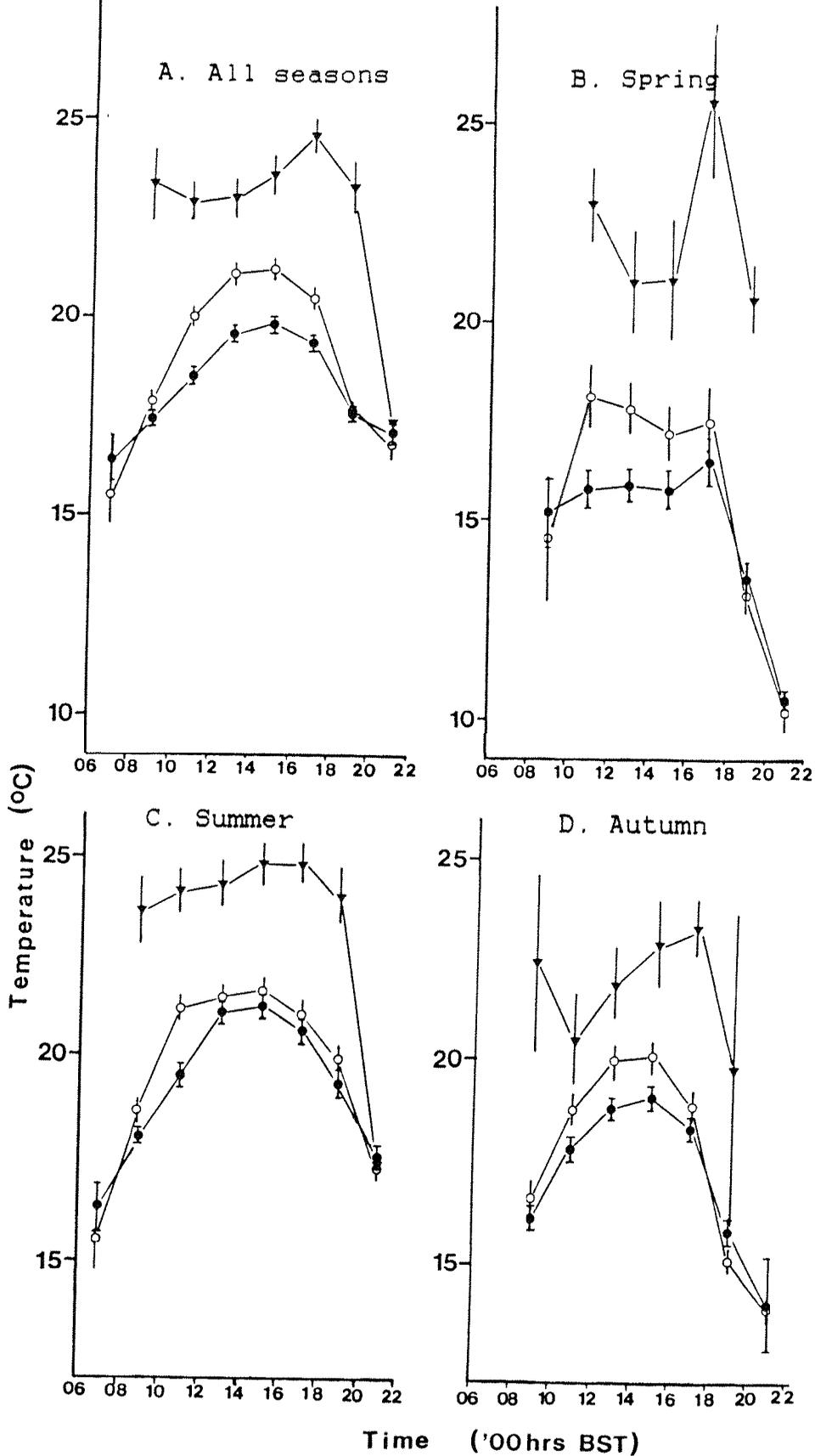


Fig. 6.13 : Diurnal variation in mean body temperature of *C. austriaca* (▼) and mean shade air temperature (●) and mean bask site temperature (○) recorded whilst observing *C. austriaca* (all ± 1 s.e.) in the field during **A.** All seasons, **B.** Spring (March-May), **C.** Summer (June-August) and **D.** Autumn (September-October) in 1984 to 1986 inclusive.

(usually captured in the open or below tin sheeting) whilst additional environmental temperature records were obtained (whilst radio-tracking) at the beginning and end of the day when the snakes were inactive. These latter records were typically associated with lower temperatures and hence these additional categories would be expected to provide different temperature values to those obtained during the rest of the day.

Notwithstanding this possible methodological difference, marked variations in environmental temperatures occurred throughout the remainder of the day. Smooth snakes appeared to maintain fairly consistent body temperatures which were in excess of both shade air and bask site temperature. This suggested that the species showed fairly precise thermoregulation. Goddard (1981) showed that *C. austriaca* on sunny days demonstrated different patterns of thermoregulation between the sexes. Males slowly warmed up to a 'plateau' level during the early afternoon whereas females maintained a warmer body temperature throughout the day. Goddard attributed this difference to more precise thermoregulation by females either through the selection of warmer bask sites or by earlier emergence. This requirement for maintaining a more elevated body temperature was suggested to be linked to viviparous reproduction. No such differences were detected on cloudy days. This observation probably reflected the difficulties associated with thermoregulation when insolation is reduced.

Whilst no distinctions were made on grounds of sex, Bont et al (1986) reported a 'tripartite' pattern of body temperatures on sunny days, i.e. showing a warming phase, a stable phase and a cooling phase. Overcast days, however, showed no such diurnal pattern of body temperature variations. This latter study measured body temperatures from early morning to late evening during the Spring time this being possible through the use of radio-telemetry. In addition four 24 hour periods were studied. These demonstrated that snakes restricted the degree to which their body temperatures cooled overnight (probably by

moving below ground to a depth of between 0 cm and 5 cm) and minimum body temperatures observed were between 12° and 14.6°C (from their Figs. 4 a. to d.).

A significant change in body temperature was observed between the seasons, this being indicated by an elevation in body temperature during Summer compared with Spring or Summer. It was likely that this variation reflected a change in the environmental temperatures; these permitting higher body temperatures to be achieved during the Summer. The longer day length associated with Summer would also have allowed longer periods of basking. Basking behaviour, however, was observed to increase in Autumn (see Chapter 4, section 4.3.9 b.). This change in behaviour is likely to have been in response to the deteriorating weather conditions and further indicated that the seasonal change in body temperatures were the result of variations in ambient temperature rather than in snake behaviour.

Goddard (1981) was unable to detect seasonal variation in body temperature. He suggested that this may result from snakes being able to expose themselves to similar conditions throughout the activity season, either through a change in bask site selection or in the length of time spent basking. Bont et al (1986) studied snakes only in Spring (between April and June). Over these months it appeared that snakes started activity ^{Successively} earlier and interrupted basking during the day with a period of submergence. These behaviours related to body temperature maintenance. In addition, Bont et al noticed an increase in the body temperature at which activity commenced and at which snakes submerged as the seasons progressed towards Summer.

Changes in body temperatures of snakes with season have been observed in other species e.g. Masticophis t. taeniatus, Crotalus viridis lutosus and Coluber constrictor mormon (Hirth and King 1969). Such variations in body temperature may also be accompanied by various physiological adaptations, for example changes in the

relationship between metabolism and temperature and the shift of critical temperatures (see Spellerberg 1982). Physiological adaptations (i.e. acclimatisation) in ectotherms may have developed to minimise disruption to the behaviour and physiology through the seasonal fluctuations in environmental temperatures (and day lengths, etc.). These would not only allow a higher body temperature to be maintained (i.e. representing metabolic homeostasis) but may also result in a shift of 'preferred' (and perhaps in some way 'optimal') body temperature. This may in turn affect the range of activity temperatures.

6.4.3. Intra-specific variation

Body temperatures were shown not to vary between the sexes during any (or all) of the seasons or throughout the day. No differences were observed in the temperatures of bask sites selected by males and females (that could not be explained by differences in the season in which they were observed or due to weather). Goddard, too, reported a similarity between the body temperatures of male and female C. austriaca although he proposed that female snakes showed a tendency to attain and maintain slightly warmer body temperatures than males. He suggested that this may be related to viviparity.

Viviparity has been shown to correlate with higher selected body temperatures in other species of snake (Hirth and King 1969). Selection of warmer bask sites would be expected to be beneficial to pregnant females in that it would promote embryogenesis. Development of the young would be enhanced by an increased body temperature of the mother. The gestation period typically extends well into September and often October. The more rapid development of embryos will be favoured as this would increase the probability of parturition prior to the deterioration of the weather at the end of the Summer and the associated submergence into hibernation. The absence of a difference between the sexes may also reflect the selection of warmer sites by males to some degree; warmth would also be required to optimise

spermatogenesis.

During the present study, neither body temperature nor bask site temperature was compared between pregnant and non-pregnant snakes. If lower body temperatures were shown by, and/ or cooler bask sites used by, non-pregnant than pregnant female snakes, then the corresponding greater values for the latter category may well be indicative of thermophilic behaviour relating to the bearing of live young.

Other aspects of individual condition can be related to changes in thermal preference. Regal (1966) observed a thermophilic response in various reptiles in the laboratory and proposed that this behaviour was largely to aid digestion. Skoczylas (1970) showed that digestion in Natrix natrix was dependent upon temperature. At very low temperatures (5°C) no digestion occurred, and it proceeded only very slowly at 15°C. Maximum rate appeared to be at 25°C with digestion rate being decreased again at 35°C. Such observations indicate that reptiles may adapt their behaviour to promote their body temperatures after feeding. Field data for C. austriaca did not support this hypothesis and no difference was observed in body temperatures between snakes in different feeding conditions.

Aspects of snake metabolism are affected by the slough condition (Taylor and Davies 1981) and this may, in turn, be expected to affect thermal behaviour. However, no differences were detected in body temperatures of C. austriaca in different stages of the skin shedding cycle in the field during the present study.

6.4.4. General comments

Maintenance of a precise body temperature can be ecologically 'expensive' in terms of time (when the animal could be pursuing other activities, e.g. foraging and mating) and energy (e.g. through repeated 'shuttling' behaviour and through loss of food intake). Other risks

associated with thermoregulation include increasing the possibility of predation and of promoting inter- and intra-specific competition for bask sites (Huey 1982). The precision of thermoregulation will therefore depend upon the relative priority of maintaining a particular or consistent body temperature and the relative increase in fitness conferred upon an animal by doing so. These factors will vary between individuals in a population and at different times within any individual.

Of primary importance is the avoidance of lethal temperatures or temperatures that will be ecologically lethal (i.e. the 'critical' temperatures). Within these limits lie a narrower band of temperatures at which various physiological (e.g. metabolic rate, hearing efficiency in lizards, digestive efficiency) and behavioural (e.g. burst speed) processes will operate optimally; although these need not all share the same optimal temperature.

Snakes are generally regarded as being less precise thermoregulators than many lizards species (Avery 1982). Field observations indicated that *C. austriaca* maintained the body temperature to within a fairly wide band of temperatures. Observation of the behaviour of the species in conjunction with body temperature measurements suggested that precise body temperature maintenance was forfeited through its basking within vegetation (possibly an anti-predator behaviour) and its frequent use of thick vegetation and forays below ground. In consequence the metabolism may have adapted to mean field body conditions (see Chapter 7). However, females did appear to spend protracted periods basking during pregnancy.

The investigation of thermal biology in the field during the present study was necessarily limited to measurements of hand captured animals. Use of bio-telemetric techniques (probably radio-telemetric devices) may help enhance the knowledge of the thermal ecology of the species by providing more abundant and unbiased measurements of body temperatures.

6.5. Summary

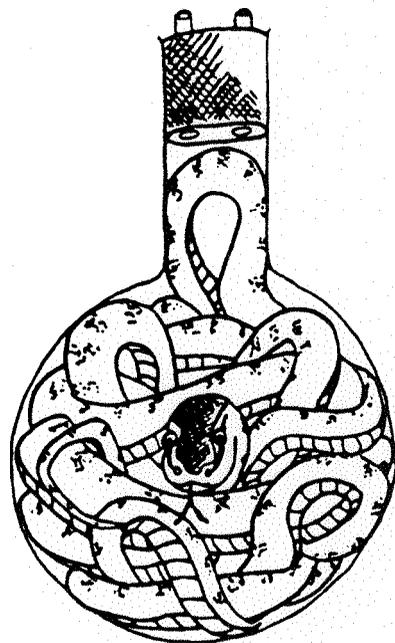
- i. Body temperatures of C. austriaca captured in the field ranged between 10.5° and 31.6°C with a mean value of 23.48°C \pm 3.95 (n= 327).
- ii. No difference in body temperature was detected between male and female snakes.
- iii. Body temperature was directly related to shade air and bask site temperatures, although in both cases body temperatures were usually higher than the corresponding environmental temperature.
- iv. Increasing cloud cover had a depressive effect on body temperatures. Body temperatures were generally decreased at any given environmental temperature as cloud cover increased.
- v. Thermoregulation by C. austriaca seems to be primarily heliothermic in nature.
- vi. Bask site temperatures correlate with, but are generally warmer than, shade air temperatures.
- vii. Seasonal variations in body temperature were observed, being greater in the Summer than in Spring or Autumn. These seemed to relate to variations in environmental temperatures. No variation was observed between the body temperatures of the sexes within any season.
- viii. Snake body temperatures did not vary during the course of a day during any season (with the exception of data for female snakes during all seasons ^{Combined} and during Spring). Body temperatures did not vary between the sexes throughout the day in any season.
- ix. No variation in body temperature was observed between snakes in different slough conditions, feeding states or

between females that were pregnant and those that were not.

x. Basking posture related to body temperature with snakes basking in medium to tight coils generally having the greater body temperature for females and for both sexes combined (but not males).

xi. Shade air and bask site temperatures varied between seasons and throughout the course of a day.

VII. Thermal Biology II: Laboratory Investigation



CHAPTER SEVEN

THERMAL BIOLOGY II

LABORATORY INVESTIGATION

7.1 Introduction

Coronella austriaca is ectothermic and poikilothermic (Spellerberg 1976), that is it derives its body warmth from external heat sources (i.e. from the environment) and consequently shows a variable body temperature. Body temperatures in most species of reptile, however, do not passively follow changes in environmental temperature but are regulated with varying degrees of precision through out much of the day (e.g. Avery 1982). In species where the body temperature does change with environmental conditions (these including many nocturnal, aquatic and fossorial species) habitat selection and regulation of activity timing are frequently employed to avoid unsuitable extremes of temperature (Avery 1982, Shine 1986). Such observations indicated that, in reptiles, activity occurs within only certain ranges of temperature and, for some species, that specific body temperatures are 'preferred' by these animals (Spellerberg 1976, Pough and Gans 1982). The thermal biology of C. austriaca in the field was discussed in Chapter 6.

Body temperatures that can be achieved and maintained in the field, however, will ultimately be determined by the conditions within the habitat. It is unlikely that conditions that permit precise thermoregulation will occur at all times. As such records measured under these conditions may not be representative of the 'preferred' body temperatures of the species. Estimates of such temperature ranges can therefore not be obtained from field studies alone. Similarly, the extreme limits to the thermal environment can not be determined in the field, as such conditions are likely to be avoided by active animals. Due to these limitations, laboratory investigation of certain

aspects of the thermal biology of C. austriaca were undertaken during the present study to supplement the observations made in the field.

Metabolism in animals will be affected by body temperature. In poikilotherms, variation in body temperature may cause variation in metabolic rate which will affect a diversity of physiological (e.g. growth, development, digestion), and consequently behavioural (e.g. movement, mating), processes in these animals. The nature and extent of variation in metabolism with temperature is therefore of interest in determining the importance and precision of body temperature regulation. Many studies of metabolic rate in reptiles have been undertaken (see reviews by Bennett and Dawson 1976, Bennett 1982) and many aspects of aerobic and anaerobic metabolism investigated.

In this chapter the thermal biology of C. austriaca is investigated via a series of laboratory experiments. These determine the temperatures 'selected' (sensu Pough and Gans 1982) by the species in the absence of limitations to the thermoregulation, the upper and lower limits to body temperatures ('maximum tolerated temperature' and 'minimum critical temperature') and the relationship between the resting (aerobic) metabolic rate and temperature. Such information is useful for the understanding of the use of the thermal habitat and for determining the metabolic requirements of the species in the field.

7.2. Methods and materials

7.2.1. Methodology

Details of the methodology used in this chapter are presented in Chapter 2 (General Methods), Section 2.3, as follows:

Section 2.3.1 : Respirometry

Section 2.3.2 : Selected body temperature

Section 2.3.3 : Critical minimum temperature

Section 2.3.4 : Maximum tolerated temperature

Data pertaining to details of study animals used and other experimental details for each experiment are presented in the relevant part of the Results section (7.3.) below.

7.2.2. Analysis

a. Weight-specific metabolism and size relationships

Regression equations and Pearson's correlation coefficients were calculated for the relationship between oxygen consumption and live body weight of smooth snakes at each of seven test temperatures.

b. Intra-specific comparisons of results

Oxygen consumption rates were compared between pregnant and non-pregnant female specimens at each test temperature between 10° and 30°C using the Student's t-test. The difference in metabolic rate between male and female smooth snakes at test temperatures from 5° to 35°C was investigated via Student's t-tests.

c. Results collectively for all specimens

Metabolic rate-temperature curves were plotted for absolute and Log_{10} values of oxygen consumption rate against test temperature. Temperature coefficients (Q_{10} values) were calculated for each 5°C interval of test temperatures and for the entire range of temperatures.

d. Selected body temperature

Mean Selected Body Temperatures for each individual and for all males, all females and all specimens were calculated. Male and female mean selected body temperatures were compared using the Student's t-test. Mean body temperatures during six 4-hour time periods across the day were

calculated for each sex separately. Temporal variation in body temperature was investigated via a one-way Analysis of Variance. Measurements of laboratory air temperature and temperatures along the thermal gradient were tested for temporal variation using a one-way Analysis of Variance.

e. Minimum critical and maximum tolerated temperatures

Mean minimum critical and maximum tolerated temperatures were calculated.

