UNIVERSITY OF SOUTHAMPTON

Faculty of Science

Department of Biology

ECOLOGY AND VAGILITY OF THE GRASS SNAKE, *Natrix natrix helvetica* LACÉPÈDE.

submitted by

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To Mum and Dad

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UNIVERSITY OF SOUTHAMPTON

ABSTRACT

FACULTY OF SCIENCE

DEPARTMENT OF BIOLOGY

Doctor of Philosophy

Ecology and vagility of the grass snake Natrix natrix helvetica Lacépède in southern Britain.

The movement ecology of free-ranging grass snakes (Natrix natrix) was examined at a site in Hampshire, England. Miniature radio transmitters were surgically implanted into 18 adult snakes for periods ranging between 7-313 days and the behaviour of the snakes observed. Several of the transmitters contained built-in thermistors which enabled the body temperatures of snakes to be remotely measured and logged.

The use of space was examined using two methods of home range analysis. Minimum Convex Polygon analysis showed that intraspecific variation in the size of home ranges was high (0.54-33.49 ha), but Multi-nuclear Polygon analysis showed that only a small percentage of each range was used intensely. Monthly range sizes were greatest in May and July and the ranges for all months overlapped considerably. The monthly ranges of individual snakes also overlapped and this is discussed.

Most daily distances moved were small and snakes did not move at all on 65% of daily observations. However, 1.5% of observations recorded daily movements over 300m. Seasonal migration was observed in both sexes but not in all cases. Movement was much reduced in the periods before ecdysis and after feeding.

The preferred body temperature of the snakes was approximately 31°C. Snakes warmed rapidly on emergence and cooled more slowly on submergence. Emergence appeared to be initiated by increased substrate temperature and submergence by decreased insolation. Body temperatures less than the preferred maximum were attained by snakes which could do so without emerging and this is discussed. Body temperatures fluctuated considerably while snakes were moving and activity was possible under a wide range of body temperatures.

The preferred habitats of snakes were deciduous woodland and grassland, and snakes showed a marked preference for linear habitats, in particular woodland edges. Snakes selected microhabitats which provided both cover and basking opportunities.

Laboratory investigation using time-lapse video showed that grass snakes exhibited a behavioral response to areas previously used by the adder Vipera berus, though no such response to areas used by conspecifics. The use of scent trailing and chemical cuing are discussed.

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Chapter One

Introduction

1.1 Taxonomy and appearance

The grass snake, Natrix natrix natrix Linnaeus is an oviparous member of the Family Colubridae, the largest and most widespread family of snakes. The Genus Natrix is widespread, appearing in Europe, North Africa, North America and Asia as far east as Japan. There are three European species of Natrix (N. natrix, N. maura and N. tesselata, of which N. natrix is the only species found in Britain.

The grass snake is olive-green in colour with vertical black markings and a vivid yellow collar. Specimens caught in the course of this study, were, with one exception, less than 1m in length, although individuals elsewhere have been reported which are in excess of 1.5m (eg Smith, 1951). Female specimens are typically larger than males in both length and girth and have relatively shorter tails, both of which features aid in the identification of sexes. Adult males typically weigh less than 100g and females 150-300g.

1.2 Distribution

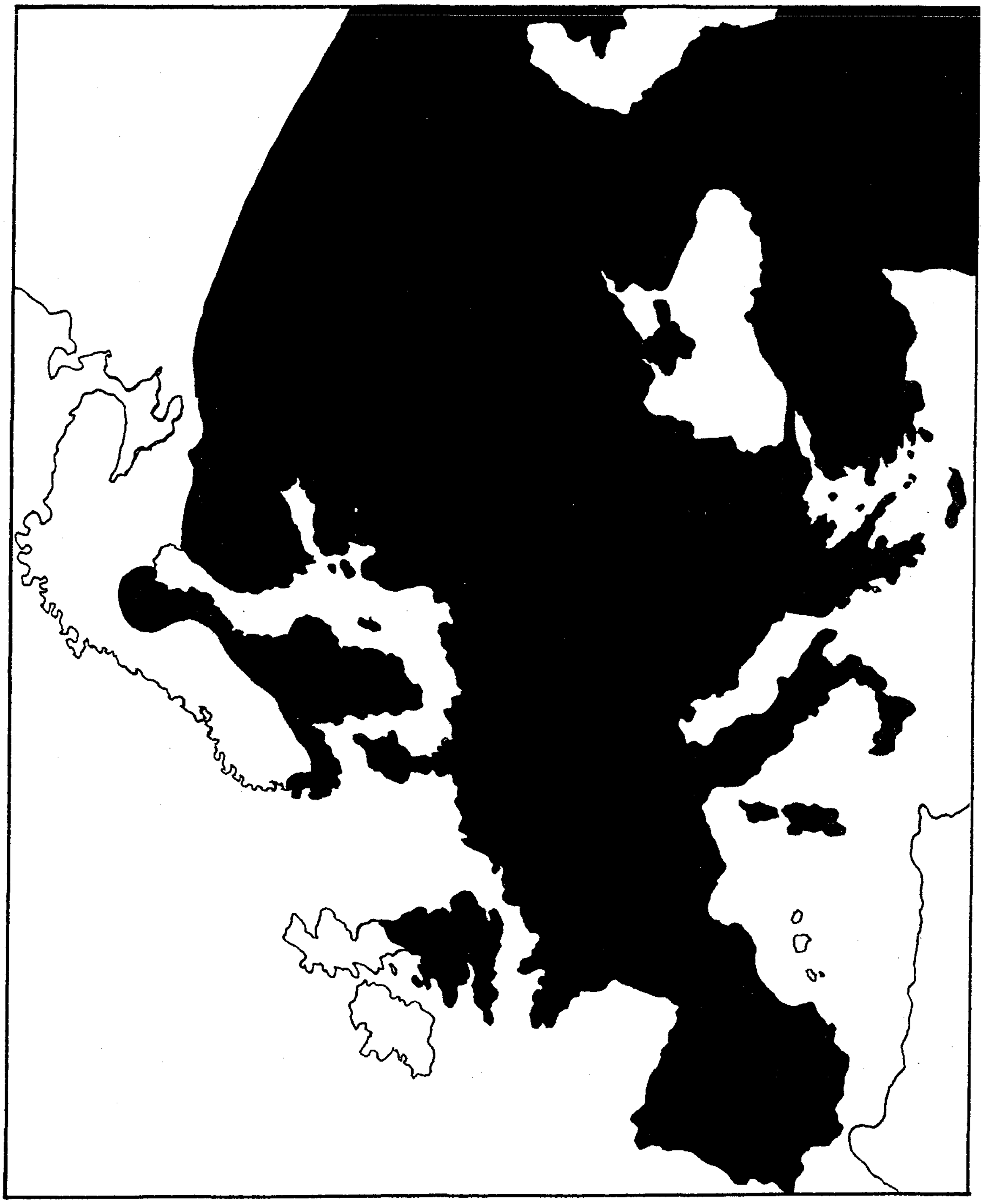
Colubridae are found in tropical, subtropical and temperate regions of the Americas, Africa, Eurasia and Australasia and comprise some 2,500 of the known 3000 (approximately) snake species recorded (Webb, Wallwork & Elgood, 1978). The species is widespread throughout western and central Europe and Asia and Northern Africa, and in Britain, can be found over most of England and Wales. The subspecies found in Britain is Natrix natrix helvetica Lacepède, which is also located in France, Switzerland, West Germany and Italy. Maps of the distribution of the species in Europe and Britain are shown in Figures 1.1 & 1.2.

1.3 General biology

The grass snake, in common with other British reptiles, overwinters in a state of torpor, thereby reducing the active season to approximately 7 months. Madsen (1984) reported communal overwintering of a large population of N.n. natrix in Sweden and that the snakes remained in the vicinity of the winter refuge until mating had occurred.

Smith (1951) and Frazer (1983) both noted that amphibians, and particularly frogs, were the preferred prey of the snake, but that toads, newts and small mammals were also taken. Prey are consumed live and digestion may not be complete for several days if large prey items have been taken.

Figure 1.1 European distribution of the snake Natrix natrix.



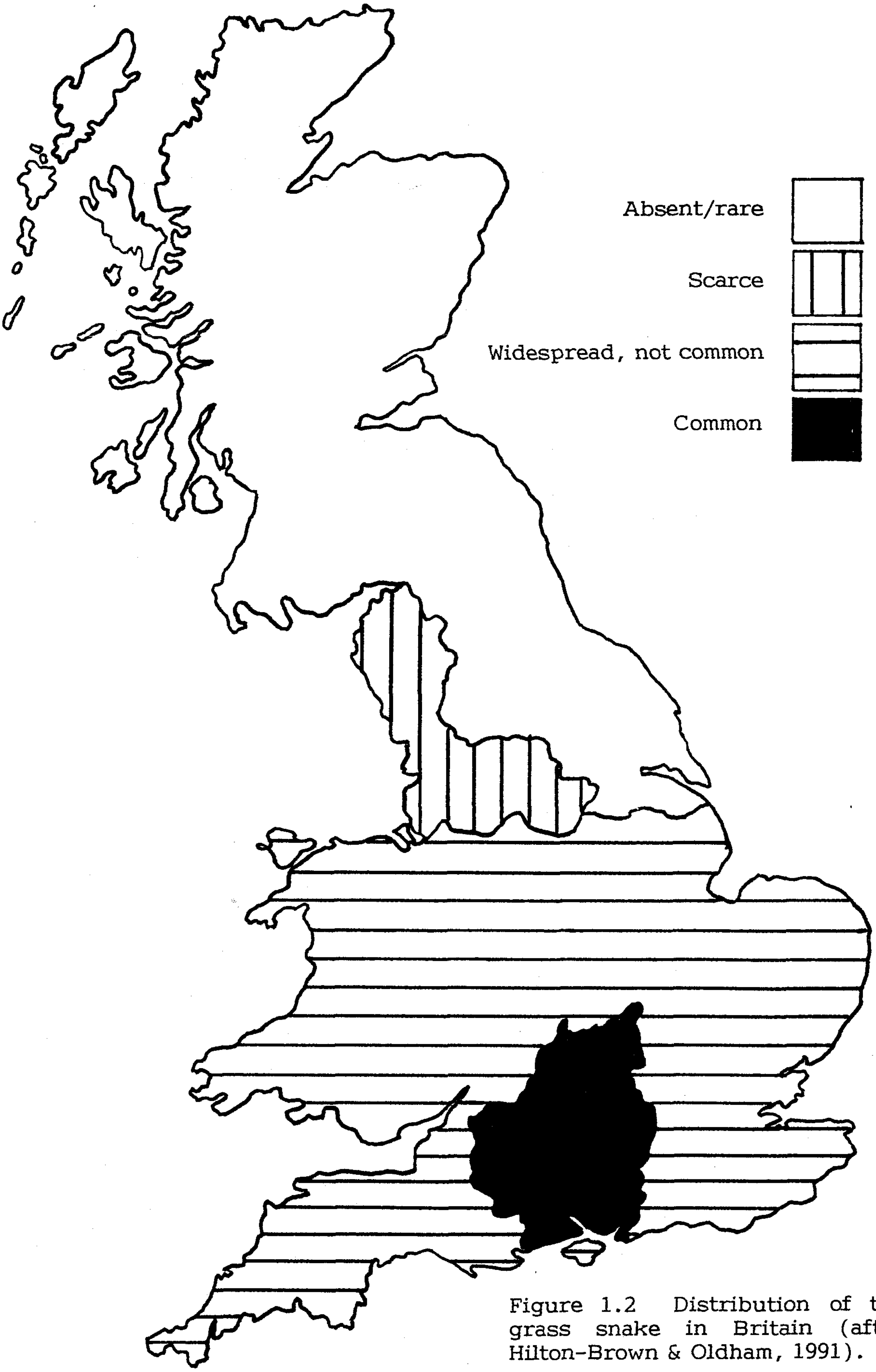


Figure 1.2 Distribution of the grass snake in Britain (after Hilton-Brown & Oldham, 1991).