7.3. Results

7.3.1. Respirometry

a. Experimental details

Values for oxygen consumption presented were recorded from nineteen experiments between May to July 1984 and May to July 1985 using seventeen specimens of C. austriaca as follows: twelve experiments used ten male snakes and a further seven experiments each used a different female snake. A further five sets of data were discarded, four due to faulty apparatus and the results from an experiment using a recently fed snake were excluded from the analysis to maintain consistency of methodology. These latter experiments are not included in the above totals.

All animals included in the analysis were assumed to be in a post absorptive condition (i.e they showed no obvious sign of having recently fed upon capture) and were all adults (male snout to vent length (SVL) = 360 to 450 mm (mean= 410.2 mm \pm 26.9, n= 10), female SVL = 395 to 496 mm (mean= 440.4 mm \pm 31.6, n= 7)). Weights of these animals were taken prior to each experiment and varied between 31.0 g and 66.3 g. Mean values recorded were 44.6 g \pm 9.8 at 10°C, 45.0 g \pm 9.7 at 20°C and 44.7 g \pm 9.9 at 30°C. Of the females five were pregnant and two were not. With the exception of one experiment, no pregnant female specimens were subjected to temperatures below 10°C.

b. Weight-specific metabolism and size relationships

The relationship between metabolic rate and body mass for smooth snakes was investigated via the regression equations from a double logarithmic plot of the two parameters ($\text{Log}_{10} \text{VO}_2$ against Log_{10} body weight), and the correlation between the two variables determined by calculating a Pearson's correlation coefficient (r), for each test temperature. The slope of the regression line is reported not to vary between test temperatures (Bennett and Dawson 1976) and a consistent value for this statistic would permit a weight-correction equation, specific for C. austriaca, to be derived and this used to standardise results for the species and permit comparisons between other published studies for other species.

Significant correlations were obtained in only four out of the seven test temperatures, these being at 15°, 20°, 30° and 35°C, ($r = 0.55$ $p < 0.02$, $r = 0.43$ $p < 0.05$, $r = -0.46$ $p < 0.04$, $r = -0.069$ $p < 0.005$ respectively). The regression equations calculated for the metabolism / weight relationship at each of these temperatures are presented below :

$$\begin{aligned} 15^\circ: \quad \text{Log}_{10} \text{VO}_2 &= 0.98 \text{Log}_{10} W - 3.11 \\ 20^\circ: \quad \text{Log}_{10} \text{VO}_2 &= 0.72 \text{Log}_{10} W - 2.52 \\ 30^\circ: \quad \text{Log}_{10} \text{VO}_2 &= -0.53 \text{Log}_{10} W - 0.16 \\ 35^\circ: \quad \text{Log}_{10} \text{VO}_2 &= -0.72 \text{Log}_{10} W + 0.37 \end{aligned}$$

where VO_2 is the oxygen consumption ($\text{ml. O}_2 \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$) and W is the body weight (g). Regression lines for the above equations are presented in Fig. 7.1. In the absence of a consistent value for the slope of the regression equation, with values even being contradictory with regards to whether the variables are positively or negatively correlated, no weight correction equation for C. austriaca could be derived from these data that would be applicable for all temperatures. Thus subsequent analysis employed weight-specific metabolic rates which were not further corrected to compensate for differences in body mass

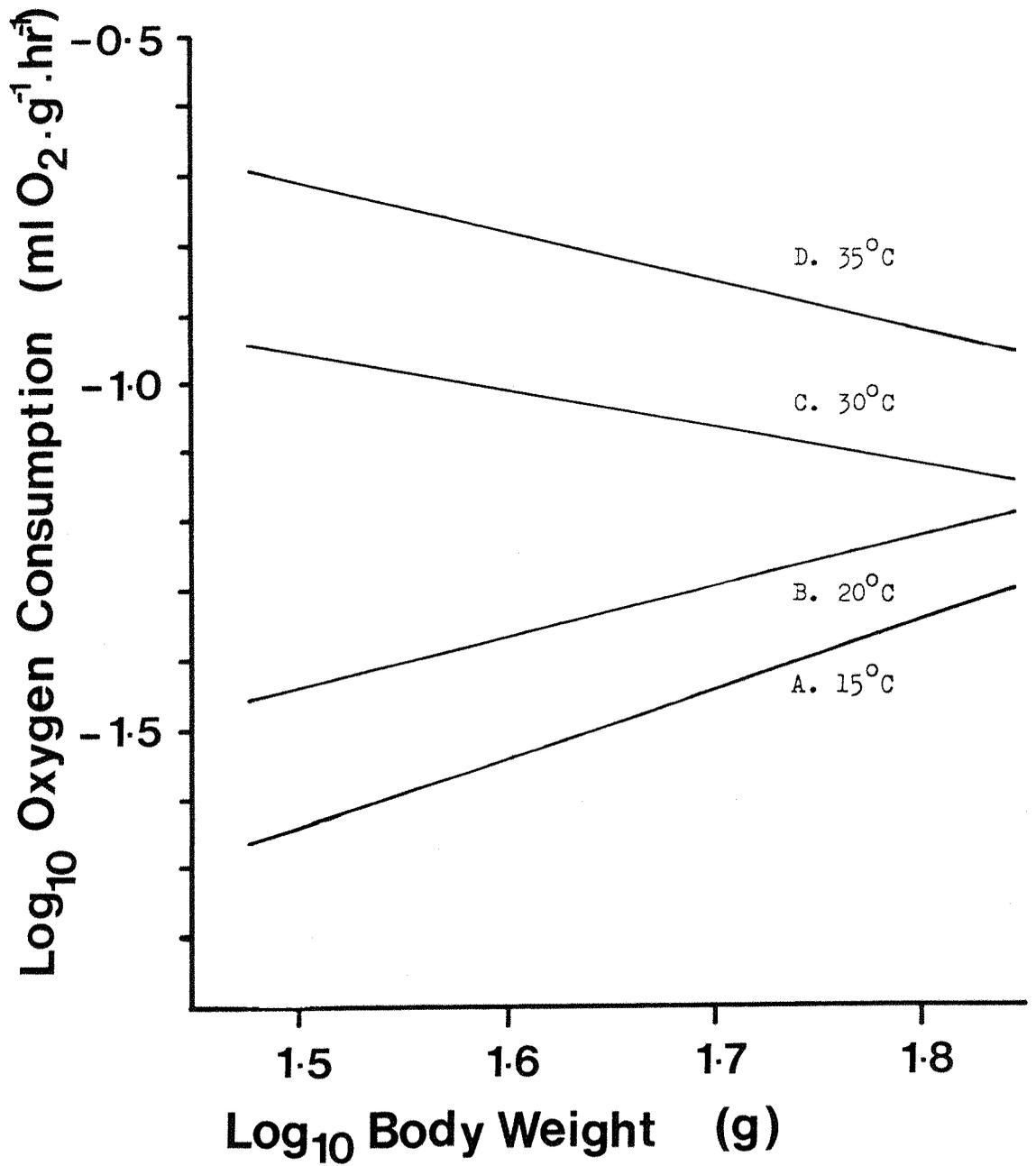


Fig. 7.1 : Regression lines for the relationship between Log_{10} Oxygen consumption and Log_{10} Body weight for C. austriaca at test temperatures where a significant correlation was detected namely A. 15°C, B. 20°C, C. 30°C and D. 35°C (n= 17 in all cases except D. where n= 13).

between the animals tested. That no weight correction was employed was further justified since the range of body weights used was small ($66.3 - 31.0 = 35.3$ g) and that the analysis was primarily concerned with intra-specific comparisons.

c. Intra-specific comparisons of results

A significant difference in oxygen consumption rates was observed between pregnant and non-pregnant females only at 25°C ($t = 2.77$, with 5 d.f., $p < 0.05$); higher metabolic rates were observed for non-pregnant females (mean = $0.079 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot \text{hr}^{-1} \pm 0.010$, $n = 2$) than for pregnant females (mean = $0.056 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot \text{hr}^{-1} \pm 0.010$, $n = 5$). No such difference was observed at other test temperatures ($t = 1.26, 1.50, 0.32$ and 2.15 with 5 d.f. and $p > 0.05$ in all cases for 10° to 20°C and 30°C respectively). Data for all female snakes were combined for further analysis because of the small sample sizes in each category and because of the overall similarity of the two sets of data.

Snakes from all four defined slough conditions were used (males: sloughing $n = 1$, post-slough $n = 8$, mid-slough $n = 2$ and preslough $n = 1$; females: $n = 0, 4, 2$ and 1 respectively). Due to the small sample sizes in each case data for all slough conditions were combined and treated together. Consequently no relationships between the metabolism and the slough status of the animals were investigated.

Data for the oxygen consumption rates of male and female snakes, both separately and as combined data, are presented in Table 7.1. A significant difference was detected between the sexes only at 35°C ($t = 2.54$ with 11 d.f., $p < 0.05$). No such difference was observed at other test temperatures ($t = 0.55$ with 12 d.f., 0.27 with 15 d.f., 0.48 with 15 d.f., 0.78 with 15 d.f., 0.17 with 15 d.f. and 0.26 with 15 d.f., $p > 0.05$ in all cases, for 5° to 30°C respectively). As all but one of the seven temperatures showed no significant difference between the sexes, further analysis was limited

STATISTIC		TEMPERATURE (°C)						
		5	10	15	20	25	30	35
Males and Females	Mean	0.008	0.021	0.034	0.048	0.063	0.094	0.150
	s.d.	0.002	0.010	0.015	0.018	0.014	0.024	0.030
	Log ₁₀ Mean	-2.131	-1.722	-1.501	-1.340	-1.211	-1.041	-0.832
	N	14	17	17	17	17	17	13
Males	Mean	0.008	0.021	0.032	0.046	0.064	0.092	0.166
	s.d.	0.001	0.009	0.016	0.017	0.015	0.012	0.016
	Log ₁₀ Mean	-2.114	-1.721	-1.521	-1.364	-1.208	-1.037	-0.781
	N	11	10	10	10	10	10	7
Females	Mean	0.007	0.022	0.036	0.053	0.062	0.096	0.132
	s.d.	0.004	0.013	0.015	0.020	0.014	0.036	0.032
	Log ₁₀ Mean	-2.194	-1.723	-1.473	-1.307	-1.215	-1.045	-0.892
	N	3	7	7	7	7	7	6

Table 7.1 : Mean values of oxygen consumption (ml O₂. g⁻¹. hr⁻¹) (of four lowest but consistent values for each animal) of C. austriaca at different test temperatures (°C) for all specimens and for males and females separately. Data collected between May and July 1984 and May and July 1985.

to the data for all specimens of C. austriaca collectively.

d. Combined results for all specimens.

The metabolic rate-temperature (M-T) curves presented for absolute (Fig. 7.2) and \log_{10} values (Fig. 7.3) of oxygen consumption rate ($\text{ml O}_2 \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$ at STP) were produced using the means of between thirteen and seventeen experimental values in each case. Each of these values was in turn derived from the mean of the lowest four (but consistent) readings obtained from each experiment.

Oxygen consumption rate increased with increasing temperature (see Fig. 7.2), but the rate of increase is not linear. The gradient of the curve becomes progressively steeper as the temperature becomes higher and hence suggests an exponential relationship. A semi-logarithmic plot (Fig. 7.3) demonstrates an approximately linear relationship between \log_{10} O_2 consumption and temperature although, even here, the gradients at low and high temperatures are steeper than those at intermediate values.

The temperature coefficients (Q_{10}) for the oxygen consumption values over various temperature intervals were derived from the equation:

$$Q_{10} = (R_2 / R_1)^{10 / (t_2 - t_1)}$$

where R_1 and R_2 are the rates of oxygen consumption ($\text{ml O}_2 \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$) at the corresponding temperatures t_1 and t_2 ($^{\circ}\text{C}$). These data are presented in Table 7.2.

The Q_{10} values for C. austriaca were greatest at the two extremes of the test temperature range. Q_{10} values gradually decreased as the temperature increased from 5-10 $^{\circ}\text{C}$, through 10-15 $^{\circ}\text{C}$ and 15-20 $^{\circ}\text{C}$, until 20-25 $^{\circ}\text{C}$. After 20-25 $^{\circ}\text{C}$ the Q_{10} values became progressively greater as the temperature increased through 25-30 $^{\circ}\text{C}$ to 30-35 $^{\circ}\text{C}$, (see

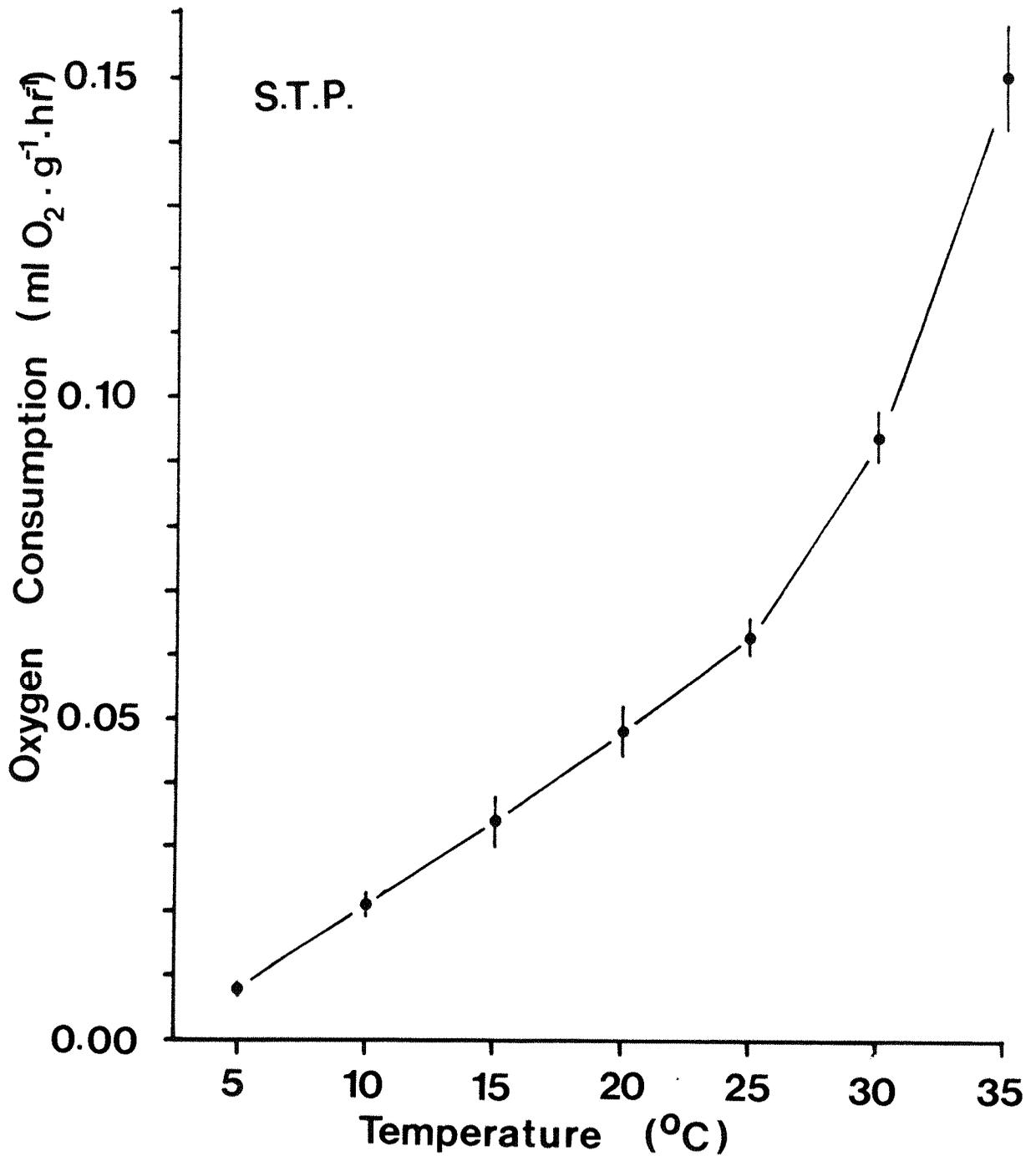


Fig. 7.2 : Oxygen consumption (ml O₂ . g⁻¹ . hr⁻¹) against Temperature (°C) (+ 1 s.e.) for C. austriaca (Males and Females in post-absorptive condition) converted to Standard Temperature and Pressure (S.T.P.). n = 17 in all cases except at 5 °C where n = 14 and at 35 °C where n = 13.