Oviposition occurs from June to July and the eggs hatch after 6-10 weeks, dependant on the temperature at which they incubate (Smith, 1951). There is no subsequent parental investment. The eggs are laid in clutches in an environment which has a higher than ambient temperature in order to facilitate development. Madsen (1984) reported that radio-tracked females at his study site all used one of two man-made compost heaps and he emphasised the importance of such places. An employee of a Hampshire County Council tree nursery stated that grass snake eggs were found each year in a heap of composting bark (anon., pers comm). In the absence of such sites, it is not known where eggs are laid.

Grass snakes have a commonly reported affinity for water and are often associated with ponds or slow running streams and ditches. In this study, grass snakes were observed in and around a pond, but were more commonly found in woodland and edge habitats such as field and woodland boundaries. Observations at ponds are probably widely reported because the animals are more easily seen in such habitats, whereas in grassland and field edges they are more cryptic.

Overwintering begins in October and it is thought that snakes may return to their previous winter refuge (Madsen, 1984).

1.4 Incidental observations of grass snake ecology

The following observations were made during the course of this research project and are intended to complement the general observations set out above. They have been placed in this introduction because they are of general interest, but are not directly relevant to the chapters that follow.

All observations made during this study indicated that the snakes overwintered in shallow underground refuges, such as rodent burrows or cavities made by tree roots. Spring emergence began in mid-March and the earliest sighting at the study site was on 23rd March in 1988, although grass snakes were reported and observed (Noble, pers comm) at other locations before this date. Male and female snakes emerged at approximately the same time and although the first individual caught in both 1988 and 1989 was female, there was no evidence to suggest that males emerged significantly earlier than females, as has been suggested for a number of other snake species (eg. Viitanen, 1967 & Prestt, 1971, Vipera berus; Brown & Parker, 1976 Coluber constrictor; Parker & Brown, 1980, Masticophis taeniatus and

Pituophis melanoleucus). A table showing the dates of emergence and a description of the snakes is shown in Table 1.1.

Mating was observed on three occasions and in each case was at an over-wintering site. In one case the female left the overwintering site the day after mating and the male with which she had mated was not subsequently observed at the site. These observations reinforce those of Madsen (1984), who stated that grass snakes remain at the overwintering site and mate before dispersal.

Snakes in the process of sloughing were observed on several occasions during this research. For several days before sloughing the eyes of the snakes became 'milky' in appearance (Figure 1.3) and the snakes noticeably less alert. Although the snakes used in this study only sloughed once a year, two distinct periods were evident during which many snakes could be observed with either the 'milky ' eyes and dull coloration typical of sloughing snakes or with the vivid coloration of snakes which have recently shed their skin. The first period was in June of each year and the majority of snakes appeared to slough at this time. Grass snakes at other locations also sloughed during June (Gaywood, pers comm; pers obs). The second period was in September and only a relatively small number (three) were observed, all in 1988 and all at Chilworth.

The association of the grass snake with water arises from the food preference of the grass snake, which feeds almost exclusively on amphibians. In the three years of this study, it was possible to identify the prey of grass snakes on 27 occasions. This was done by faecal analysis, analysis of regurgitated stomach contents and by watching snakes consuming prey in the field. Prey at Chilworth consisted exclusively of toads Bufo bufo, which were abundant at the site. Frogs Rana temporaria, newts triturus sp. and one small unidentified bird were also taken by snakes in either the New Forest or at Whiteparish in Hampshire. Figure 1.4 shows a female grass snake which contains a large food bolus and Figure 1.5 shows a chart of prey species taken by grass snakes during this study.

In captivity, grass snakes were offered frogs, toads and goldfish, and ate each of these, although goldfish were frequently regurgitated before digestion was complete. Neonate grass snakes were offered toad tadpoles, which were taken one or two at a time. Captive adults were also known to eat earthworms and one was observed taking worms fed by hand. Captive snakes always refused dead prey.

a)

Date	Sex	SVL	TL	Weight
21-3-88	♂	450	140	80
21-3-88	♀	700	140	168
23-3-88	♂	550	160	65
24-3-88	♂	580	150	83
26-3-88	♂	570	150	87
28-3-88	♀	680	90	172
5-4-88	♂	540	150	55
5-4-88	♀	590	160	161
12-4-88	♂	600	170	84
22-4-88	♀	620	120	132

b)

Date	Sex	SVL	TL	Weight
24-3-89	♂	480	140	93
24-3-89	♀	710	140	176
24-3-89	♀	630	140	152
27-3-89	♂	500	130	71
29-3-89	♀	690	120	132
29-3-89	♀	580	120	148
30-3-89	♂	520	120	50
1-4-89	♂	520	160	84
4-4-89	♂	570	160	80
5-4-89	♀	680	130	171

Table 1.1 Dates of emergence and details of the first ten snakes caught each year at known overwintering sites in a) 1988 and b) 1989.

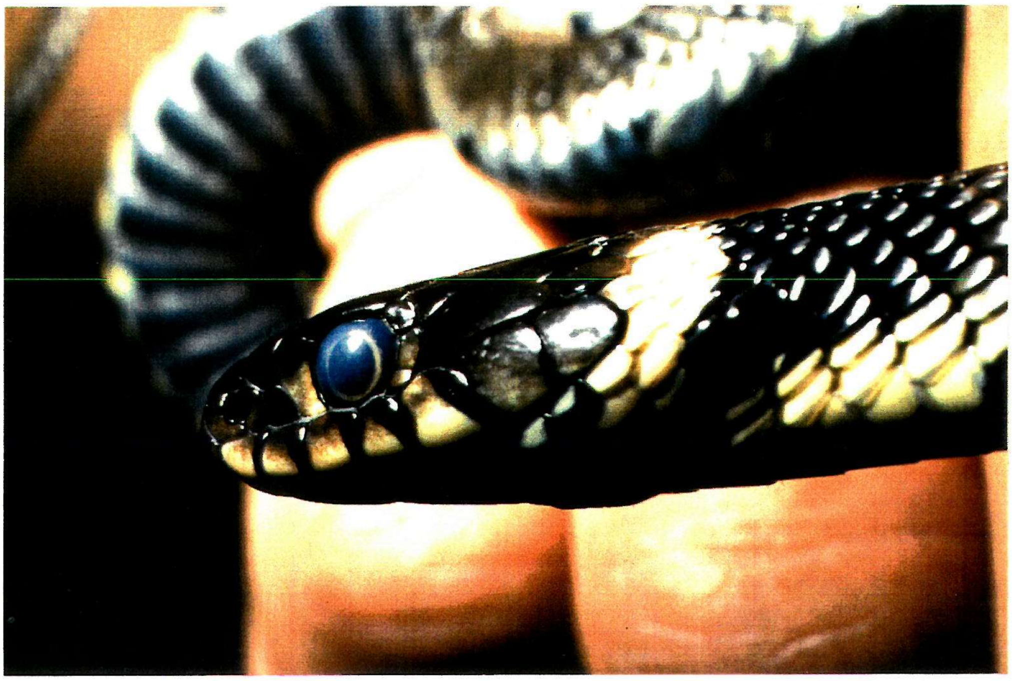


Figure 1.3 'Milky' eyes of snake about to slough (x 2½).

Figure 1.4 Recently fed 80cm snake containing food bolus.

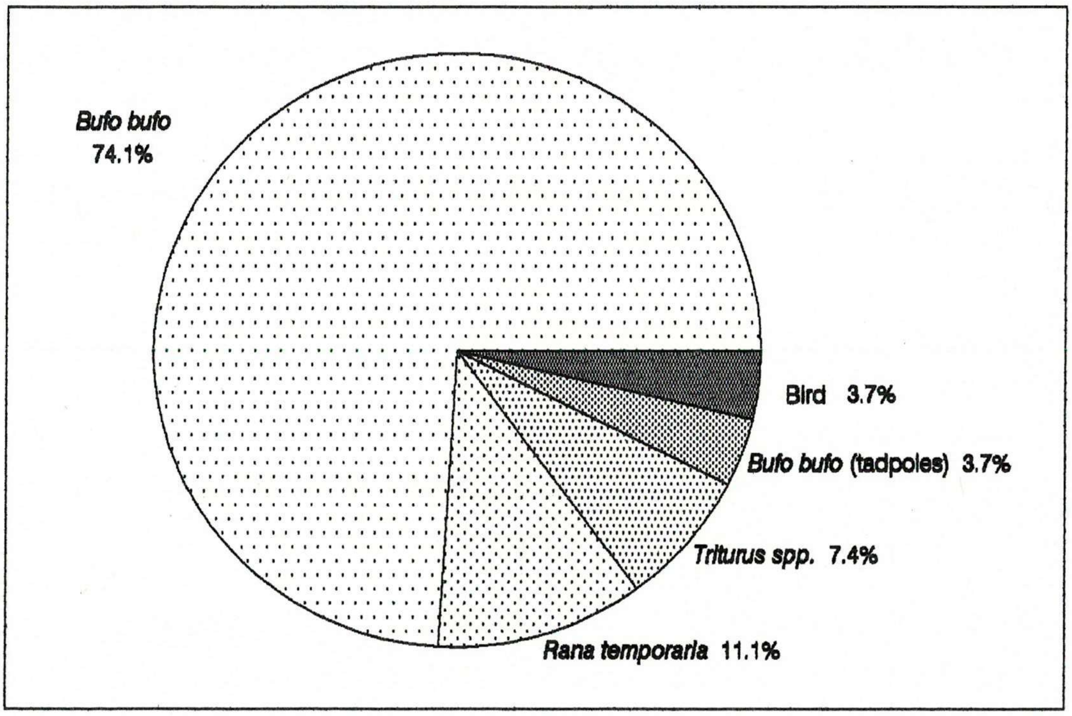


Figure 1.5 Prey species taken by grass snakes. Data is taken from radio-tracked animals and other observations made during this study.

Little data is presented in this thesis in respect of egglaying behaviour, because only one gravid snake was used experimentally and it died in the field shortly after release. No eggs were found at the main study site, although neonates were found in 1988, 1989, 1990 and 1991. However, one site which contained several clutches of eggs was located in a garden at Whiteparish in Hampshire and the behaviour of snakes studied for a period of several weeks.

The site consisted of a large compost heap covered with black plastic sheet weighted down with tyres. Three clutches of eggs were found containing 28, 42 and 52 eggs respectively. A large female taken from a nearby site produced 62 eggs in captivity. The temperature of the immediate site of the eggs was between 24-26°C and the relative humidity over 95%; both remained constant over a three week period.

The exact date on which the eggs hatched is not known, but one clutch hatched in the last two weeks of August, 1988. Dispersal away from the site occurred more or less immediately and no neonate snakes could be found at the site at the end of August. The site is apparently used every year by grass snakes as the landowner stated that hatched eggs were found every winter when the compost was used. He also stated that grass snakes were not seen at other times of the year at the site.

1.5 Status in Britain

The status of the grass snake in Britain is not well known at the present time. Cooke & Scorgie (1983) reported that the snake was widespread and fairly common in England although it had suffered a moderate decline in central and southern England during the 1970's. Hilton-Brown & Oldham (1991) reported a decline in the status of the species in the West Midlands and in south-west and north-west England in the 1980's and no change over the rest of the country.