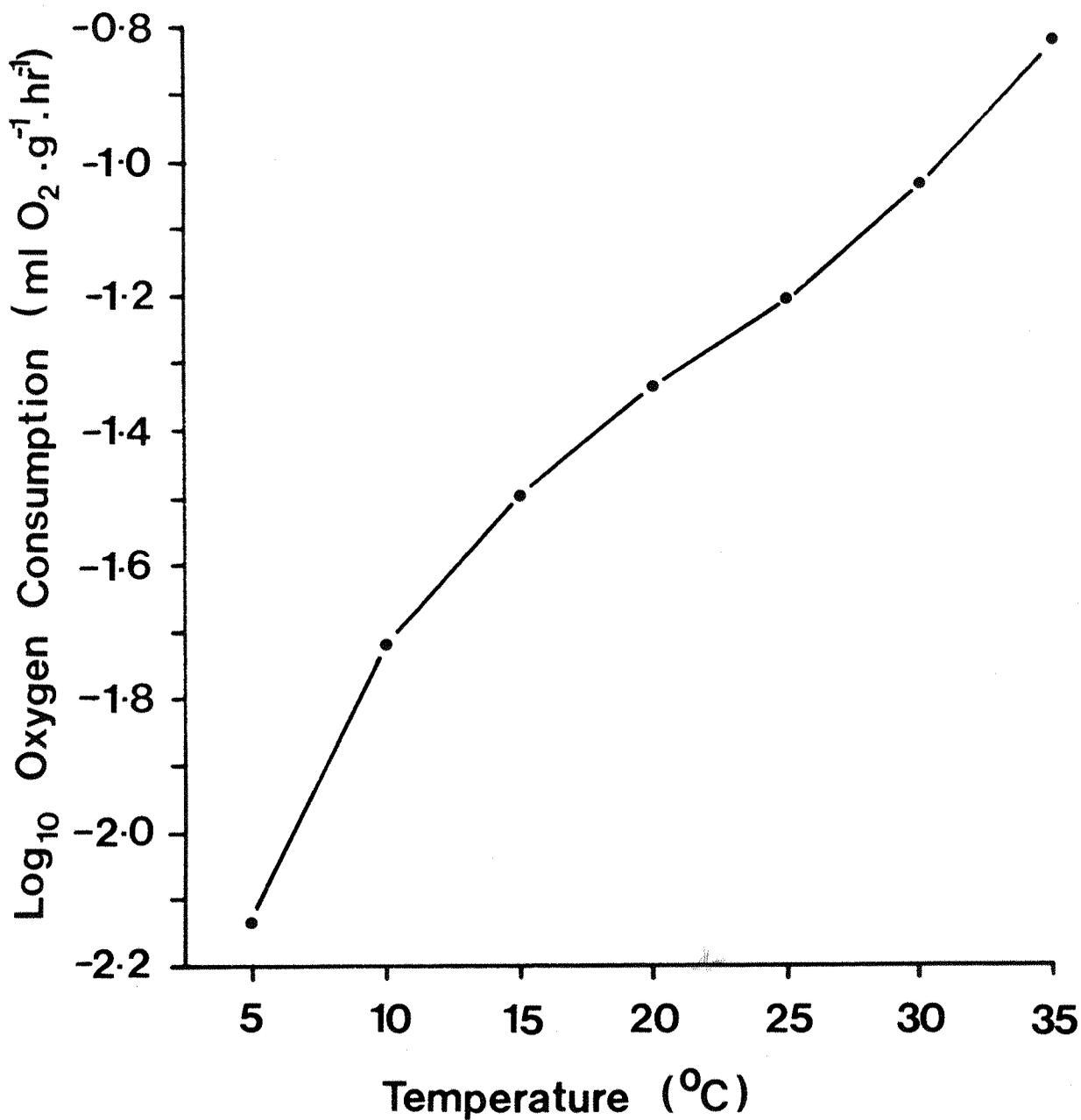


Fig. 7.3 : Log₁₀ Oxygen consumption (ml O₂ · g⁻¹ · hr⁻¹) against Temperature (°C) for C. austriaca

(Males and Females in post-absorptive condition) converted to Standard Temperature and Pressure (S.T.P.). n = 17 in all cases except at 5°C where n = 14 and at 35°C where n = 13.

<u>Experimental Temperatures (°C)</u>	<u>Q₁₀ Values for mean of oxygen consumption</u>
5-10°	6.89
10-15°	2.62
15-20°	1.99
20-25°	1.72
25-30°	2.23
30-35°	2.55
<u>Overall</u>	2.66

Table 7.2 : Q₁₀ values for oxygen consumption rates for C. austriaca at 5° intervals and over all test temperatures (all specimens).

Table 7.2). The rate of increase of oxygen consumption rate therefore decreased as temperatures increased to 20–25°C and thereafter the rate of increase became increasingly rapid.

An overall 'average' Q_{10} value for 5–35°C was calculated as 2.66, indicating that oxygen consumption almost trebles for each 10°C increase in temperature over that range.

7.3.2. Selected body temperature (Voluntary temperature)

Body temperatures were measured by radio-telemetry from a total of seven specimens of C. austriaca (four males and three females) housed in a thermal gradient chamber over 22 days during May to July 1985 and June 1986. Data from seven experiments (using four males and three females) lasting between 1.5 and 2.8 days each are suitable for analysis. Due to discrepancies between calibration curves at the start and finish of the experiments, the results presented below are to an accuracy of between $\pm 1^\circ$ and $\pm 2^\circ$ C in each case.

Mean Selected Temperatures (sensu Pough and Gans 1982) for each individual and for pooled data are presented in Tables 7.3 and 7.4 respectively together with the standard deviations of these means and ranges of recorded body temperatures. Mean selected temperatures for individual animals ranged between 28.4 and 31.3°C. Pooled data indicates a mean selected temperature of 29.6°C \pm 3.15 for C. austriaca, however a significantly higher mean selected temperature was observed for females (30.3°C \pm 2.17) than males (29.2°C \pm 3.65), ($t = 3.09$ with 322 d.f, $p < 0.01$). As such, data for the two sexes are hereafter treated separately.

Temporal variation in selected body temperatures was investigated separately for each sex by dividing the day into six 4-hour time blocks, corresponding with the artificial lighting, to approximate to dawn (05–0900 hr), morning (09–1300 hr), afternoon (13–1700 hr), evening (17–

Animal	Sex	Mean Body Temperature (°C)	s.d	Number of Observations	Range
H10	M	29.0	2.84	47	20 to 33
H27	M	29.1	4.11	48	20 to 38
B 3	M	28.4	3.15	62	19 to 35
B 4	M	31.2	4.37	29	20 to 37
H31	F	31.3	1.88	54	27 to 34
S 3	F	29.3	1.96	57	23 to 33
L 1	F	30.1	2.20	27	25 to 36

Table 7.3 : Mean body temperatures (°C) of each specimen of C. austriaca used in Selected Body Temperature Experiments, (M = male, F = Female).

	Number of Individuals	Mean Body Temperature (°C)	s.d.	No. of Obs.	Range (°C)
All Data	7	29.6	3.15	324	19 to 38
Males	4	29.2	3.65	186	19 to 38
Females	3	30.3	2.17	138	23 to 36

Table 7.4 : Mean body temperatures (°C) of specimens of C. austriaca and standard deviations (s.d.) using data from all Selected Body Temperature experiments showing the number of individuals used and the number of observations made (No. of Obs.).

2100 hr) and two periods of night (21-0100 hr and 01-0500 hr). Differences in selected body temperatures between time periods were tested for using a one-way Analysis of Variance. Mean selected temperatures for each time period are presented in Table 7.5. Male *C. austriaca* demonstrated a difference in selected body temperature over the day ($F=9.237$ with 5 and 180 d.f, $p<0.001$) being lowest ($26.4^{\circ}\text{C} \pm 3.94$) at dawn and slowly rising to a peak value ($31.5^{\circ}\text{C} \pm 2.42$) just after dark (21-0100 hrs). No significant variation in the selected body temperatures of female smooth snakes was observed throughout the day ($F=1.015$ with 5 and 132 d.f, $p>0.05$). Body temperatures of male and female snakes differed significantly from each other during three of the six time periods, namely 0500-0859 hr, 1700-2059 hr and 2100-0059 hr (values for 't' and significance levels are presented in Table 7.5). During the first two of these periods body temperatures of female snakes were greater than those of male snakes and during the latter period body temperatures of males exceeded those of female specimens.

Changes in body temperature may occur as a result of the snake moving along the thermal gradient and actively selecting a temperature regime or may, alternatively, be a passive response to changes in the temperature of the gradient at the location of the snake. To test this latter possibility, temperatures at five locations along the thermal gradient and the laboratory air temperature were monitored hourly (between 8th and 12th September 1986), using an automatic temperature recorder. Although these data were collected after all Selected Body Temperature experiments had been completed, the temperatures recorded in the thermal gradient during this latter period were believed to be representative of those experienced by the study animals as laboratory air temperatures and natural day lengths were similar during both periods. The thermal gradient was subjected to the same light: dark cycle as the final series of selected body temperature experiments (light:dark = 16:8). Consequently fluctuations in both air temperature and the temperatures along the gradient were

Time	<u>Males</u>			<u>Females</u>			<u>t-test</u>	
	Mean	s.d.	n	Mean	s.d.	n	t	p
01-05	29.9	1.89	31	30.0	1.47	21	0.204	>0.05
05-09	26.4	3.94	30	29.8	1.97	21	3.641	<0.001
09-13	27.7	5.03	27	29.9	2.74	22	1.839	>0.05
13-17	29.6	3.01	30	30.3	2.67	21	0.855	>0.05
17-21	29.5	2.94	34	31.0	2.25	28	2.217	<0.05
21-01	31.5	2.42	34	30.3	1.65	25	2.151	<0.05

Table 7.5 : Mean body temperatures ($^{\circ}$ C) observed during different time periods for Male and Female specimens C. austriaca as measured during Selected Body Temperature Experiments. Values obtained from t-tests are presented, showing the value of 't' and the significance level(p).

also assumed to have been similar.

Temperature data were pooled to yield the six 4-hour time periods used in the above analysis of diel changes in selected body temperature and these compared to assess whether significant changes in temperature were observed at each position during the day by employing a one-way Analysis of Variance.

Highly significant changes in the laboratory air temperature ($F= 64.09$ with 5 and 94 d.f., $p<0.001$) and in the temperatures at all five positions along the thermal gradient ($F= 54.54$, $F= 65.90$, $F= 88.56$, $F= 107.05$, $F= 46.41$ with 5 and 94 d.f. and $p<0.001$ in all cases, for positions 1 to 5 along the thermal gradient respectively) were recorded (see Table 7.6).

For a comparison between fluctuations in temperatures observed in the laboratory and in the thermal gradient with the observed body temperatures of both male and female C. austriaca, the two sets of data were combined in Fig. 7.4.

7.3.3 Minimum critical and maximum tolerated temperatures

The mean critical minimum temperature of C. austriaca was calculated as $1.98^{\circ}\text{C} \pm 1.14$ ($n= 7$, four individuals: all males) (range= 0.6 to 3.86°C).

The maximum tolerated temperature experiments proved unsuccessful using C. austriaca. The specimens seemed rather agitated and frequently moved from under the tin sheeting at quite low body temperatures. On these occasions it seemed improbable that the movement was related to attaining an uncomfortably high body temperature and hence these data were discarded. An estimate of the maximum tolerated body temperature of $36.63^{\circ}\text{C} \pm 1.27$ ($n= 2$, both males) (range= 35.78 to 37.58°C) was obtained using this method. This value is comparable with the maximum values recorded in the selected body temperature experiments in the thermal gradient.

Time	Shade Air	Position Along Thermal Gradient											
		Temp.	1	2	3	4	5	.					
	n	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.	mean	s.d.
0100-0500	16	17.6	0.5	36.9	0.9	26.3	0.8	17.0	0.8	13.1	0.7	-2.0	1.0
0500-0900	16	17.3	0.7	37.1	1.2	27.2	0.9	17.6	0.9	14.3	0.8	-1.8	1.1
0900-1300	17	19.4	1.5	39.6	2.4	29.5	1.7	20.5	1.8	17.1	1.7	0.5	2.0
1300-1700	19	21.5	1.1	43.7	2.5	32.6	1.8	24.1	1.6	20.1	1.3	3.2	1.6
1700-2100	16	20.9	0.5	44.2	1.3	32.1	1.0	23.6	1.1	19.5	0.8	3.1	1.0
2100-0100	16	18.7	0.5	39.6	1.2	28.1	1.1	19.0	1.2	15.3	1.1	0.1	1.1

Table 7.6 : Mean laboratory shade air temperatures (°C) and mean temperatures at five points along the thermal gradient chamber (°C) during six 4-hour periods between 8th and 12th September 1986.

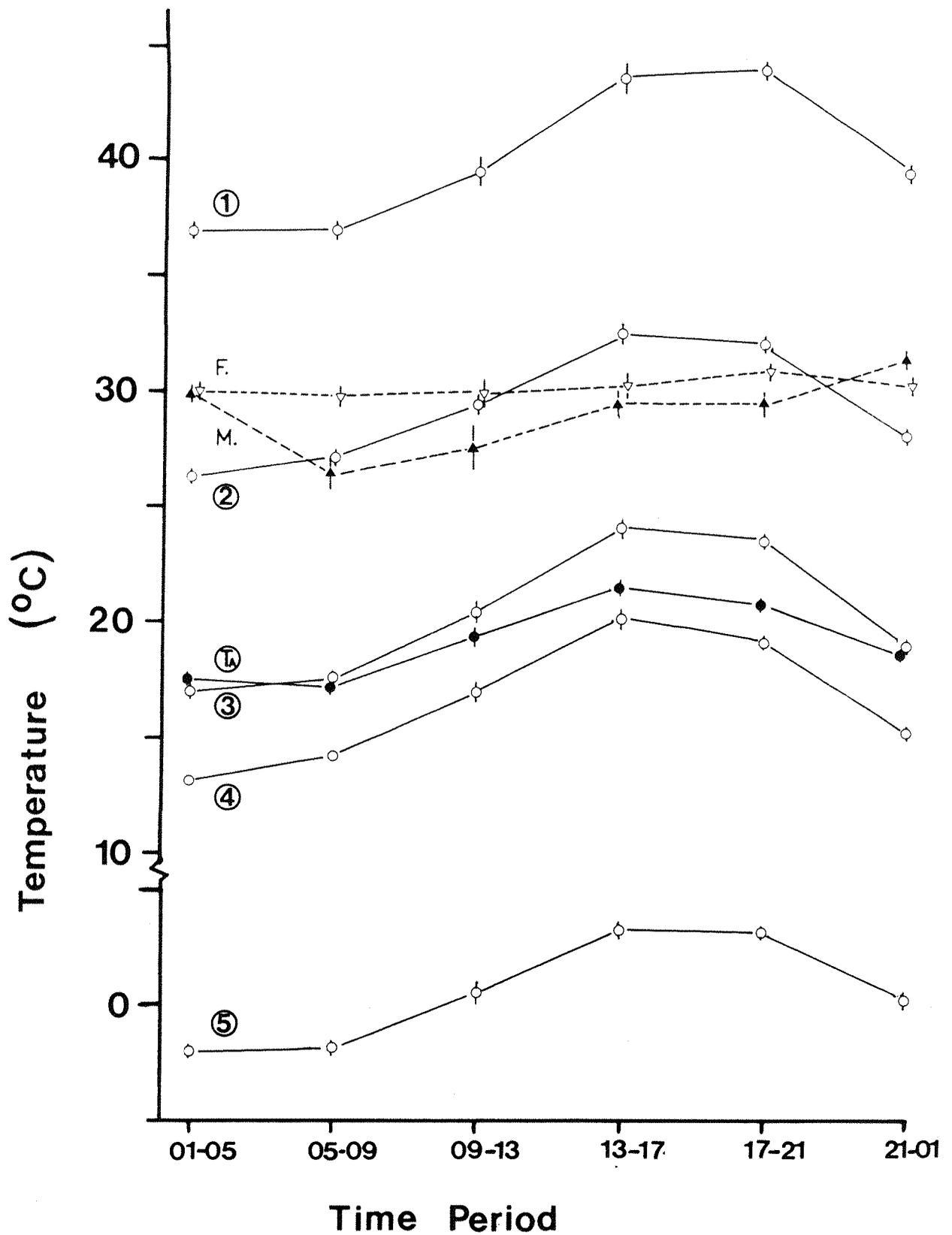


Fig. 7.4 : Mean Selected Body Temperatures of Male (closed triangles, M) and Female (open triangles, F) *C. austriaca* in the Thermal Gradient, Laboratory Shade Air Temperature (closed circles, T) and Temperatures at Five Positions along the Thermal Gradient Chamber (open circles, 1 to 5) during six time periods through out the day. Error bars indicate ± 1 s.e.

7.4. Discussion

7.4.1. Metabolism

a. Weight correction

The relationship between metabolic rate and body size has long interested biologists studying many taxa. With increasing size an increase in net metabolism is observed; the metabolic rate per unit weight, however, decreases. This relationship has been dubbed the "Mouse-Elephant" curve and has been reported within and between many invertebrate and vertebrate (both ectothermic and endothermic) taxa (Scholander et al 1953, O'Connor 1963, Bennett and Dawson 1976). These metabolic rate-weight relationships have the general form:

$$M = aW^b$$

or $M/W = aW^{(b-1)}$

where 'M' is the metabolic rate (often expressed in ml O₂.hr⁻¹) and 'W' is the body weight. The constants 'a' and 'b' are empirically determined and represent the metabolic rate of a 1.0 g animal and the slope of the regression line on a double logarithmic plot respectively. The value of 'b' can yield useful information about the nature of the relationship (for example a value of 0.67 indicates that metabolic rate is directly proportional to the surface area of the animal) and the comparison of the value between taxa is useful for determining how consistent the Rate - Weight relationship is between studies.

Such expressions have been determined for the Reptilia (Bennett and Dawson 1976). Using data from published studies of different species, Bennett and Dawson (1976) calculated regression relationships for oxygen consumption rates (ml O₂. hr⁻¹) and weight (g) for snakes at 20°C (n= 35) and 30°C (n= 13). These were as follows:

1. At 20°C: $\text{ml O}_2 \cdot \text{hr}^{-1} = 0.120 \text{ g}^{-0.77}$

or : $\text{ml O}_2 \cdot \text{g}^{-1} \cdot \text{hr}^{-1} = 0.120 \text{ g}^{-0.23}$

2. At 30°C: $\text{ml O}_2 \cdot \text{hr}^{-1} = 0.280 \text{ g}^{-0.74}$

or : $\text{ml O}_2 \cdot \text{g}^{-1} \cdot \text{hr}^{-1} = 0.280 \text{ g}^{-0.24}$

The 'b' values obtained from these studies indicate that the relationship between metabolic rate and weight is not simply determined by surface area relationships.

Using Bennett and Dawson's equations, metabolic rates for C. austriaca were predicted as being $0.050 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$ (95% confidence limits: 0.049 to 0.051) at 20°C and $0.112 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$ (95% confidence limits: 0.110 to 0.116) at 30°C. These predictions compare with observed values of $0.048 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$ (95% confidence limits: 0.039 to 0.057) at 20°C and $0.094 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$ (95% confidence limits: 0.083 to 0.105) at 30°C. Thus the observed value at 20°C encompassed the range predicted by these equations yet the observed metabolic rates at 30°C were lower than those predicted for this latter temperature.

Davies and Bennett (1981) reported that predicted values of metabolic rate determined from the above equations were consistently higher than observed metabolic rates of juvenile Natrix natrix and adult and juvenile N. maura. These authors believed the variation to be partially due to scatter of data in Bennett and Dawson's regression equations resulting from inconsistency of methodology between studies. Variation within their own data between animals of different ages, however, indicated that a single regression equation for snakes is probably too simplistic (Davies and Bennett 1981). Nonetheless, the relationships suggested by Bennett and Dawson provide a useful 'average' for all snakes against which results from an individual study can be compared.