In both studies, the principal reason given for the decline in the status of the species was the loss of suitable habitat. Agricultural 'improvement', forestry, public pressure and urban development were all quoted as specific examples of habitat loss. In neither study was predation considered to be a key factor in the decline of the species. In this study, a significant number of tagged snakes were killed by predators and the remains of untagged snakes found on two occasions. The magpie Pica pica, which has increased in numbers in most parts of Britain in recent years, possibly because of the decrease in the use of organochlorine chemicals in agriculture and an increase in urban tree planting (Marchant et al, 1990), was a suspected predator of grass snakes during this study (pers obs). It was not uncommon to observe grass snakes which had lost part of their tail, which suggested that they had been attacked at some time in the past. Predation may thus be a more important factor than has been previously considered.

In addition to snakes known to have been killed in the field, four snakes disappeared during the radio-tracking period. Whilst this may have been due to predation and associated tag damage, it may also have resulted from long-distance migration or tag failure. The tags proved thoroughly reliable in tests carried out both by the author and by the tag manufacturers and although it cannot be ruled out, this seems the least likely to account for loss of the snakes. Loss by long-distance migration was minimised or eliminated by extensive searches for 'lost' snakes, and three animals were indeed lost for between 2-14 days before relocation. Extensive and wide ranging searches were carried out for these snakes, although it was pragmatic to accept that a search could only be carries out over a reasonable area.

No overwintering mortality was known to have occured in free-ranging snakes. Emerging snakes at Chilworth all appeared to be in good condition, although Redding (pers comm) observed emerging grass snakes at a Dorset site which had bite marks possibly caused by small mammals.

Until the Wildlife and Countryside Act, 1981 was enacted, grass snakes had no protection at all and were undoubtedly victims of negative prejudice by the public, which may have had a serious effect on local populations. The Act (as amended) makes it illegal to take grass snakes from the wild and illegal to kill grass snakes. The enforceability of this legislation though is questionable.

1.6 Previous research

The elusive and secretive nature of the grass snake make it a difficult animal to study in the wild. Few worthwhile studies have been carried out into the ecology of the animal and most of the current knowledge has come from largely anecdotal works such as Smith (1951), Appleby (1971) and Frazer (1983). Phelps (1978), made a cursory examination of seasonal movements in all three British snakes, but relied on visual observations and his assumptions were of a general nature.

The availability of reliable miniature radio transmitters provided a solution to the problem of relocating individual specimens and Madsen (1984) carried out a more detailed study of grass snakes using this method. His work at a site in southern Sweden used basic techniques to explore the range, frequency and extent of movement and use of different habitat types. Further work by Madsen (1983, 1987) examined other aspects of grass snake ecology such as growth and life-history tactics and these also were novel studies on the species.

1.7 Objectives of the study

This study aims to examine the behaviour of the grass snake in the field, with particular reference to movement and the use of space and has both a pure and applied component. Comparison of the behaviour of the grass snake with other species of snake will add to the body of knowledge of snake ecology in general and will enable comparative studies to be made with other studies of the same species, such as those of Madsen (1983, 1984 & 1987).

The use of various types of home range analyses has been the source of much discussion by various workers (Jenrich & Turner, 1969; Dixon &

Chapman, 1980; Rose, 1982; Samuel et al, 1985; Worton, 1987). In this study, a method is used which is novel in the study of snake ranging behaviour and which has a particular suitability not only to the study of snakes, but also to any study of other animals in a heterogenous environment.

In a more applied sense, knowledge of the vagility and habitat use of the grass snake may assist in the management of the species by landowners and conservation bodies. One instance of this has already arisen, in which a small archaeological organisation, in their efforts to protect a site of some archaeological importance, also expressed a desire to include conservation of the resident grass snake population in a management plan for the area. Information obtained directly from this study was used when offering advice to the organisation.

In addition to home range, movement and habitat analyses, part of the research attempts to explain the reasons underlying grass snake behaviour. In common with other ectotherms, behaviour is certain to be affected by many variables, both biotic and abiotic. Biotic variables include age and sex of the animal, its physical condition, the annual cycle of the animal, familiarity with its environment and intra- and inter-specific interactions. Abiotic variables are predominantly factors associated with weather and time. Many of these variables are included in analyses of the behaviour of the snakes during this research. Particular importance has been placed on the body temperature of individuals as this is likely to be of specific relevance to any terrestrial ectotherm.

Finally, the interactions of grass snakes both with conspecifics and with the adder, Vipera berus has been examined in a controlled situation in an attempt to explain the importance of such interactions in the field.

1.8 Layout of the thesis

The chapters of the thesis have been arranged in an order that makes it possible, in the main, to read the work in sequence. Cross references to future chapters have been minimised wherever possible, although on occasions this was unavoidable. Each chapter is sub-divided conventionally into introduction, methods, results and discussion and each of these in turn is further sub-divided into logical sections.

Chapter two examines the methods used throughout this study which are common to several or all of the other chapters.

Chapter three analyses the ranging behaviour of grass snakes using appropriate methods which are themselves critically assessed. The use of space within ranges, changes in ranging behaviour with time and overlap of ranges with conspecifics are analyzed and discussed.

Chapter four is concerned with the vagility and movement behaviour of grass snakes and variation in movement between sexes, over time, with body temperature, with environmental variables and with the physical condition of the snakes.

Chapter five investigates the thermal ecology of free-ranging grass snakes, with emphasis on stationary animals, although some data from moving snakes is presented. The body temperature of the snakes is examined in relation to environmental variables at all times of the day and during various snake activities. The effects of ecdysis and feeding on body temperature are analyzed and discussed.

Chapter six examines habitat selection and the use of the physical microhabitat. A number of biotic and abiotic variables were examined collectively in an attempt to understand the requirements of basking snakes.