That a relationship between metabolism and body weight is

observed suggests data need to be standardised prior to comparisons between inter- and intra-specific groups. Failure to compensate this relationship may mean that important ecophysiological relationships may be obscured in comparisons between animals of different sizes, with larger snakes showing apparently lower weight-specific metabolic rates. The data obtained throughout this study were primarily intended for intra-specific study and, due to the small amount of variation in body sizes used, such 'weight-correction' would therefore not be necessary. The absence of any consistent weight related effect on metabolism (see section 7.3.2) further suggested that such manipulation would be unwarranted here. Comparisons with published studies, however, would require such standardisation and to this end data were 'weight corrected', via the formula given in Davies and Bennett (1981), and these values are presented in Table 7.7. This formula (derived from Bennett and Dawson 1976) is as follows:

$$\text{Log}_{10} a = \text{Log}_{10} \text{VO}_2 + 0.235 \text{Log}_{10} W$$

where W = body weight (g) and VO_2 = O_2 consumption rate ($\text{ml O}_2 \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$). 'a' = antilog of Y intercept of metabolism against body weight regression and hence will represent the oxygen consumption rate of a hypothetical 1.0 g animal.

In all cases the weight corrected data were greater than the observed values. Whereas this value allows comparison between studies, the unweight corrected values were preferred for subsequent discussion of intra-specific comparisons and of metabolic requirements.

b. Metabolic rate

The relationship between metabolic rate and temperature has been investigated in many groups of animals and this represents one of the most studied aspects of reptilian physiology (see reviews by Bennett and Dawson 1976 and Bennett 1982). Reptiles are almost exclusively ectothermic and the majority experience variation in body temperature.

STATISTIC		TEMPERATURE (°C)						
		5	10	15	20	25	30	35
Males and Females	Mean	0.018	0.052	0.084	0.119	0.153	0.227	0.368
	s.d.	0.005	0.026	0.041	0.046	0.033	0.054	0.062
	Log ₁₀ Mean	-1.738	-1.286	-1.078	-0.925	-0.814	-0.645	-0.434
	N	14	17	17	17	17	17	13
Males	Mean	0.018	0.049	0.078	0.110	0.152	0.220	0.398
	s.d.	0.003	0.020	0.042	0.043	0.036	0.029	0.031
	Log ₁₀ Mean	-1.735	-1.309	-1.110	-0.961	-0.820	-0.658	-0.400
	N	11	10	10	10	10	10	7
Females	Mean	0.018	0.056	0.092	0.132	0.156	0.237	0.333
	s.d.	0.010	0.034	0.041	0.051	0.032	0.079	0.074
	Log ₁₀ Mean	-1.747	-1.251	-1.037	-0.879	-0.807	-0.625	-0.478
	N	3	7	7	7	7	7	6

Table 7.7 : Mean values of weight-corrected oxygen consumption ($\text{ml O}_2 \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$) (using the equation of Davies and Bennett 1981) (of four lowest but consistent values for each animal) of *C. austriaca* at different test temperatures (°C) for all specimens and for males and females separately. Data collected between May and July 1984 and May and July 1985.

A knowledge of the effect of such changes on metabolism is therefore important to the understanding of the use of the thermal environment in the field. During the present study the temperatures measured in respirometry experiments were ambient temperatures relating to the inside of the 'animal chamber' of the apparatus; as the animal was inactive and maintained in the dark, ambient temperatures were assumed to be very similar to the body temperatures of the snake.

The metabolism of an animal, like any chemical reaction, will be affected by temperature. Van't Hoff's generalisation states that the rate of a biochemical reaction will double with every 10°C rise in temperature and consequently will show an exponential rate of change (Gordon et al 1982). Metabolic rates of C. austriaca increased with increasing temperature (see section 7.3.1, Figs. 7.2 and 7.3). The overall Q_{10} between 5° and 35°C was 2.66 which indicated an approximately exponential relationship between rate and temperature. This relationship is common to most other reptiles where the majority of species show increases in metabolic rates of a factor of between two and three for every 10°C rise in temperature (Bennett and Dawson 1976, Spellerberg 1982). However a general overview of the whole curve tends to be too simplistic and will overlook differences that occur throughout the different portions of the curve.

The most noticeable feature of the semi-logarithmic plot of oxygen consumption against temperature (Fig. 7.3) is the diminished rate of increase between 15° and 25°C. The Q_{10} values associated with the two five-degree intervals here were both less than 2.0. This temperature range encompassed those body temperatures most frequently encountered by active C. austriaca in the field (see Chapter 6) and, as such, this 'slight levelling of the curve' may be indicative of a degree of metabolic homeostasis over 'normal' body temperatures in the field. The mean body temperature recorded in the field was 23.48°C \pm 3.95 (95% confidence interval= 23.26° to 27.70°C) (see Chapter 6). This body temperature is equivalent to an oxygen

consumption rate of $0.058 \text{ ml.O}_2 \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$ (and those associated with the 95% confidence interval for the mean body temperature are 0.057 to $0.059 \text{ ml.O}_2 \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$) (from Fig.7.2).

Maintenance of any particular body temperature will be very difficult for an ectotherm and it is likely that even the most 'precise' thermoregulators (sensu Gibson and Falls 1979) will show a degree of fluctuation around their 'preferred' body temperature. Metabolic homeostasis will therefore provide a compensatory effect which would decrease disruptive physiological effects resulting from slight changes in body temperature within the activity temperature range. In addition such physiological adjustment may preclude the need for behavioural thermoregulation in order to sustain a consistent, and perhaps in some way optimal, level of metabolism (Davies and Bennett 1981). Such a homeostatic system could therefore be useful in decreasing the need for energetically expensive locomotory behaviours.

As temperatures progressively increased or decreased from this intermediate range, this control over metabolic rate was lost. Between 10° and 15°C and between 25° and 35°C values for the Q_{10} were between 2.0 and 3.0 which suggested an approximately exponential rise in the metabolic rate. The observed rates approximate to those associated with simple biochemical reactions, thereby indicating that no homeostatic mechanism was in operation here. Increasing body temperatures above 25°C would therefore yield noticeably increasing metabolic rates. Such rapid increases in the metabolic rate would be beneficial for promoting physiological processes, such as muscular activity, digestion or the development of ova; nonetheless, these benefits would be offset by increased energetic 'costs' arising from the increase in metabolic rate. For decreases in body temperature below 15°C the converse would be true. The rapid decrease in metabolic rate, associated with falling body temperatures here, would have the beneficial consequence of a marked reduction in energy expenditure but

would also be detrimental to the animal in that physiological processes would be impeded.

Associated with a rise in temperature from between 10° and 15°C to between 25° and 35°C, the metabolic rate-temperature curve was displaced to the right. Thus, a reduction in temperature below a certain threshold would cause an instantaneous relative increase in oxygen consumption (and conversely an increase in temperature above this threshold level would yield a relative decrease in oxygen consumption rate). This displacement indicates an adaptation to cool temperate climates as it would permit efficient metabolism throughout the activity temperature range. This shift may be caused through the temperature activation of isoenzymes with affinities for substrates at different temperatures (Aleksiuk 1971) or through the differential permeability of mitochondrial membranes relating to temperature (such phenomena having been observed in plant cells (D.A. Morris, pers. comm.)). Such a shift has been reported elsewhere, e.g. for Thamnophis sirtalis (Aleksiuk 1971), Lacerta vivipara (Tromp and Avery 1977) (see also Al-Sadoon and Spellerberg 1985a).

A much higher Q_{10} was observed below 10°C (i.e. 6.89) than would be expected on the basis of the Van't Hoff generalisation. This rapid change in metabolic rate may relate to the rapid onset of torpor with decreasing temperatures, thus reducing metabolic costs at sub-activity temperatures, whilst allowing a rapid return to a suitably high metabolic rate to permit activity once adequate temperatures are reached. Thus such a system would provide a temperature dependent metabolic 'switch', changing between active and subsistence metabolic rates with the change between activity and sub-activity temperatures. These temperatures coincide with likely minimum emergence temperatures reported for C. austriaca in Chapter 4 (this study) and by Bont et al (1986).

Many factors have been reported as affecting the metabolic rate - temperature relationship (Bennett and Dawson 1976,

Davies and Bennett 1981). Within and between species, the metabolic rate - temperature relationship shows variation that relates to climate and season. Reptiles from cooler climates show a displacement of the rate - temperature curve to the left, so that relatively higher metabolic rates are shown at a given temperature (Aleksiuk 1971, Bennett and Dawson 1976, Davies and Bennett 1981, Al-Sadoon 1983, Al-Sadoon and Spellerberg 1985a, 1985b). Such variation can be inherently determined, e.g. in northern and southern subspecies of Thamnophis sirtalis (T. s. parietalis and T. s. sirtalis) (Aleksiuk 1971), Natrix natrix and N. maura (Davies and Bennett 1981), or achieved through acclimation / acclimatisation e.g. Podarcis hispanica, Psammodromus hispanicus and Anguis fragilis (Patterson and Davies 1978), Lacerta vivipara (Al-Sadoon 1983 and Patterson and Davies 1978).

Terrestrial ectotherms inhabit thermally heterogenous environments and are therefore able to regulate body temperature through thermoregulatory behaviour. As such, these animals are less dependent upon variation in environmental temperature than ectotherms that occupy more homogenous yet variable environments, such as aquatic organisms (Scholander et al 1953). Terrestrial ectotherms are therefore likely to show less pronounced acclimatory responses to environmental change. Those reptiles that do show acclimatory responses tend to be those that encounter the greatest variation in environmental conditions, e.g. temperate cf. desert species (Al-Sadoon and Spellerberg 1985b). C. austriaca is a temperate species and is likely to show seasonal variation in metabolism. The data here relate to experiments conducted in May to July. Consequently these data may not be applicable to all seasons.

A further seasonal adjustment in metabolic rates has been reported. A displacement of the metabolic rate - temperature curve to the right during hibernation has been reported from in vitro studies of T. s. parietalis tissue (Aleksiuk 1976) and from Lacerta vivipara (Patterson and

Davies 1978a). These studies showed a decrease in metabolic rate at any given temperature which would serve to reduce energy consumption during the hibernation period. No records of metabolic rate were obtained from dormant C. austriaca and whether or not such depression of metabolism is observed in this species is a matter for speculation.

Metabolic rate can vary between individual animals within a species in relation to aspects of their condition. Intra-specific investigation of metabolic rates for many parameters was confounded during the present study due to the small sample sizes involved. Significant variation was observed between sexes at one test temperature (35°C) with males having a greater metabolic rate. Lower metabolic rates have been reported from female specimens when compared with male specimens in several studies of lizards, e.g. Urosaurus ornatus (Vance 1953) and Uta stansburiana (Roberts 1968), and snakes, e.g. Storeria dekayi (Clausen 1936), (see Bennett and Dawson 1976). This difference may have related to hormone levels or inherently different activity levels between the sexes.

In female snakes breeding condition has been shown to affect metabolism in Storeria dekay (Clausen 1936), with gravid animals showing higher metabolic rates than non-gravid specimens. Generally no difference was observed between female breeding condition during the present study, except at 25°C where non-pregnant specimens had higher metabolic rates than pregnant ones. However small sample sizes may have obscured the true variation between snakes in the two breeding conditions.

Smooth snakes from different slough conditions were used during the present study although due to small sample sizes the effect of this variable on metabolism was not investigated. The stage of the sloughing cycle has been reported to affect the metabolic rate - temperature relationship (Taylor and Davies 1981). Consequently the incorporation of different slough conditions in the present study may have increased the variability of the data.

Feeding condition has been reported to affect metabolism, with the metabolic rate of fed animals being increased by two- to seven-fold compared with unfed individuals (see Bennett and Dawson 1976). In most studies only post absorptive animals were used. The effect of feeding condition on the metabolic of C. austriaca was not investigated during the present study.

Two aspects of the metabolism of reptiles that relate to movement potential were not investigated for C. austriaca during the present study but are worthy of a brief mention. These are the maximal oxygen consumption (activity metabolism) and anaerobic metabolism. These latter aspects have been reviewed by Bennett (1982).

The study of resting metabolism yields little information about the potential for activity in a species. Metabolic rate studies have been extended to investigate the difference between oxygen consumption of a resting animal and that of a fully active specimen. This difference between resting and maximal oxygen consumption rates has been termed the aerobic scope or metabolic aerobic scope (Bennett 1982). Maximal oxygen consumption rates are typically between six and ten times the resting level; these active oxygen consumption rates, like resting oxygen consumption rates, increase with increasing temperature. Larger aerobic scopes are observed in species that are more active than in those more sedentary species.

Maximal oxygen consumption levels relate to the sustained activity potential of an animal. As movement rate increases oxygen consumption increases until this maximal level is achieved. Movement rate however can be increased beyond that associated with this maximal oxygen consumption; this movement is sustained through anaerobic metabolism. Anaerobiosis yields comparatively less energy per unit of substrate metabolised and produces lactic acid as bi-product. High levels of lactic acid cause acidosis which, amongst other things, disrupt haemoglobin and enzymatic function. A build up of lactic acid causes exhaustion and

muscle fatigue. Consequently the potential for anaerobic respiration is not unlimited. Anaerobic metabolism however can sustain short bursts of activity these being followed by periods of relative inactivity, during which lactic acid levels are reduced through excretion and gluconeogenic resynthesis (lactate reconverted to glycogen). This may explain the low overall dispersal of C. austriaca, interspersed with occasionally large movements, observed in the field during this present study (see Chapter 4).

7.4.2. Selected body temperature (Voluntary temperature)

Laboratory thermal gradient experiments have been used in numerous studies to observe the range of body temperatures exhibited by a thermoregulating reptile (see review by Spellerberg 1977, Lillywhite 1980). These temperatures are termed the 'Selected body temperatures range' (Pough and Gans 1982), although the terms 'Voluntary temperature range' and 'Preferred temperature range' have also been employed to describe this range of temperatures. The arithmetic mean of the observed temperature is referred to as the 'mean selected temperature' and this value is often regarded as being indicative of an optimal body temperature for a species.

The mean selected body temperature of C. austriaca obtained from the present study was $29.6^{\circ}\text{C} \pm 3.15$ (range 19 to 38). Such a body temperature, however, would appear high when considered in the light of the metabolic rate - temperature relationship. The associated level of oxygen consumption was high ($0.092 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$) and occurred at a portion of the curve where little metabolic homeostasis appeared to occur.

Selected body temperature data for two and three specimens of C. austriaca have been published by Spellerberg and Phelps (1975) and Spellerberg (1976) respectively. The former authors reported mean day time selected body temperatures of 25.8°C (range = 11.0 to 36.0°C) and 28.4°C (range = 23.0 to 33.0°) and night time mean selected body

temperatures of 25.8°C (range = 10 to 34°) and 19.8°C (range = 10 to 31°) for two specimens respectively. Spellerberg (1976) gave the 'voluntary range' for C. austriaca as 20 to 34°C with a mean value of 27°C (based on three individuals). The results from the present study suggest a higher selected body temperature from that observed in either the studies of Spellerberg and Phelps (1975) or Spellerberg (1976). This discrepancy may be due to the difference in methodology employed between the studies. The former authors measured the temperature of the tissue above the heart as a measure of body temperature whereas in the present study the cloacal temperature was used. Such measurements might not be directly comparable as gradients of temperature have been reported throughout the body lengths of snakes (Bartholomew 1982).

The body temperatures of snakes measured in the laboratory were significantly higher than those recorded in the field during the present study (29.6°C ± 3.15, n= 324 cf. 23.48°C ± 3.95, n= 327 (see Chapter 6, section 6.3.1.), t= 21.84 with 649 d.f., p<0.001). A similar observation was noted by Spellerberg and Phelps (1975) in that the field data yielded a lower mean temperature than the laboratory data (25.8°C, range= 17.0 to 31°C, n= 88). Goddard (1981) reported similar field body temperatures with voluntary means of 24.42° (n= 297) and 23.96°C (n= 51) for snakes basking in the open and below cover respectively. Laboratory data from this present study however were very similar to field data recorded from a radio-telemetric study of C. austriaca in the Netherlands, where body temperatures during the day time were typically maintained at 29 to 33°C (Bont et al 1986).

Field data recorded during this present study and by Spellerberg and Phelps (1975) and Goddard (1981) were likely to be biased towards snakes that were captured whilst basking and therefore probably in the process of warming up. In addition data were collected over a variety of environmental conditions and consequently mean body temperatures would be lowered by a large number of

observations of comparatively cool snakes.

Body temperatures that can be achieved and maintained in the field will be the product of many behaviours. Thus observed body temperatures are likely to reflect a compromise level depending upon the importance of each behaviour at any particular moment. Hungry Teju lizards (Tupinambis teguixin), for example, allow their body temperature to fall below their 'preferred' level in order to feed (Cabanac 1985) and basking behaviour in Anolis spp., and hence the precision with which body temperatures are maintained, is related to the antipredator behaviour (Huey and Slatkin 1976, Huey 1982). The observed behaviour in the laboratory therefore indicates that, in the absence of other behavioural requirements and with no thermal limitations on body temperature, smooth snakes thermoregulate to maintain a high body temperature. This thermophilic behaviour may be advantageous to an ectotherm that would often be prevented from 'precise' thermoregulation because of climatic and behavioural considerations. These climatic and behavioural requirements are likely to effect a reduction in body temperatures of C. austriaca observed in the field in cool temperate climates.

Maximum field body temperatures reported by Spellerberg and Phelps 1975, Goddard 1981 and in the present study were comparable with data recorded in the laboratory during this study and those reported by Bont et al (1986); these were 31°, 31° and 31.6°C respectively. These upper field body temperatures seem likely to be more representative of the 'preferred body' temperature of C. austriaca. Apparent metabolic homeostasis at intermediate temperatures indicates that metabolism is adapted to body temperatures most frequently attained in nature. The observations from this study therefore suggest that the 'selected body temperature' may, in fact, not be the optimum temperature for metabolism.

Selected body temperatures differed between the two sexes with a higher mean temperature being maintained by the

female. In addition females kept a constant temperature throughout the day whilst males let their temperature fall during the early morning. This latter behaviour did not simply follow diel temperature fluctuations at any fixed position in the gradient (see section 7.3.2., Fig 7.4). These observations suggest differences in the thermal ecology of the two sexes in C. austriaca. Pregnant female smooth snakes may select consistently high body temperatures, where possible, as an adaptation to maximise the rate of development of embryos; chances of survival of newborn snakes will be enhanced the earlier they are born in Autumn. Non-pregnant females may also benefit from maintaining higher body temperatures. Increased metabolism would favour rapid assimilation of food and perhaps encourage the repletion of reserves following pregnancy during a previous year. The 'cost' of reproduction for males, however, is less great (Shine 1980) and consequently the need to maintain high digestion and assimilation levels will be lower. Indeed, maintaining an unnecessarily high metabolic rates will be disadvantageous as it will lead to a much higher food intake requirement. Thus male C. austriaca may adopt a strategy that decreases metabolic expenditure by selecting a decreased body temperature during the inactive phase of the daily cycle. Such 'voluntary nocturnal hypothermia' (sensu Huey 1982) is likely to be subject to feeding condition. Recently fed snakes are likely to select higher body temperatures where possible to prevent food spoilage and selecting cooler environments would benefit most those individuals that have not recently fed.

Diurnal variation in body temperature was suggested for one of the two specimens of C. austriaca studied by Spellerberg and Phelps (1975), but not the other, and was reported for the species by Spellerberg (1976). The sex of these snakes, however, was not reported and consequently these data can not be used to support or refute the above hypothesis.

The maintenance of a constant body temperature will confer both advantages and disadvantages. Precise temperature

regulation will allow the optimal performance of some, but not necessarily all, physiological processes. In some species, recently fed snakes show a thermophilic response such that higher temperatures are selected to achieve maximum rate of digestion and assimilation (Regal 1966, Skoczylas 1970), although such observations are by no means universal (Lillywhite 1980). Unfed animals may benefit from cooler temperatures such that metabolism is not accelerated to an inefficient level. Growth rate depends upon thermoregulatory behaviour in relation to food availability; high metabolic rates facilitate growth rates when food is abundant, through allowing frequent foraging (and therefore a high level of food intake) and rapid assimilation, but are detrimental to them when food is in short supply (Huey 1982, Avery 1984). Thus a range of optimal temperatures may exist, dependent upon environmental and physiological conditions, and production of a single value for a 'selected temperature' for a species may be somewhat misleading. For many reptiles, being permanently kept at the selected temperature can even be damaging (Huey 1982).

7.4.3. Minimum critical and maximum tolerated temperatures

The mean critical temperature for C. austriaca determined in the present study was 1.98°C which was over 1.5°C lower than the value calculated by Spellerberg (1976); the value reported from this latter study was 3.5°C. Discrepancies may have resulted from differences in the methodology, particularly through differences in the rate of cooling. Critical minimum values reflect the degree to which ectotherms are adapted to cold climates and lower values for the critical minimum temperature are observed for reptiles from cooler climates than are observed for specimens from warmer areas (Spellerberg 1976). Differences in methodology preclude comparisons between the values obtained during the present study and those published elsewhere. Nevertheless the observed value indicates that C. austriaca can sustain activity until very low temperatures are reached. Low critical minimum temperatures

have been reported for all three species of British snake, with notably higher values being reported for congeneric species that occur in warmer climates (Spellerberg 1976). The southern smooth snake C. girondica had a lower critical temperature of 5°C, which was 1.5°C higher than the equivalent value for C. austriaca (Spellerberg 1976).

Critical temperatures will vary between seasons with lower critical minima being observed during cooler months. A similar depression of this temperature can be achieved through acclimating animals to low temperatures. In addition to the acute Summer time critical minimum temperature of several species of reptile, Spellerberg (1976) presented their 'ultimate temperatures'; these are the critical values after a period of acclimation at very low temperature and therefore would be similar to critical temperatures during the Winter. These values were lower than the acutely determined values in all cases, and sometimes quite noticeably so. Spellerberg's values for the ultimate temperature of C. austriaca was 0.3°C.

The critical minimum is a useful parameter in that it determines the absolute minimum acute temperature that can be tolerated by a species in the wild. At this temperature the animal is immobilised and would be unable to avoid any further reduction in temperature, that may itself be lethal, or predation (Pough and Gans 1982). All animals would be expected to seek cover long before this temperature fell to the critical minimum. Spellerberg (1976), however, reports an occasion where some specimens of C. austriaca were found dead following a night where a rapid fall in temperature to below the critical level occurred before they were able to seek shelter.

The maximum tolerated temperature is the body temperature at which an animal will move from cover to select a cooler body temperature and as such is similar in definition to the maximum voluntary temperature. This temperature will represent the upper temperature tolerated by C. austriaca in nature. The method employed yielded a value of 36.6°C

(range= 35.78 to 37.58°C). Animals that approach this body temperature in the wild would therefore be expected to actively seek conditions that would permit body temperature to fall. The observed maximum tolerated temperature is similar to the maximum body temperature recorded in the thermal gradient in both definition in and value. The observed upper selected body temperature in the thermal gradient during the present study was 38°C.

The term 'maximum tolerated temperature' does not refer to the same concept as 'critical thermal maximum'; the latter refers to the value at which increasing temperature causes the locomotory activity to become disorganised and hence the animal becomes incapable of avoiding conditions that would lead to its death (Pough and Gans 1982). No measurements of critical thermal maximum temperature were undertaken during the present study.

7.5. Summary

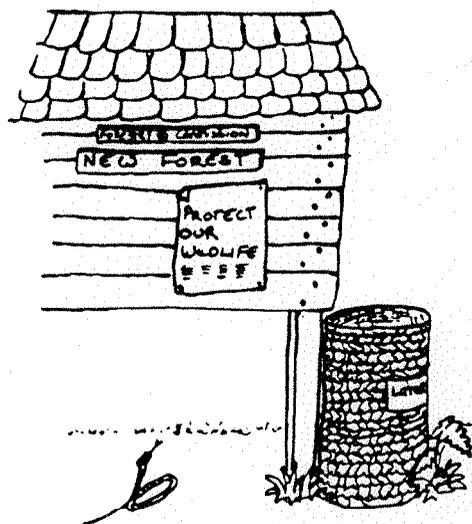
i. The metabolic rate of C. austriaca was investigated. The relationship between temperature and oxygen consumption was almost semi-logarithmic. Intermediate temperatures of 15 to 25°C showed a slight levelling of the curve suggesting possible metabolic homeostasis over these temperatures where oxygen consumption rates of 0.034 to 0.063 ml O₂. g⁻¹. hr⁻¹ were observed. These temperatures represent those most frequently encountered in the field. At temperatures slightly above and below this intermediate range, metabolic rates varied in relation to Van't Hoff's generalisation. At temperatures below 10°C a large Q₁₀ was observed; this may have related to emergence and submergence behaviour.

ii. High mean selected temperatures were found, averaging 29.6°C (range 19 to 38°C). This temperature yielded a metabolic rate of 0.092 ml O₂. g⁻¹. hr⁻¹. This value seemed inconsistently high when compared with the position of the minimum Q₁₀ values on the rate temperature curve. High temperatures were likely to have been selected where possible so that an intermediately high mean body

temperature can be maintained in nature. The Rate - Temperature curve suggested that metabolism was adapted for maximum efficiency at a value approximating the mean body temperature in the field.

iii. Minimum critical and maximum tolerated temperatures were calculated as 1.98°C and 36.63°C respectively.

VIII. General Discussion



CHAPTER EIGHT

GENERAL DISCUSSION

8.1. Introduction

An integrated investigation into the movement, range use and thermal ecology of the smooth snake in southern Britain was undertaken via a combination of field and laboratory study. Various vegetational, faunal and thermal aspects of the habitat of C. austriaca were also investigated during this study.

In this chapter the various behavioural and habitat related topics investigated in previous chapters and their relationship to each other are discussed. The application of the results of this research to conservation and management practices is also considered.

8.2. Discussion of methodology

The cryptic coloration and secretive behaviour of C. austriaca has, in the past, made difficult the detailed study of many aspects of the ecology of the species. Visual location of snakes can at best allow the unpredictable collection of data which will be prone to observer bias (both in the selection of areas sampled and the location of animals within these areas) and be influenced by prevailing weather conditions. Regular relocation of animals is required for the investigation of movement biology and an unbiased location technique needed for the study of habitat selection. To these ends, radio-tracking was used in the present study to aid the observation of free ranging C. austriaca.

Data collected from radio-tagged animals may be subject to certain limitations, not least the effect of the transmitter upon the behaviour of the snake. Quantification of the effect of the methodology upon the behaviour of free

ranging animals is difficult, since very often the aspects under study are difficult to observe by other means.

Radio-tagged animals generally appeared to behave in a similar manner to untagged animals that were observed during the study, with regard to the timing of activity, duration of basking and movement behaviour. The weight of the externally attached transmitter was not regarded as being unduly detrimental to the snakes' behaviour but its physical bulk did seem to affect movement of snakes through vegetation and below ground. On several occasions, some snakes were observed snagged in amongst heather and similar structurally complex herbage. Several periods of observation were terminated early because of snakes becoming caught in vegetation or below ground. In other cases it is possible that the rate of movement was affected by the attachment of the radio-tag. Bont et al (1986) reported a similarity in behaviour between tagged and untagged *C. austriaca* using force fed radio-transmitters. However, these authors discounted data collected during the first day of radio-tracking since snakes were observed to travel long distances during this time. No such changes in behaviour were observed during the present study and radio-tracking sessions were too short to allow such long periods to be discounted.

The need for externally attached transmitters arose from the large size of the transmitter relative to the body size of the snake. This meant that force feeding was undesirable. Surgical implantation was both impractical (again due to the size of the transmitter and the requirement for a fairly long aerial) and undesirable due to the protected status of the snake. The short battery life (typically lasting up to 21 days) also meant that surgical implantation could not be considered.

The radio-tag was attached to the snake by surgical adhesive tape, a method that assured that the package was held firmly in place whilst providing a smooth, low friction binding. Surgical tape was also placed around the

body to reduce the possibility of abrasion from the transmitter against the skin. This method of attachment often caused slight scale damage (by removing the very top layers of integument from a few scutes) when transmitters were removed. In these cases, healing was rapid and the scales soon regained their smooth and shiny appearance, although these were usually darker in colour than previously. Very occasionally snakes would pull the transmitter and tape from their tail and this could cause more extensive scale damage at the site of transmitter attachment. No serious skin damage or bleeding was observed with the exception of a very small cut at the anterior end of the tape attached to one snake where the skin appeared to have been caught by vegetation which had snagged under the transmitter.

A single fatality occurred which was probably attributable to the attachment of a radio-transmitter. This snake was found draped over a small mound of grass with the attached transmitter caught in the grass. A series of wounds along the animals side indicated that it had been caught by another animal, perhaps a bird of prey, and pulled, thus causing the transmitter to become snagged. It is, however, possible that the wounds were self inflicted, by the animal holding against a rusting chicken wire fence to try to pull the transmitter free from the grass.

The rate of change of body weight can provide information about the effect of methodology, and quantitative data can be collected to compare radio-tagged and non-tagged snakes in the field. Body weight changes were recorded from radio-tagged snakes over periods of observation between 0.754 and 9.705 days and these compared with all body weight changes of free ranging, untagged snakes which were measured over the same range of intervals (but excluding cases where the snake was handled in that period). Body weight changes over these periods varied between -19.0 to +2.6 g for radio-tracked snakes and -21.7 to +16.8 g for visually located snakes. These data included one case each where a snake gave birth to a litter of young and, for visually located

data, one animal that consumed a large meal in the intervening period.

Rates of change of body weight varied between -2.508 and $+3.046$ g. day⁻¹ for radio-tagged snakes and -4.159 and $+5.590$ g. day⁻¹ for visually located animals. The distributions in each case were slightly positively skewed and the majority of observations were of negative weight gains. Mean body weight changes were -0.540 g. day⁻¹ \pm 0.932 (n= 41) and -0.110 g. day⁻¹ \pm 1.067 for radio-tagged and untagged snakes respectively. The variance for the body weight changes associated with the two methods were homogenous ($F_{max} = 1.312$ with 40 d.f., $p > 0.05$) and the means of the two samples were significantly different ($t = 2.220$ with 127 d.f., $p < 0.05$). Body weights decreased significantly more quickly in radio-tagged snakes than in those without transmitters; this may in part be explained by the absence of any observations of radio-tagged snakes feeding. Radio-tracking may therefore serve to reduce food intake rather than cause a more rapid reduction in body weights of non-feeding snakes.

With the view to objectively assessing the effect of radio-transmitters on behaviour, the activity of captive animals was analysed using video recordings. Details of the methodology and results are presented in Chapter 2, section 2.3.5. These experiments indicated that, in general, there was no difference in activity patterns, movement rates, use of vegetation and cover or differences in the rate of change of body weight between animals that were attached with transmitters and those that were not. A recent study by Wilkinson (1988) also showed that the behaviour of the adder Vipera berus was not affected by the attachment of thermistor transmitters.

Collection of data by radio-tracking was hampered by the occasional malfunction of transmitters or by the transmitter being shed (for details see Chapter 4, section 4.2.1.). Transmitter malfunction may have been caused by the need to break open the araldite potting around the

transmitter to change the battery. Longer battery life could help decrease this problem. With further miniaturisation surgical implants could be developed for use on small snakes. This technique has been well developed for use with larger snakes (e.g. Reinert and Cundall 1982, Madsen 1984) and in these cases many of the problems relating to transmitters become snagged or being shed are avoided.

8.3. Food requirements and general ecology

8.3.1. Food requirements

Energy requirements of resting C. austriaca in the field can be estimated using field body temperature measurements (Chapter 6) and respirometry data (Chapter 7). A mean body temperature of 23.48°C was observed in the field and this has a corresponding oxygen consumption rate of 0.058 ml O₂. g⁻¹. hr⁻¹ (from Fig. 7.2). The diet of C. austriaca is primarily small vertebrates and therefore the respiratory quotient (Mol. CO₂ / Mol. O₂) is assumed to equal 0.8, i.e. approximately the value for protein metabolism. An equivalent energy conversion value is 20.35 J. ml O₂⁻¹ (from Gordon et al 1982). At mean field body temperature this is equivalent to 1.18 J. g⁻¹. hr⁻¹, which for a typical 40 g smooth snake would give a value of 47.21 J. hr⁻¹.

The energy value for whole mouse tissue is 24.61 KJ. g⁻¹ dry weight, which is equivalent to 9.05 KJ. g⁻¹ fresh weight (R.J. Putman pers. comm.). Therefore 1 g (fresh weight) of mouse tissue would provide sufficient energy to sustain the standard metabolism of a 40 g smooth snake for 191.7 hours at mean field body temperature. No such energy equivalents were available for body tissue of reptilian prey species.

No body temperatures were recorded outside the day time activity period but it is likely that the body temperature would fall at night to a value between 10°C and 15°C, the value recorded below ground (from Fig. 6.12 and Bont et al

1986). These night time temperatures are equivalent to a metabolic expenditure of 0.427 to 0.692 J. g⁻¹. hr⁻¹. Taking an average value, this represents a rate of 22.385 J. hr⁻¹ for a 40 g snake. With a 12:12 hour day to night ratio 835.16 J would be consumed in 24 hours and hence the equivalent of 1 g of 'mouse' could sustain the resting metabolism for 260.1 hours (10.84 days). Thus a typical 5 to 10 g meal could sustain the standard metabolic rate of a 40 g smooth snake for 54 to 108 days at typical field temperatures. Extrapolating these data further, a 40 g snake would need to consume 19.2 g of 'mouse tissue' to sustain its metabolism in a typical activity season (estimated at 208 days; see Chapter 5).

Clearly these estimates of energy requirements rely on many assumptions and, as such, care must be taken when applying these calculations to animals in the field. These calculations are based upon the metabolic rates of resting snakes and no investigation into the active oxygen consumption rates was undertaken during this study. Al-Sadoon (1983) presented values for oxygen consumption of active Lacerta vivipara. These were typically 1.5 to 3.5 ml O₂. g⁻¹. hr⁻¹ above the resting values (aerobic scope) which represented an approximate ten fold increase in oxygen consumption rate (although the magnitude of this increase varied between test temperatures). Consequently the estimated rate of energy expenditure and food requirement calculated above would represent a gross underestimate for active animals.

The calculation of rate of food consumption also makes unrealistic assumptions (e.g. constant body temperatures, 100% conversion of energy from the mouse tissue, etc) and a more accurate estimate of food requirements may be obtained by direct observation of captive animals. Published data on feeding of a juvenile specimen of V. berus were available (Fawcett 1976). This specimen consumed 89 g of food in 118 days. Assuming the same food energy value as above (i.e. 9.05 KJ. g⁻¹) this was equivalent to an energy consumption of 6.82 KJ. day⁻¹. Assuming the voluntary temperature

(30°C) (Spellerberg 1976) was maintained all day (which was permissible by the provision of heat lamps) and stayed at 22°C at night (temperatures of 20 to 25°C being maintained) a value for the energy requirement of 3.21 KJ. day⁻¹ was obtained for this specimen (mean weight= 22.25 g) (from Al-Sadoon, unpublished data).

Although inaccuracies are inherent in this latter comparison, e.g. the comparison of data from a juvenile snake (i.e. data from Fawcett 1976) with metabolic rate-temperature curve from adult specimens (i.e. data from Al-Sadoon, unpublished), the two values of energy requirement are fairly similar. This comparison suggests that a reasonable estimate of field energy requirements may be obtained by increasing the calculated theoretical value by a factor of two. As such, a typical 40 g specimen of C. austriaca would need to consume 38.4 g of 'mouse' tissue (i.e. 19.2 g x 2) during a typical activity season (i.e. 208 days) .

These low rates of food consumption seem to be borne out by observations in the field. In most cases smooth snakes were captured with no detectable item of food in the gut, and only very occasionally after having just eaten a meal. During the study no smooth snakes were observed catching or consuming a meal; this latter observation further indicates that relatively few prey items are taken during the course of a year.

8.3.2. General biology and ecology

The maintenance of only an intermediately high body temperature in the field may in part explain the fairly low food intake by C. austriaca. In addition, metabolism in C. austriaca seems adapted to maintain a fairly consistent level of energy consumption at a typical range of field body temperatures. These observations suggest that C. austriaca is a species that is adapted to a 'low energy' mode of life. The adaption towards having a low level of energy throughput has been described for other snake

species, e.g. Acrochordus arafurae (Shine 1986). A summary of the interaction of physiological, behavioural and ecological parameters that suggest the tendency towards low energy specialisation in C. austriaca is illustrated in Fig. 8.1. 'Low energy specialists' would be expected to demonstrate a low movement rate, this resulting in a decreased energy consumption which in turn reduces the need to move (through a reduction in the need to forage). A reduced movement rate may or may not be reflected by a smaller lifetime home range area, although short term range areas are likely to be smaller than those shown by more active 'high energy' species.