Chapter seven documents a laboratory study which investigated scent recognition in grass snakes. Conspecifics and sympatric adders were used in a comparative study of behaviour following exposure to the scents of other snakes.

Chapter eight is a general discussion which incorporates information from all analytical chapters in the thesis.

In addition to the main body of the work, appendices are included which detail observations made during the surgical implantation of the transmitters and which briefly document the results from a largely unsuccessful attempt to examine the behaviour of grass snakes which were caught at Whiteparish and introduced to the main study site.

Chapter Two
General Methods

2.1 Study sites

In 1987, three study sites were used, two in the New Forest and one at Chilworth, near Southampton. The New Forest sites were chosen because of their apparent suitability for the study. The reported population of grass snakes was high in one case and the other consisted of habitat known to be favoured by the snakes. Permission was obtained from the Forestry Commission to use specific sites in the Forest and initial radio-tracking work was carried out at the two sites. As the season progressed, it became clear that the area around Chilworth supported a higher than expected population of grass snakes and its' proximity to the University and relative lack of intrusion from the public made it a desirable site at which to work. Traffic congestion in the New Forest meant that much time could be lost in a day and disturbance by tourists and naturalists became a considerable distraction, so in 1988 and 1989, research was only carried out at the Chilworth site. On balance, it was felt that it would be more productive to cover this one site more thoroughly, despite the obvious value of a comparative study between two or more sites.

The New Forest sites consisted of two areas which were assessed as being suitable for a long term study. Both sites proved to have resident populations of grass snakes, as well as other reptile species, and for the first year of the study were intensively studied.

Burbush Hill railway cutting (SU 19 01) is a one mile long cutting, very badly drained, with standing water along much of its length. Vegetation in the wet areas is dominated by Juncus effusus and in the damp areas by Molinia caerulea. The north facing slope is covered with plantation conifers except at the extreme west of the site, where it opens out into a flatter and drier area dominated by gorse Ulex europaeus. The south facing slope is a mixture of dry heath with associated ericaceous vegetation, gorse breaks and woodland dominated by conifers. The surrounding areas on both sides of the cut comprise extensive dry heath and on the north side is a large pond which contains a small breeding population of frogs and toads. Grass snakes were common here, but the area was popular with walkers and naturalists and undisturbed work was rarely possible.

Bentley Enclosures, Fritham (SU 23 13) is an area of damp grassland bordered on three sides by plantation conifers. Dominant vegetation is again M. caerulea and there are several developing stands of alder carr together with beech and birch thickets as well as more open lawn areas. Only one female snake was tagged here and extensive searches for other snakes were not undertaken, although grass snakes were known to be present (Gaywood pers. comm.). The area was popular with tourists and again, undisturbed work was difficult.

Chilworth Manor, SU 40 18; owned largely by the University of Southampton, the site has three main distinct areas. The first is a formal garden consisting of lawns and flower beds of non-native species; the second is a meadow managed for wildlife and education and the third and most extensive is an area of deciduous acid woodland. The estate is bordered by a Forestry Commission conifer plantation, a motorway (M27), a riding school and stables and a tree nursery; grass snakes were commonly seen in all of these areas. Bracken Pteridium aquilinum dominates all three of the sites from June onwards and at Chilworth, brambles Rubus fruticosus form a virtually continuous ground layer in the deciduous woodland.

A map of the Chilworth site is shown in Figure 2.1 and an aerial photograph in Figure 2.2.

Initially, Chilworth was used largely because of ease of access and because work could be carried out without disturbance. Once it became apparent that a worthwhile population of grass snakes was present here, the New Forest sites were abandoned in its' favour. Neither of the Forest sites was extensively mapped as this process was very labour intensive and since most of the data presented in this study represents work carried out at Chilworth, mapping was not considered worthwhile.

2.2 Snake capture and handling

The capture of snakes in the field can be fraught with difficulty for a number of reasons. Venomous snakes pose particular problems, but even non-venomous species can often be difficult just to locate. Camouflage, extreme wariness, secretiveness, speed of escape and often a low population density all contribute to the problem of catching even moderate numbers of snakes over a relatively short period of time.

Most workers have caught snakes by hand, either by transecting areas known to be used by the snakes (eg. Gregory, 1984; Fitch & Shirer, 1971; Fraker, 1970; Gent, 1988) or by catching snakes at areas where aggregations occur such as overwintering sites or breeding areas (Gregory & Stewart,

Dw	Deciduous wood
Cw	Coniferous wood
Mw	Mixed wood
Gg	Grazed grassland
Ug	Ungrazed grassland
Mg	Managed grassland
W	Wet grassland
Fg	Formal garden
P	Pond
A	Arable land (cereals)
C	Cultivated (tree nursery)
S	Stream
B	Built environment
╱	Roads

Fig. 2.1 Map of the Chilworth study site

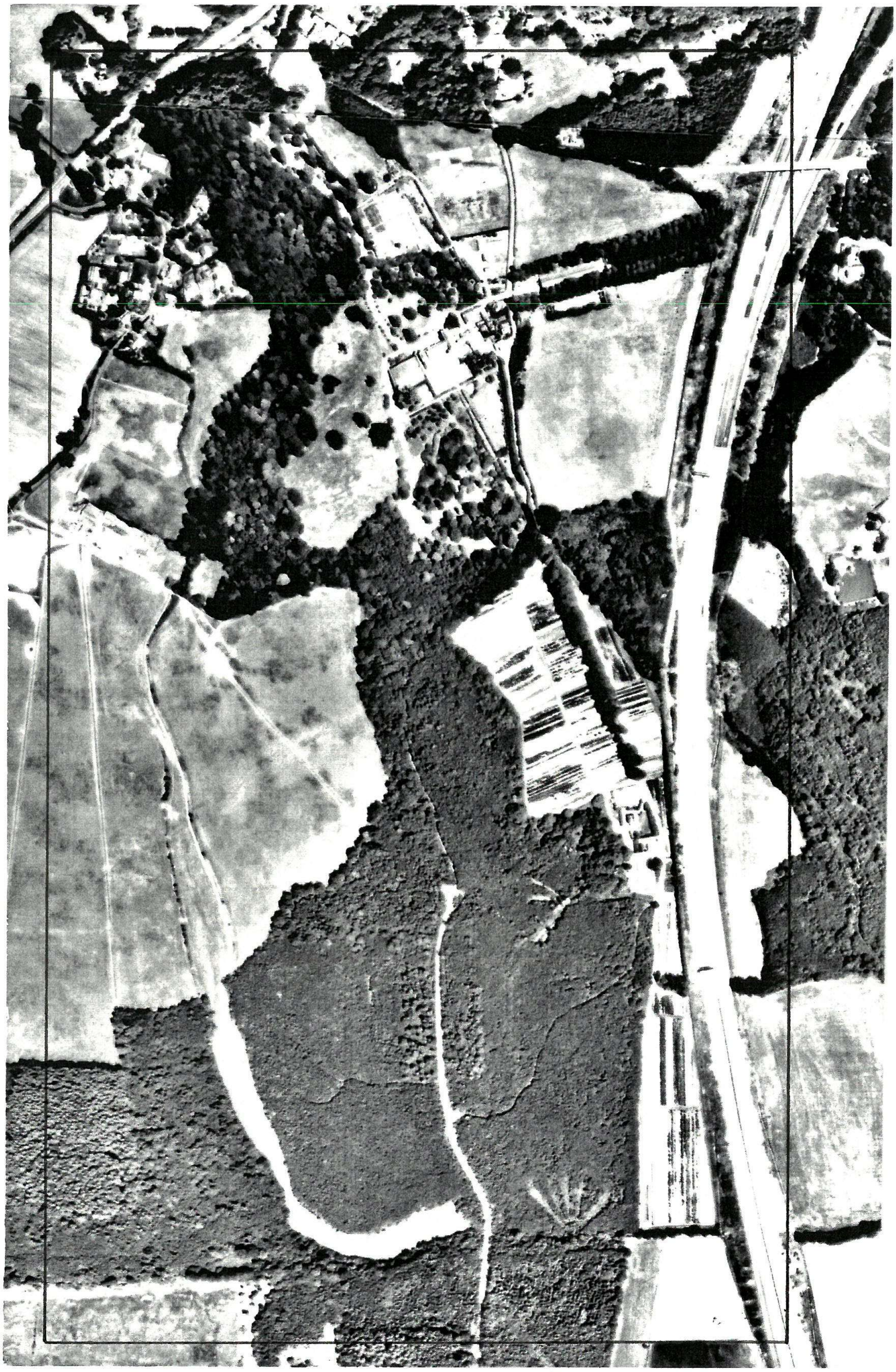


Figure 2.2 Aerial photograph of the Chilworth study site. The boxed area represents the extent of the map shown in Figure 2.1.

1975; Brown & Parker, 1976; Gannon & Secoy, 1985). Some researchers have used drift nets to guide snakes to pitfall traps (eg. Woodbury, 1951; Gibbons & Semlitsch, 1987), but the method has met with only limited success and works better for small snakes whose length is less than the depth of the pit (Fraker, 1970; Fitch, 1987).

Artificial cover appears to provide the best method for trapping snakes in temperate regions where they cannot regularly maintain high body temperatures and is a method that seems to work well for all British snakes. Gent (1988) made use of small pieces of corrugated iron for trapping smooth snakes, Coronella austriaca in southern England and he found these were also used by both adders and grass snakes.

In this study, most snakes were captured by searching the field site, although the snakes propensity for hiding under pieces of tin was used to advantage and several snakes were captured in this way, particularly in mid-season, when they were often difficult to locate in other areas. At each study site, snakes were usually temporarily removed for weighing and measuring, although this was sometimes done in the field. Snakes considered suitable for fitting with transmitters were removed to the laboratory and processed as rapidly as possible to ensure return to the wild with the minimum loss of time and stress to the animal. In the case of implants, this was between one and two weeks, depending on the recovery rate of the animal. Fitting of external tags was usually done in the field and the snake released at the point of capture.

Several methods can be used to accurately sex snakes and grass snakes proved very straightforward in this respect, even to the extent of sexing some snakes which were not caught. Female grass snakes are considerably larger both in length and girth than males. Secondly, the head of the adult females is broader and somewhat spade shaped, whereas that of the males is narrower. Finally, the tail length of the females is considerably smaller than that of the males when taken as a ratio of the total body length and tapers rapidly away from the vent whereas the tail of the males tapers evenly away from the vent. Smith (1951) counted the sub-caudal scales of grass snakes and observed that males had 51-61 and females had 61-73; in this study, all the captured snakes conformed to this pattern.

Evidence for these features was provided during the course of this research in a number of ways. In the latter two years, three mating pairs were caught or observed and in each case, the appearance of each sex fitted the descriptions as above. In 1988, a known oviposition site in a private garden was visited twice at the start of the egg-laying period and five gravid females were observed. The eggs were identified by careful palpation and the snakes all had the broad heads and short, rapidly tapering tail typical of females. A further visit to the site identified three gravid females and two smaller snakes, both of which fitted the above pattern for males and neither of which contained eggs. A series of visits to the site after the oviposition period revealed three large snakes, all of which had loose, stretched and ill-fitting skin which apparently resulted from the loss of body mass following oviposition. Such a phenomena was never seen in the smaller snakes identified as males. Two large snakes taken into captivity before oviposition both produced clutches of eggs and subsequently had stretched and loose-fitting skin. Snakes observed but not caught or handled at this time at other sites also fitted the descriptions above.

In the course of the research, three of the experimental animals died or were killed by predators and their bodies recovered (see Table 2.2); post-mortem showed that the sex of each had been correctly identified.