A reduced movement rate may also be reflected by an increased reliance upon crypsis as an anti-predator behaviour. Selection of partially concealed bask sites enhances the effect of the animal's cryptic coloration and may, additionally, provide shading which prevents the body temperature of a basking animal rising too rapidly or too greatly. Low energy species may also be expected to show a low growth rate. Goddard (1981) compared the growth rate of C. austriaca against those obtained for six North American species from previous studies. From these data Goddard concluded that the growth rate of C. austriaca is similar to that shown by other species of snake. However a species that has a low energy throughput need not necessarily show a lower rate of growth. An efficient digestive system and low energy expenditure on activity may maximise the utilisation of energy towards growth.

Similarly, a low energy specialist may be expected to show a small reproductive effort or a low reproductive rate. Litter sizes for C. austriaca vary between one and 16 (NCC 1983). Goddard (1981) reported weight losses of between 30 and 80% of body weight upon parturition. Thus a fairly large reproductive effort is made by the species. As a consequence of not maintaining a high body temperature in the field reproductive rate may be reduced which, in turn, may be detrimental to the survival of both the offspring and post-partum females.

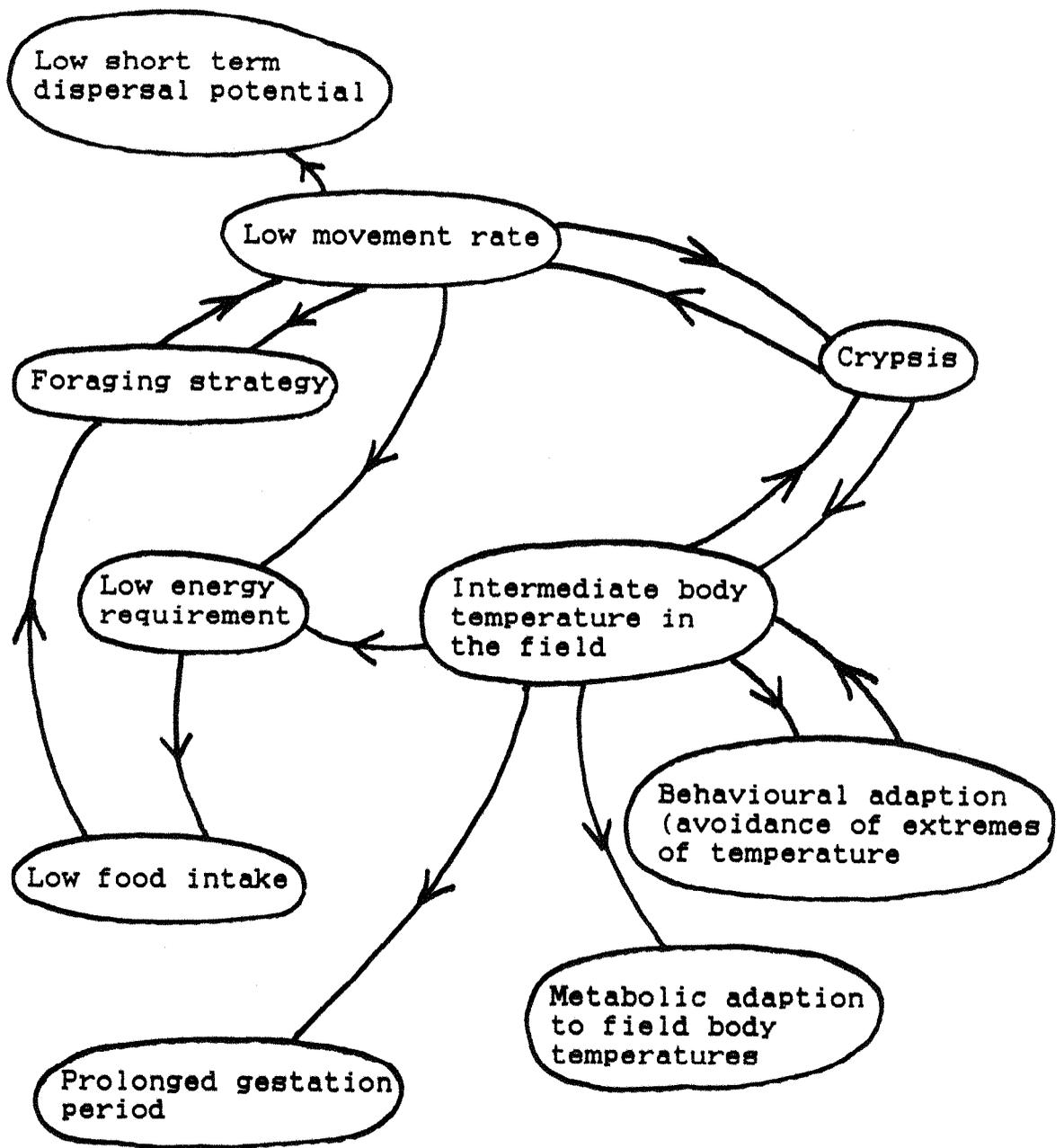


Fig. 8.1 : A schematic summary of the interaction between physiological, behavioural and ecological factors showing 'low energy specialisation' by C. austriaca in southern Britain.

Goddard described the life history strategy of C. austriaca as being typical of a K-selected species; that is, a species that is generally long lived, has a small reproductive effort relative to the expenditure on growth and consequently maintains a fairly small and stable population size determined by the carrying capacity of the environment. These features could also typify the strategy shown by 'low energy specialists', although in these latter species a fairly large carrying capacity would be expected for the environment due to the reduced energetic demands of each individual.

Comparison of data obtained during the present study with the generalised equations for snakes (Bennett and Dawson 1976) indicated a similarity between the metabolic rates of C. austriaca and other species of snake at 20°C; the former species, however, showed a lower metabolic rate at 30°C than would have been expected from the generalised equation. The observation at 30°C may indicate that C. austriaca has a low energy requirement at higher temperatures (relative to other snakes); the similarity at the lower temperature may suggest that low energy strategies are in fact widespread in the Ophidia. This latter inference could be expected for a group of animals in which a large proportion of species feed upon relatively large items of prey, each of which will sustain the animal for long periods of time before another meal is required. Low energy specialisation is likely to be less common in animals that need to ingest many, smaller items of prey.

It is also worth speculating whether such behaviour would be found across the geographic range of the species. A low energy life strategy may be favoured where the precise maintenance of a high body temperature is not possible. A reduction in mean body temperature would favour metabolic adaption to lower temperature regimes and a reduced movement rate, both of these in turn favouring an adaption towards low energy specialisation. Where higher body temperatures can be maintained, higher metabolic rates and

greater activity would lead to an increased energy demand and hence favour a greater energy throughput. Low energy specialisation may also be favoured where food is in short supply. Optimal temperatures for growth (and reproduction) will be affected by food availability. Higher temperatures increase the metabolic rate, and hence the rate at which food can be assimilated, and such conditions will be optimal when food is abundant. Where food is scarce optimal temperatures for growth will be lower, this being a consequence of the reduced rate of energy consumption for metabolism.

8.4. Habitat requirements

8.4.1. Components of habitat selection

The individuals of any species will need to encounter all the elements that ensure both the short and long term survival of themselves and the persistence of the species within their lifetime ranges. These elements are both biotic and abiotic and represent the major components of habitat. Some of these factors will limit the range of habitats that can be occupied by animals both in the short and long term since the presence or absence of certain conditions may make an area unsuitable for occupation. Others will affect the use of the environment within the range of acceptable habitats by making some areas more 'favourable' at any particular time.

The habitat selected by an individual may represent a behaviour that reflects the need to optimise a single aspect (or a limited number of aspects) of the animal's biology. Alternatively, habitat selection may represent a behaviour that is a compromise between the satisfaction of several different, and possibly conflicting requirements. The expression of a behaviour is generally triggered by the need to benefit from its outcome (for example a hungry animal will forage, a warm animal seek cooler environments and an animal that is being pursued by a predator will flee or demonstrate some other anti-predator behaviour). In

turn, these needs will vary between various physiological conditions, seasons, times of day, etc., and be influenced by interactions with the biotic and abiotic environment. At any one time these different considerations will create differing priorities for each of the various aspects of an animal's biology. The use of the (biotic or abiotic) habitat at any particular time is likely to be determined by behaviours responding to which ever aspect (or aspects) have the highest 'priority' at that time.

For an ectotherm body temperature regulation will be largely influenced by habitat usage. The precision of body temperature regulation will be affected by both the physical (e.g. the range of temperatures available) and by the biotic components of the environment (e.g. shading by plants, intra- and inter-specific competition, anti-predator behaviour, foraging and breeding behaviours). Even for ectotherms that are not 'precise' thermoregulators (sensu Huey and Slatkin 1976), thermal considerations will be important. The avoidance of extremes of temperatures (both high and low) and the need to ensure that body temperatures are maintained within the upper and lower critical temperatures (ecologically lethal temperatures) will restrict the range of habitats occupied by a species. In practice C. austriaca maintained a considerably narrower range of body temperatures in the field (between 10.5° and 31.6°C). Body temperature fluctuations outside this relatively narrow range would cause muscular co-ordination to be impaired and various physiological processes retarded.

Temperature maintenance is therefore an important consideration for an ectotherm at all times and variations in environmental temperatures may create a higher priority for thermal homeostatic behaviour. Many aspects of smooth snake ecology are probably determined primarily by thermal considerations. Comparison between laboratory selected body temperatures and body temperatures attained in the field suggests that C. austriaca are frequently prevented from precise control of body temperatures. The factors that prevent such control are likely to be both biotic and

abiotic in nature.

Cover within the environment will also be important to C. austriaca. Apart from its role in moderating the thermal habitat, ground cover provides physical shelter that offers protection from predators. Vegetation also enhances the cryptic coloration of snakes which both increases the degree of protection from predators and the likelihood of capturing its prey species. Snakes were often found basking below vegetation and it was assumed that this was primarily in connection with anti-predator behaviour. Such behaviour was by no means universal and snakes were often seen basking in patches of quite open ground. However, in all such cases, snakes were in close proximity to some form of cover into which escape would be possible. The presence of some form of cover therefore may affect habitat selection at all times of day and during all seasons.

Smooth snakes seem to feed only infrequently and as such the distribution of prey will not necessarily influence site selection at all times. However, for unfed reptiles foraging behaviour may be the major factor in determining the use of the habitat, e.g. hungry lizards forgo the precise control of body temperature in order to obtain food (Cabanac 1985).

Breeding only occurs at distinct periods in the year. Searching for mates and mating will be important for C. austriaca during Spring (and possibly in the Autumn (see Chapter 3, section 3.3.1 c.) and during these times these behaviours may take precedence over other activities. In the apparent absence of agonistic behaviour between conspecifics, however, the presence of other smooth snakes is unlikely to affect habitat selection throughout the remainder of the year.

Habitat use is therefore determined by a series of differing requirements throughout the diurnal and annual cycles. Determination of an 'optimal' smooth snake habitat is therefore difficult as some environments produce ideal

conditions for certain aspects of the species biology but not others. Vegetation communities that represent 'good' smooth snake habitat will vary throughout the year, with variations in the animal's physiology and changes in the habitat itself. Traditionally 'optimal' habitat for C. austriaca has been taken as meaning mature dry heathland and suggestions that other vegetation types may also be important (or even offering 'optimal' conditions for any aspects of the species biology) have been treated with severe sceptism (e.g. Corbett 1980). While the importance of dry heathland to C. austriaca should not be underestimated, the belief that observations away from this habitat simply represent the short term persistence on 'secondary refuges' may be an over simplification. The potential for including such areas in nature reserves (or managing them to promote the survival of the species) has, to date, been largely overlooked.

8.4.2. Factors limiting geographic distribution

The reproductive effort of many individuals is likely to be needed to ensure the persistence of a species in any area. Consequently the colonisation of an area may be prevented if the immigration of a sufficiently large number of individuals to establish a viable population is not possible. Hence even 'partial barriers' to dispersion may preclude the occupation of potentially suitable sites. The distribution of smooth snakes therefore may be limited to a great extent to their historic range.

Temperature is likely to be a major factor restricting the range of C. austriaca and will affect both active snakes (by limiting the duration of daily and seasonal activity) and those in hibernation (especially where very cold winters cause deep and long lasting frosts). The distribution in Britain, Norway and Sweden (at the northern limits to the range) is likely to be restricted through temperatures being too low (e.g. for precise body temperature regulation), or seasons too short (e.g. to allow development of embryos, etc.), whereas in southern

Europe and Asia Minor temperatures that are too high would limit the range. The use of lowland habitats by the northern populations and higher altitudes by southern snakes (Arnold and Burton 1978) may allow the occupation of latitudes that would be thermally unsuitable at some intermediate height above sea level. Thus the combined effect of both latitude and altitude on ambient temperature may serve to define the geographical limits to distribution.

Climate alone does not appear to completely explain the distribution of C. austriaca in Britain. Although the climate is relatively warm all year round in the southern areas of the range (south Dorset and south Hampshire), smooth snakes are also found in northern Dorset, northern Hampshire and Surrey. These latter areas have a similar pattern of climate to a much larger area of southern and eastern Britain from which the species is absent.

To the north of the known range in Dorset and Hampshire lie areas of downland. The greater height above sea level may in part explain the absence of smooth snakes from these areas as may the vegetation associated with this habitat. Downland is generally covered by short vegetation or allowed to develop to woodland. Either of these vegetational extremes would be unfavourable to thermal requirements of C. austriaca, since the former would be particularly exposed to frosts in Winter whilst the latter would be too shaded to provide sufficient warmth in Summer. Areas of East Anglia offer similar vegetational and temperature conditions to other areas occupied by both C. austriaca and L. agilis yet neither of these species have been recorded there (Beebee 1978). Beebee suggested that other climatic factors, such as prevailing winds, may make these areas thermally unacceptable.

Neither climatic nor vegetational hypotheses can explain the absence of C. austriaca from large expanses of heathland such as the Ashdown Forest in Sussex. Vast tracts of forest once covered the Weald area of Sussex and Kent

(until about the 17th century) and it is likely that these would have prevented smooth snakes from dispersing to such areas. Their absence from such areas would relate to their restricted distribution in recent history and not upon the suitability of the habitat. However, it may also be possible that smooth snakes were once more widespread throughout southern England, thriving in the open forests (mainly of Betula spp.) associated with post glacial England during a period when the climate was warmer than today (Spellerberg 1982). The discovery of smooth snake fossils at Ightham near Sevenoaks in Kent (dating from about 9500 years before present) (Holman 1985) may in part support this possibility. In this latter scenario, local extinction of the species would explain the absence of C. austriaca from Kent and Sussex. Beebee (1978) discussed the possible constraints upon the distribution of C. austriaca, Lacerta agilis and Bufo calamita. He felt that the distribution could, in part, be explained by the availability of 'corridors' of suitable habitat in recent historic times, and these accounted for the presence of L. agilis in areas as remote as Lancashire and Dorset, Hampshire and Surrey and the even more widespread distribution of B. calamita which additionally includes western counties in the English midlands and parts of East Anglia.

Smooth snakes are typically associated with areas of coarse sandy soils (Beebee 1978) and the geology of an area is regarded as being a possible cause of the limitation to the species' distribution. Vegetation will be largely determined by soil type, and a dependence on dry heathland would be reflected by occupation of drier, sandy soils. Topography will also be determined by geology. Sandy soils are associated with lower ground and these may be more favourable due to the relationship between temperature and altitude and thus the relationship with soil type may be coincidental. Soil type will also affect the thermal property of the ground through the structure of soil and the ability to retain water. Drainage may also affect the survival of animals, particularly where they occupy

underground refuges for over wintering (a time when the soil is particularly prone to waterlogging).

Beebee (1978) felt that whilst thermal restrictions limited the distribution of the rare reptiles, they did not explain the reason that C. austriaca was more restricted in distribution than L. agilis (and in particular as the former species is viviparous and the later oviparous). He attributed the more restricted range of the snake to the higher trophic level and especially due to its dependence upon lizard prey. Adult C. austriaca will take a variety of prey species (Spellerberg and Phelps 1977, Goddard 1981) and thus this limitation would not appear to be applicable. Juvenile snakes, however, do appear to favour reptilian prey (Goddard 1981). A requirement for reptilian prey for juveniles would be a factor that further restricts the range of habitats and geographic locations that can be occupied by the species.

The range of C. austriaca in Britain is probably restricted through a variety of considerations, which are primarily temperature related. Short and comparatively cool activity seasons (further reduced by many cloudy or rainy days) will affect an individuals seasonal growth and the ability to build sufficient reserves to survive the period of winter inactivity. Decreasing mean temperatures and reduction in the length of the warm period with increasing latitude will further limit the potential for growth and assimilation of energy reserves. Increasing latitude may also delay emergence from hibernation (and consequently mating). Parturition would in turn be delayed, possibly until late Autumn, which would reduce the likelihood of survival by juveniles and post-partum females over winter. Soil conditions which promote high ground temperatures and provide good drainage will favour precise body temperature regulation and hence facilitate the development of embryos. Thus while it is likely that individual smooth snakes can survive in cooler climates, these would prevent successful reproduction and consequently viable populations could not persist under such conditions.

The climate in Britain is reportedly deteriorating (having, on average, cooled by about 0.25°C over the past 25 years), as it is in parts of Scandinavia, Europe and Canada against a world wide trend where the atmosphere is apparently become warmer (Gribbin 1988). The effect of this local cooling upon ectotherms at the northern most limits of their range could be disastrous and could cause extinctions in some regions. A more restricted distribution in Britain in the near future, due to climatic change, is therefore possible.

8.5. Conservation

The conservation of Britain's rare reptiles (C. austriaca and Lacerta agilis) has primarily concentrated upon the conservation of mature, dry heathland. Management practices used include the removal of invading pine (Pinus spp.) and birch (Betula spp.) trees and control of growth of bracken (Pteridium aquilinum) (using herbicides such as 'Azulam'). The formation of large heathland reserves has undoubtedly preserved good reptile habitat in areas that are traditional strongholds for these species, e.g. on the Isle of Purbeck in Dorset. In the light of the association between smooth snakes and heathland aspects of heathland conservation shall be considered here and discussed in the context of nature reserve design in general.

Many theoretical considerations can be addressed when designing a nature reserve or when considering the merits of designating or managing an area for that purpose. One of the more commonly considered criteria is the area of the land in question. Area has been related to species richness. MacArthur and Wilson (1967) devised a simple model which considered the species richness of hypothetical islands. The number of species found on any island would be the consequence of the equilibrium between the rate at which species colonised the island and the rate of extinction of species on that island. Extinction rates in turn would be determined ^{by} island size and immigration rates

would be affected by the proximity of a reservoir from which potential colonisers would originate. These rates would also be affected by the number of species already established on the island (Diamond and May 1981).

Since its conception, the relationship between area and species richness has been applied to nature reserve design with nature reserves being considered analagous to 'islands' of suitable habitat surrounded by 'seas' of inhospitable ground. Diamond (1975) applied MacArthur and Wilson's 'equilibrium theory of island bio-geography' to simple reserve designs and suggested these should be as large as possible and close to, and preferably linked to, adjacent 'islands' and as near circular in shape as possible. These factors maximised immigration and minimised the possibility of extinction.

Margules et al (1982) were critical of the assumptions implicit in such models and cautioned the use of 'island bio-geographic theory' to nature reserve design, not least because many of the concepts involved were unsubstantiated by empirical evidence. For example, in some cases large islands did contain more species than two smaller islands of same total area whereas in other cases the converse was true. This observation may partially be explained by the different collections of species which would occur on each of the smaller islands, yielding upon occasion a greater total number than were found on the larger islands. A further important consideration was habitat type. Island bio-geographic^t theory is limited to comparison between homogenous habitat types. Clearly, comparisons of area between different habitat types would be confounded by the relative species richness of the different habitats. Indeed habitat heterogeneity has been advanced as a major factor contributing to greater species diversity (Reed 1983), and the greater diversity of habitats that are likely to be found on larger areas may greatly contribute to the greater species richness of such sites.

The application of the above theories to nature reserve

design has the implicit assumption that high species richness is desirable, and the rationale behind this approach is questionable. Webb and Hopkins (1984) noted a negative relationship between the species richness of certain invertebrate taxa and the area of heathland fragments when sampling at the centre of the site. These authors attributed this result to the large number of 'edge species', i.e. species that were not typical to the heathland community that had immigrated from adjacent habitat types. Thus simple island bio-geographic theory cannot be applied to relatively species poor 'islands' in 'seas' which are likely to be comparatively species rich. Heathland surrounded by woodland, farm land and urban development is likely to be typical of such a scenario. In such cases the invasion of non-heathland species may be detrimental to the heathland community. For example, a greater number of predators may be found, which may not usually be associated with heathland. Foxes Vulpes vulpes, badgers Meles meles and hedgehogs Erinaceus europaeus (which thrive in woodland and in association with urban development) and domestic animals, such as cats Felis domesticus, may extend their ranges into small heathland fragments and may cause serious declines of some heathland fauna. Invasion by non-heathland plant species may also provide adverse competition for the heathland flora. The question of 'typicalness' of community structure should therefore be addressed in preference^{to} species richness when considering the design of a particular reserve. A diversity of ecological communities should be conserved to ensure a great species richness at the national level.

Other, more subjective, criteria are also considered including rarity (of habitat type and/ or component species), vulnerability (to human activity and natural processes) and other qualities such as 'usefulness', educational interest and aesthetic appeal. Dry and wet heathlands are becoming increasingly rare, both nationally and internationally, and are inhabited by many rare species (see Chapter 1, section 1.5. b.). Shortage of land in southern Britain has made dry heathland particularly

vulnerable to urban development, agriculture, mineral extraction and forestry. In addition, recreational activity has increased its vulnerability, both through increased risk of fire and the high sensitivity of heathland to trampling (Harrison 1981). Thus conservation measures should be directed towards the preservation of large 'representative' heathland communities per se, and within these communities habitat improvements can be made to benefit specific groups, such as reptiles.

Heathland is a plagio-climax, and therefore must be managed to prevent natural succession to climax woodland. This management can be by grazing (by domestic stock, such as cattle, sheep and ponies, or by wildlife, such as hares Lepus capensis), by manual removal of tree growth, by mowing or by burning. Each of these methods have their advantages and disadvantages. Mature heathland offers poor quality grazing and where heathlands are grazed by livestock the heather is usually managed additionally by burning or mowing (Hazel 1983). In addition livestock will trample vegetation and, if grazed at too high a density, may cause the replacement of heathers by grasses. Manual removal of trees is labour intensive and can only be considered on reasonable small areas of heathland. Heather has traditionally been managed by burning. Although burning is confined to winter months (1st October to 31st March) the potential for directly killing wildlife is still high. The removal of cover by burning renders often quite large areas of heathland uninhabitable during the following season to many species. It appears likely that burning will prevent the occupation of an area by reptiles for possibly as long as seven years (Chapter 5, section 5.4.2.). In addition heathland that has been burnt often becomes invaded by bracken Pteridium aquilinum. Mowing heather can provide a substitute for burning, provided the cut stems are removed. However, this method may damage root stock, especially of older heather and growth of bracken and Molinia caerulea after cutting is not uncommon.

Corbett (1980) advocated that habitat management for

reptiles should concentrate upon the provision of mature stands of heathland. However, the generality of this suggestion was not substantiated by the current research and reptiles were observed in a variety of habitat types. Moreover, heathland management often has to include wider concerns. In the New Forest heathland burning for the provision of grazing is a traditional obligation, and a certain acreage must be so managed each year. Wildlife too may benefit from such practices. Woodlarks Lullula arborea, for example, benefit from areas of short heather for nesting and feeding (Sharrock 1976). Heather also shows more vigorous growth after burning. Thus heathland management should encourage the diversity of heather structures, by creating a mosaic of managed (burnt) heath of different ages interspersed with areas that have been allowed to reach maturity, and thus promote diversity of plant and animal species and ensure the vitality of the heather. It would appear that this diverse habitat structure would favour C. austriaca. Burning should, however, be restricted to small areas (generally less than 1 ha) and should ensure that sufficient mature heath (in excess of seven years of age) is near at hand, both to provide cover for species that inhabited the burnt area and to provide a reservoir from which recolonisation of the burnt heath can take place in the future. Where bracken or birch invasion seems likely, these species should be controlled. Although they are used by reptile species, such vegetation will be detrimental to the heathland community as a whole.

Additional measures can be incorporated to encourage reptiles. Species such as the sand lizard and grass snake require egg incubation sites, namely patches of open sand and compost heaps/ piles of wood shavings/ decaying vegetation respectively, and the provision of these may greatly enhance the suitability of a reserve. C. austriaca seems not to be limited by such requirements, although the apparent attraction of banks and patches of open ground to pregnant females suggested such structures were favoured within the range. Provision of banks and ditches on a reserve will provide greater habitat heterogeneity and

serve to increase the effective ground area of the reserve.

So far the discussion has concentrated upon the conservation of heathland. C. austriaca used many habitat types throughout the present study, indicating that the species is far more catholic in habitat use than is generally reported. Thus, when considering potential reserves, areas adjoining bog, wet heathland and even bracken covered grassland or newly planted coniferous forests should not be discounted. Provided that the diversity of habitat structure offered by these offers all requirements for the species (see section 8.4.1. above) throughout the year there is no reason why these should not support viable populations of C. austriaca. The role of trees in affecting habitat use by smooth snakes is the subject of debate. Although the species is observed in amongst both coniferous and deciduous trees of all ages, coniferous plantations should not be considered suitable habitat once the canopy has closed. Therefore, although primary consideration should be given to conserving sites known to be important to smooth snakes, with the increasing pressure on land use attempts should be made to maximise the conservation value of all land that is available.

Of particular importance to a species with a low short term dispersal potential and a high susceptibility to barriers to dispersal, is the provision of corridors of habitat between adjacent populations. Typical barriers include roads, agricultural land, forests, urban and industrial developments. Corridors can be provided through each of these without detriment to their functional or commercial role; tunnels and footbridges across roads can be provided for wildlife, hedges and field boundaries can be left fallow or actively managed for wildlife, verges to forest rides can be left unplanted and landscaping of industrial and residential areas can use plant species which are beneficial to a variety of wildlife. These corridors could, however, be further managed to provide refuges and even permanent habitat for many species and, in particular, reptiles. Road side verges and embankments have the

potential for providing ideal reptile habitat and planting with ericaceous shrubs could help offset the effect of heathland loss, especially where the course of the road links natural patches of heathland. Such benefits will be even more apparent along motorway embankments which are generally wide and may continue for considerable distances. Similar benefits will be offered from conservation management along railway embankments.

Maintenance of wide unplanted ride verges in forestry plantations benefits a variety of wildlife and also facilitates certain management practices (e.g. deer control) (P.R. Eccles, pers. comm.). The minimum width which should be left unplanted for reptile management depends, amongst other things, on aspect, ride width and the height to which opposite and adjacent trees will grow. Dent (1986) recommended a width of at least 5 m for the persistence of populations of Lacerta agilis. It would seem likely that C. austriaca would also benefit from such management. In addition sensitive management of forests could ensure the persistence of open spaces as reptile habitat for as long as possible without any reduction in the total area of timber planted.

Further consideration should be given to publicity and education as means of promoting the conservation of all wildlife, and in particular the rare species. Much effort is currently expended on promoting wildlife conservation, although the majority of this is directed to audiences already aware of conservation issues. Attempts to target information at people who are unaware of, or generally uninterested in, their role in environmental conservation should therefore be considered and in particular where people are likely to come into contact with wildlife. Advice that certain species are protected under national law and local by-laws should be displayed, for example, at car parks and tourist information centres. Warnings of the possible penalties that may be incurred as a result of breaching such laws could be considered to emphasise the relevance of such legislation to all who use the

countryside.

The promotion of nature conservation is being undertaken at many levels, for example through conservation societies, museums, libraries and schools, using a wide variety of media. As a consequence many large industrial companies are keen to improve their public relations by showing a more environmentally sensitive approach. The importance of such attempts should not be underestimated and a constructive dialogue between conservationists and industrialists may serve to provide both financial support and the use of 'surplus' land as nature reserves. This latter situation could greatly benefit such species as C. austriaca which may become increasingly dependent upon marginal areas of habitat with increased urbanisation and commercial and agricultural development throughout its range in southern Britain.

8.6. Further research

The merits of undertaking further research upon a rare species need to be considered prior to undertaking such study. Where the results are of applied conservation value, further research should be encouraged. For academic studies the use of commoner species should be considered, whilst those pieces of research that advocate the destruction of rare animals should generally be discouraged (NCC 1983). In this discussion, research which may be beneficial to the conservation of C. austriaca is considered primarily.

Prior to discussing areas that may benefit from further research, a brief comment on the need for cooperation between the various interested parties should be made. Many aspects of conservation and wildlife research become 'political' and this is particularly so where rare and endangered species are involved. Differing opinions are valuable for stimulating debate and alternative interpretations should therefore be welcomed. However, unless these differing views can be constructively aired with view to determining a common conservation policy,

valuable contributions from many and varied investigators and observers may be overlooked in attempts to substantiate opposing dogmatic attitudes.

When dealing with a rare and secretive species, whose range extends over a reasonably large area, reliance upon many different sources may be needed to collate a complete picture of its ecology, distribution and status. Thus the efforts of both amateur and professional researchers are valuable, although the relative merits of each contribution should be seriously considered before their inclusion in any general statements about the species. Such consideration should also take into account any consequences of methodological biases.

The status of rare species needs to be determined and regularly monitored, to determine priority areas for management and research and to assess the success of existing management techniques and conservation policies. The distribution of C. austriaca in Britain has been described in several publications (see NCC 1983) but needs to be the subject of continual review so that changes in geographic range can be monitored. A survey of C. austriaca sites has been recently undertaken by the British Herpetological Society under contract from the Nature Conservancy Council (G.A.D. Haslewood, pers. comm.). The survey monitored known and presumed smooth snake sites with the view to determining the current status of the species at each. Whilst this approach has its merits (particularly since most contributors could only do survey work part time), the results will be limited to observations at sites chosen a priori. An objective approach to monitoring population changes should therefore be developed at various sites across the range of the species and the results obtained should be related to habitat variation.

Similar objectivity would be required for determining habitat selection. Much of the present knowledge is biased towards observations at known sites on habitat assumed to be in some way optimal. Systematic sampling of varied

habitat types should be considered. Such an objective approach was attempted during this present study, using small grids of tin sheeting. The expansion of this method (using more and larger pieces of tin) could prove worthwhile if sites can be chosen that avoid public interference. The application of this method to determining the effect of heathland burning on smooth snakes would be worth considering further.

Habitat selection, incorporating the quantification of many components of biotic and abiotic habitat for multivariate analysis, offers a potentially rewarding project provided that representative locations can be obtained. Once radio-transmitters become sufficiently miniaturised and battery life sufficiently long to allow the attachment or implantation of tags for long periods of time, radio-telemetry could provide a useful method for the collection of the necessary data. Improvements in radio-telemetry will also offer the potential for more research upon movement and ranging behaviour, perhaps tracking animals over one or more complete seasons; questions that could then be addressed include accurate determination of range size, intra-specific variation in ranging behaviour and the determination of hibernation sites. This latter aspect could have considerable implications towards the design of nature reserves.

Comparison of ecological and physiological parameters between British and non-British specimens may be instructive. Differences in habitat use have been reported between *C. austriaca* in the United Kingdom and in other countries (see Chapter 1, section 1.1). However the causal factors have not been quantified and it is possible that differences in habitat use may reflect, for example, the selection of one or more habitat parameters (such as temperature) common to the different habitats. The elucidation of common factors between smooth snake habitats throughout the range could provide useful information for the conservation of the species at the limits of its distribution. Comparison between various physiological

parameters across the range may also have conservation applications. Determination of the selected body temperature, the critical temperatures and mean field body temperature and their relationship to metabolism may serve to separate different races within the species. This information may help determine the origin of the British population of C. austriaca and serve to identify those non-British populations most closely related to those in England. Identification of similar races would be necessary if continental stock were ever considered for introductions or for providing individuals for captive breeding programmes.

8.7. Summary

i. Radio-tracking greatly enhanced the quantity and quality of data collected. The method seemed to affect the behaviour of the snakes only slightly, this being due to the physical bulk of the transmitter.

ii. Low food requirements were apparent and these together with low movement rates suggested a tendency towards 'low energy' specialisation. This specialisation enhances the role of crypsis as an anti-predator behaviour.

iii. C. austriaca can use a variety of habitat types provided that within their lifetime ranges the requirements of several criteria are met. These are diversity of thermal habitat to permit thermoregulation, adequate cover, provision of ample food (prey species) and the presence of mates. Not all of these are required at any one time and consequently the variety of potentially suitable habitats is great in the short term.

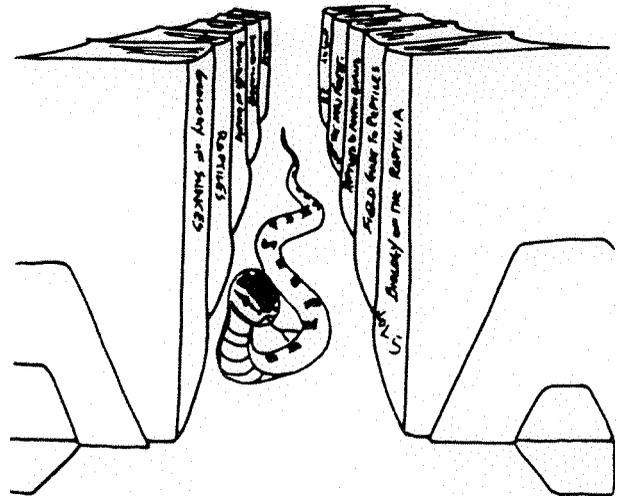
iv. Medium height to intermediately tall vegetation preferably of uneven structure and with a soft substratum is likely to provide the most suitable habitats as these are able to satisfy many of the snakes physiological and ecological requirements for much of the time.

- v. Where habitats that provide all elements in abundance are occupied vagility and range size might be expected to be low.
- vi. The range of the species in Britain is likely to be limited primarily by the thermal requirements of pregnant female snakes and the rate at which embryos consequently can develop. Shorter activity seasons with increasing latitude further decrease the chances of survival for new born snakes. Suitable habitats may therefore be limited to lowland in only the southern most regions of Britain, and made more favourable by a sandy substratum.
- vii. Conservation of heathland should be encouraged for the preservation of this distinct ecological community and for the coincidental benefit to reptiles. Large areas are favourable to promote the 'typicalness' of the heathland community.
- viii. Heathland burning should be restricted to small areas ensuring adequate unburnt heather nearby to provide cover for all ground dwelling heathland fauna and a source from which subsequent recolonisation can take place. Slight habitat management, e.g. the provision of an uneven topography, may help reptile populations.
- ix. The provision of 'corridors' of inhabitable vegetation (which may be diverse in nature) between adjacent populations will be important for the conservation of C. austriaca and of other animals with poor short term dispersal capabilities.
- x. Road side verges and embankments and forestry ride verges and edges to agricultural fields should be managed for wildlife, both as refuges and as 'corridors' for dispersion.
- xi. Further research should concentrate upon aspects of direct conservation value and should address the distribution and status of the species locally and

nationally, aspects of habitat selection and ecological and physiological comparisons between British and non-British specimens.

xii. The cooperation between all interested parties is imperative to maximise the benefits from the research efforts of both professional biologists and dedicated naturalists to the academic study and conservation of C. austriaca.

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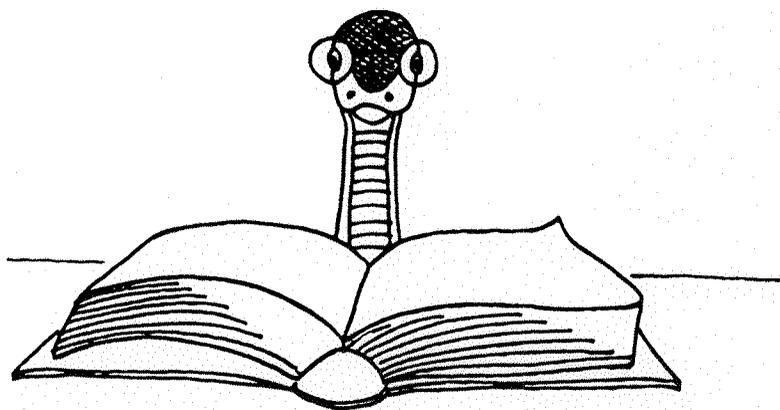
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Glossary



GLOSSARY

- Abiotic factors:** Characterised by the absence of life. These include temperature, humidity, pH and other chemical and physical influences. (cf. biotic factors).
- Acclimation:** Physiological adaptation by an animal to a change in a single, or only a small number of, environmental variable(s) (e.g. temperature, photoperiod) in the laboratory. (cf. acclimatisation).
- Acclimatisation:** Physiological adaptation by an animals to a change in many inter-related environmental variables (e.g. temperature, photoperiod) associated with natural variations (such as those associated with seasons, climate or altitude). (cf. acclimation).
- Aerobic metabolism:** Metabolism that requires oxygen. (cf. anaerobic metabolism).
- Aerobic scope:** (Aerobic metabolic scope) The difference between the resting metabolic rate and the maximumal oxygen consumption (see Bennett 1982).
- Agonistic** A term to describe all types of behaviours shown in relation to threat, territoriality and fighting (see Manning 1979).
- Anaerobic metabolism:** Metabolism that does not use oxygen. (cf. aerobic metabolism).
- Arboreal:** Living in trees (associated with living in trees).
- Aquatic:** Living in water (associated with living in water).
- Bio-telemetry:** Monitoring of an organism or a biological

process within an organism (e.g. physiological process such as heart rate) by a remote detector. Such a detector is frequently a radio-receiver monitoring radio-signals (radio-telemetry). (see also radio-telemetry, radio-tracking).

Biotic factors: Environmental factors caused by plants, animals, fungi and micro-organisms . (cf. abiotic factors).

Circadian: With reference to activity rhythms with a pattern relating to day length. (From Latin 'circa diem' meaning 'about a day').

Crepuscular: Active during the early morning and late evening (cf. diurnal, nocturnal).

Critical temperatures: (Minimum/ Maximum). The temperature at which an ectotherm loses coordination over its motor functions as a consequence of falling (minimum) or increasing (maximum) temperatures (Pough and Gans 1982). Thus these temperatures are regarded as ecologically lethal.

Crypsis: The phenomenon of an animal showing a visual resemblance to part of their environment, resulting in them becoming difficult to see (often through body coloration). Animals having such appearance may enhance its effect behaviourally. (also: Cryptic= pertaining to crypsis).

Diel: During the daily (day and night) cycle usually used in the context of activity patterns.

Diurnal: Active during the day-time (or occurring during the day-time). (cf. nocturnal, crepuscular).

Ecdysis: (Molting/ sloughing/ shedding). The process of shedding the skin in relation to growth.

- Ectotherm:** An organism that derives bodily warmth from extraneous sources (viz. the environment). Often referred to as "cold blooded" in common parlance. (cf. endotherm).
- Endogenous:** Derived from within; a pattern or cycle of behaviour controlled by an inherent and internal 'biological clock mechanism' (of activity patterns). (cf. exogenous).
- Endotherm:** An organism that derives bodily warmth from its metabolism. Often referred to as "warm blooded" in common parlance. (cf. ectotherm).
- Eury-:** (prefix) Having a wide range of tolerances to a particular factor (e.g. Eurythermal- wide range of temperatures tolerated) (cf. steno-).
- Exogenous:** Derived from or controlled from outside; a pattern or cycle of behaviour controlled by external factors (e.g. light, temperature) (cf. endogenous).
- Fossorial:** Living in soil or litter layer (associated with living in soil or litter layer).
- Heliothermy:** A method of thermoregulation by ectotherms where by the most important source of warmth is derived from radiant energy (sunlight). (cf. thigmothermy).
- Herpetology:** The study of reptiles and amphibians. Hence the term 'Herptiles' which is sometimes used to collectively describe members of the classes Reptilia or Amphibia. (also Herptile= any reptile or amphibian species).
- Hibernation:** A period of inactivity over the winter months which is generally associated with a physiological change that effects a reduction in metabolic rate. (Many definitions of this term have been proposed,

some of which are exclusive of reptiles, which vary between describing any period of winter inactivity to definitions that are based upon particular and precise sets of physiological conditions).

Homeostasis A regulatory physiological or behavioural process by which certain aspects of an organism's biology (e.g. body temperature, blood oxygen levels, etc.) are maintained within particular limits.

Homoiotherm: (homeothermic) An animal that maintains a constant body temperature (Spellerberg 1976). (cf. poikilotherm).

Lethal temperatures: Upper (Maximum lethal) and lower (minimum lethal) temperatures that are fatal to an organism. Usually defined as the temperature where a fixed per cent (usually 50%) of organisms succumb to rising or falling temperatures in laboratory studies.

Maximum tolerated temperature: (laboratory determined). The point at which an ectotherm moves to seek cooler temperatures in response to rising body temperature (Pough and Gans 1982).

Nocturnal: Active during the night-time (or occurring during the night-time). (cf. diurnal/ crepuscular).

Ophidia: (formerly Serpentes) A taxonomic Sub-order of the order Squamata which contains the snakes. (also: Ophidian= pertaining to the Ophidia).

Plagio-climax: A development stage in the successional progression of vegetation communities at which further succession (towards a climax community) is prevented due to some non-vegetational factor (e.g. burning, grazing).

Poikilotherm: An organism that has a variable body

temperature (Spellerberg 1976). (cf. homoiotherm).

Radio-telemetry: Bio-telemetric study using radio signals, with a radio-transmitter sending information to a remote radio-receiver. Such methodology includes radio-tracking, remote measurement of activity from radio-signals and monitoring of body temperatures via temperature sensitive transmitters.

Radio-tracking: An aspect of radio-telemetric study where radio-tagged animals are located using a radio-receiver so that details of their movement, behaviour and or habitat, for example, can be studied.

Reptilia: A taxonomic Class of vertebrate animals which contains the snakes, lizards, crocodilians, totoises and turtles and rhycocephalians together with extinct forms. (also: Reptilian= pertaining to the Reptilia).

Selected Body temperature: (Voluntary temperature). Mean body temperatures obtained during laboratory studies in which ectothermic animals are allowed to thermoregulate freely in a thermal gradient (Pough and Gans 1982).

Standard Metabolic Rate (SMR): The resting metabolism of an ectothermic species calculated at Standard Temperature and Pressure.

Standard Temperature and Pressure (STP): A temperature of 0°C (273 K) and a pressure of 760 mmHg (1013.25 mB) used to standardise results of experiments using volumes of gas.

Steno-: (prefix) Having a narrow range of tolerances to a particular factor (e.g. Stenothermal- narrow range of temperatures tolerated) (cf. eury-).

Squamata: A taxonomic Order which contains the snakes (Ophidia) and lizards (Lacertilia).

Taxon: (Taxa (plural)). Any level of taxonomic grouping.

Temperate: Relating to mild climates with seasonally varied weather. (cf. tropical).

Thermoconformer: An ectotherm whose body temperature fluctuates passively with changes in environmental (ambient) temperature (Huey and Slatkin 1976).

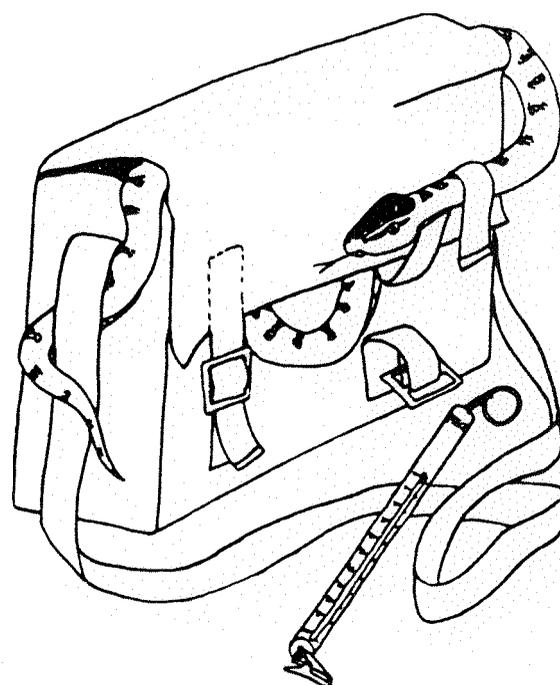
Thermoregulation: The behavioural regulation of body temperature (usually in the context of ectotherms).

Thigmothermy: A method of thermoregulation by ectotherms where by the most important source of warmth is derived from conducted heat through contact with the substrate. (cf. heliothermy).

Tropical: Relating to climates with hot and humid climates and usually without marked seasonal changes in weather. (cf. temperate).

Vagility: Rate of movement.

Appendices



APPENDIX I

Definitions of Vegetation Categories used in the description of Quadrats in Habitat Usage experiments. The quadrats measured 0.5 m x 0.5 m and were assessed by viewing from head height. Vegetation species were recorded as percentage cover within each quadrat and it upon the basis of these percentages that the vegetation categories below were defined.

- i. **Dry Heath I:** 90% or over Calluna vulgaris.
- ii. **Dry Heath II:** Calluna vulgaris and Erica cinerea in excess of 50%, but with Calluna vulgaris being less than 90%.
- iii. **Humid Heath:** Calluna vulgaris and Erica tetralix in excess of 50%, but with Calluna vulgaris being less than 90%.
- iv. **Grass/Dry Heath:** Grass spp (usually primarily Agrostis setacea) and dry heath spp (Calluna vulgaris/Erica cinerea) in excess of 50% but each component comprising less than 50%.
- v. **Grass/Humid Heath:** Grass spp (usually primarily Molinia caerulea) and humid heath spp (Calluna vulgaris/Erica tetralix) in excess of 50% but each component comprising less than 50%.
- vi. **Grass I:** Fine bent grasses, usually Agrostis setacea, in excess of 50%..
- vii. **Grass II:** Coarse grasses, usually Molinia caerulea, in excess of 50%.
- viii. **Grass III:** Diverse mixture of grass spp. associated with prostrate 'lawn' plants in excess of 50%.
- ix. **Bog/Wet Heath:** A combination of any of Molinia

caerulea, Erica tetralix, Myrica gale, Sphagnum sp. and Juncus sp(p). in excess of 50% (but with M. caerulea and E. tetralix each less than or equal to 50%), except where M. caerulea and E. tetralix were the commonest species and represented over 50% (i.e. vegetation type v.) or Sphagnum sp. was in excess of 50% (i.e. vegetation type xii.).

- x. **Gorse:** Gorse Ulex europaeus, and/or gorse litter, in excess of 50%.
- xi. **Bracken:** Bracken Pteridium aquilinum, and/or bracken litter, in excess of 50%.
- xii. **Bryophytes:** Moss sp(p)., Sphagnum sp. and/or lichen sp(p). in excess of 50%.
- xiii. **Bare ground:** Bare substratum regardless of substratum type, not covered by vegetation or litter, in excess of 50%.
- xiv. **Deciduous tree / litter:** Deciduous tree sp(p). and/or litter of deciduous tree sp(p). in excess of 50%.
- xv. **Pine tree / litter:** Pine tree Pinus sp(p). and/or the litter of pine tree sp(p). in excess of 50%.
- xvi. **Other conifer sp(p). / litter:** Coniferous tree sp(p). (other than Pinus sp(p).) and/or the litter of such coniferous tree sp(p). in excess of 50%.
- xvii. **Bramble:** Bramble Rubus fruticosus in excess of 50%.
- xviii. **Deciduous and heath:** Deciduous tree sp(p). and/or litter and C. vulgaris, Erica sp(p). and/or Ulex sp(p). in excess of 50% but each component comprising less than or equal to 50%.
- xix. **Dry heath and open / prostrate spp:** C. vulgaris and/or E. cinerea in combination with bare ground,

moss sp(p)., lichen sp(p). and/or grass sp(p). in excess of 50% but each component comprising less than or equal to 50%. Where dry heath and grass are the two commonest components these equalled less than or equal to 50% (otherwise classified as vegetation type iv.).

- xx. **Gorse and understorey:** Gorse Ulex europaeus in combination with Pteridium aquilinum, dry heath sp(p)., humid heath sp(p)., grass, bare ground, Nepeta cataria and/or Pinus sp(p). in excess of 50% but with each component less than or equal to 50%.
- xxi. **Gorse and bramble with other spp:** Gorse Ulex europaeus and bramble Rubus fruticosus in combination with Nepeta cataria, bare ground and/or dicot sp(p). in excess of 50% but with each component being less than or equal to 50%.
- xxii. **Deciduous and understorey:** Deciduous tree sp(p). or litter of deciduous tree in combination with grass sp(p)., dicot sp(p). and/or Nepeta cataria in excess of 50% but with each component being less than or equal to 50 %.
- xxiii. **Bracken and tree sp(p).:** Bracken Pteridium aquilinum in combination with deciduous and/or coniferous tree sp(p). and/or litter of such tree sp(p). in excess of 50% but with each component being less than or equal to 50%.
- xxiv. **Heath and bracken / catmint:** Dry or humid heath sp(p). (C. vulgaris and/or Erica sp(p).) in combination with bracken Pteridium aquilinum and/or catmint Nepeta cataria in excess of 50% but with each component being less than or equal to 50%.
- xxv. **Bracken and understorey:** Bracken Pteridium aquilinum in combination with grass sp., Senecio jacobaea, dry heath sp(p)., Pinus sp(p). in excess of 50% but with

each component being less than or equal to 50%.

- xxvi. **Deciduous and bramble with understorey:** Deciduous tree sp(p). and/or the litter of deciduous tree sp(p). and bramble Rubus fruticosus in combination with grass sp(p). and/or Pteridium aquilinum in excess of 50% but with each component being less than or equal to 50%.
- xxvii. **Grass sp(p). with open / moss:** Any grass sp(p). (including M. caerulea and Agrostis sp(p).) in combination with bare ground and/or moss sp(p). in excess of 50% but with each component less than or equal to 50%.
- xxviii. **Bramble and understorey:** Bramble Rubus fruticosus in combination with Nepeta cataria and/or grass sp(p). in excess of in excess of 50% but with each component less than or equal to 50%.
- xxix. **Prostrate sp(p). and bare ground:** Moss sp(p). and/or lichen sp(p). in combination with bare ground in excess of 50% but with each component less than or equal to 50%.
- xxx. **Dry heath and pine:** Dry heath sp(p). (C. vulgaris and/or E. cinerea) in combination with Pinus sp(p). in excess of 50% but with each component less than or equal to 50%.
- xxxi. **Fern sp(p).:** Any sp(p). of fern in excess of 50%.
- xxxii. **Catmint:** Catmint Nepeta cataria in excess of 50%.
- xxxiii. **Tin / tile:** Tin or tile in excess of 50%. Where snakes were found under tin/tile such that the tin/tile covered less than 50% of the quadrat the vegetation was classified according the vegetation surrounding the tin/tile.

APPENDIX II

English and scientific names of plant species

Anemone,	
Wood anemone	<u>Anemone nemorosa</u>
Asphodel,	
Bog asphodel	<u>Narthecium ossifragrum</u>
Beech	<u>Fagus sylvatica</u>
Bilberry	<u>Vaccinium myrtillus</u>
Birch,	
Silver birch	<u>Betula pendula</u>
Bog myrtle	<u>Myrica gale</u>
Bogbean	<u>Menyanthes</u> sp.
Bracken	<u>Pteridium aquilinum</u>
Bramble	<u>Rubus fruticosus</u>
Buttercup	<u>Ranunculus</u> sp.
Catmint	<u>Nepeta cataria</u>
Chestnut,	
Sweet chestnut	<u>Castanea sativa</u>
Clover	<u>Trifolium</u> sp.
Crucifer	f. Cruciferae
Cypress	f. Cupressaceae
Daisy	<u>Bellis perennis</u>
Dandelion	<u>Taraxacum</u> Sect. <u>Vulgaria</u>
Fir,	
Douglas fir	<u>Pseudotsuga menziesii</u>
Frogbit	<u>Hydrocharis morsus-ranae</u>
Gentian,	
Marsh gentian	<u>Gentiana pneumonanthe</u>
Gorse,	
Dwarf gorse	<u>Ulex minor</u>
European gorse	<u>Ulex europaeus</u>
Gladiolus,	
Wild gladiolus	<u>Gladiolus illyricus</u>
Grass,	
Bristle bent grass	<u>Agrostis setacea</u>
Purple moor grass	<u>Molinia caerulea</u>
Harebell	<u>Campanula rotundifolia</u>

Hawkweed,	
Mouse-ear hawkweed	<u>Hieracium pilosella</u>
Hawthorn	<u>Crataegus monogyna</u>
Heath,	
Bell heather	<u>Erica cinerea</u>
Cross-leaved heath	<u>Erica tetralix</u>
Ling	<u>Calluna vulgaris</u>
Holly	<u>Ilex aquifolium</u>
Honeysuckle	<u>Lonicera periclymenum</u>
Ivy	<u>Hedera helix</u>
Larch,	
European larch	<u>Larix kaempferi</u>
Marestail	<u>Hippuris vulgaris</u>
Moss,	
Shpagnum	<u>Sphagnum sp.</u>
Nettle	<u>Urtica dioica</u>
Oak	<u>Quercus robur</u>
Orhid,	
Heath spotted orchid	<u>Dactylorhiza maculata</u>
Pennywort,	
Marsh pennywort	<u>Hydrocotyle vulgaris</u>
Pine,	
Scots pine	<u>Pinus sylvestris</u>
Corsican pine	<u>Pinus nigra</u>
Plantain	<u>Plantago major</u>
Primrose	<u>Primula vulgaris</u>
Ragwort	<u>Senecio jacobbaea</u>
Reed sp.	<u>Phragmites australis</u>
Rose,	
Dog rose	<u>Rosa canina</u>
Rush sp.	<u>Juncus sp.</u>
St. John's wort,	
Marsh St. John's wort	<u>Hypericum elodes</u>
Sedge sp.	<u>Carex sp.</u>
Strawberry	<u>Fragaria vesca</u>
Spruce,	
Norway spruce	<u>Picea abies</u>
Sitka spruce	<u>Picea sitchensis</u>
Thistle	<u>Cirsium sp.</u>

Tormentil

Vetch

Yarrow

Potentilla erecta

Vicia sp.

Achillea millefolium