These characteristics apparently also hold true for adders; in the three years of research, three dead adders (and three grass snakes) were found and dissected and male/female identification features found to hold true.

Snakes that contained an obvious food bolus when caught were rarely handled for long or taken into captivity to avoid the near certainty that they would void their gut of food, probably to increase their escape chances. Similarly, gravid females were rarely handled for long to minimise the possibility of damage to the eggs or the snake.

2.3 Identification of individuals

Several methods have been used by workers to mark snakes for future recognition. Scale clipping as described by Blanchard & Finster (1933) has been the most common method of identifying individual snakes in the field and has been used in many studies (e.g. Prestt, 1971; Goddard, 1984). It does however have the disadvantage that clipped scales quickly regrow or are sloughed off, leaving little or no trace of the marks. Furthermore, on smaller snakes, it is difficult to make a sufficiently deep cut without damaging the animal. Lewke (1974) used freeze branding which proved humane and quick, but necessitated taking very cold liquids into the field. Weary (1969) used a portable heated needle, the marks from which were still visible after two years, but the equipment, although portable, was relatively expensive.

Hailey and Davies (1984), in a study of *Natrix maura* used the scale patterns on the ventral surface of the snake to identify individuals. It was found that these patterns were unique and could be coded numerically for ease of use in the field. Although in this study the ventral patterns of *Natrix natrix* have not been coded, the pattern of ventral scale markings was reproduced onto a blank template as shown in Fig 2.3. These patterns appear to be permanent and do not change after sloughing, and present a simple way of identifying individuals in the field. Carlström & Edelstam (1946) photographed the ventral scale patterns of grass snakes and noted that there was no change in the pattern even after a considerable increase in size.

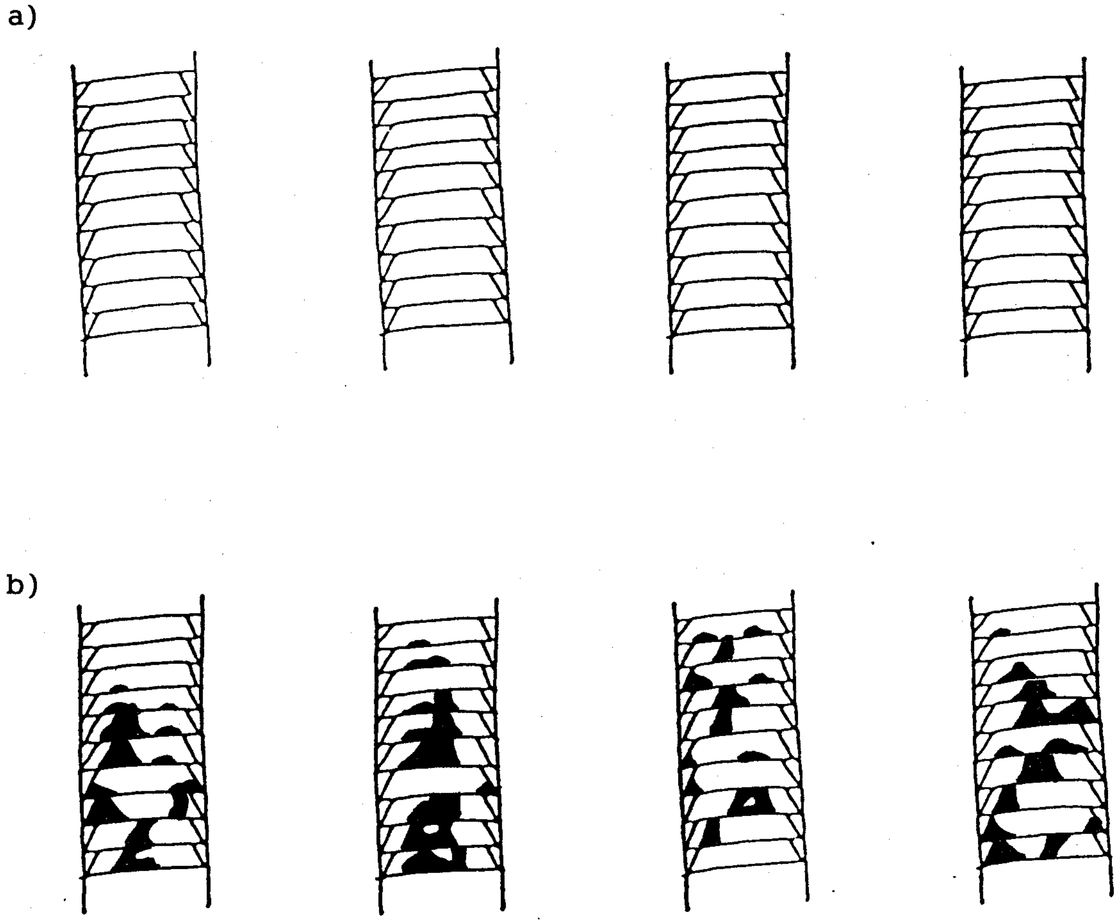


Fig 2.3 Recognition of individual snakes from the ventral scale markings.
a) Sample of blank templates.
b) Sample of completed templates as used in the field.

Snakes were captured and put into a perspex tube, which was then stopped at each end with a rubber bung. It was then a simple matter to accurately copy the scale pattern onto the template. Only the first ten complete scales were used on each occasion and in practice it was always possible to positively identify the animal from these.

2.4 Radiotracking

2.4.1 General

Radiotracking in the field was undertaken using an AVM LA12 receiver with a three element yagi antenna, which allowed the animals to be pin-pointed exactly. The wavelength permitted for radio-tracking in Britain is 173.20-173.35MHz, and the transmitters used (radio tags) operated across this range, allowing several animals to be tracked simultaneously, although care had to be taken to ensure that the signals were sufficiently spaced to allow differentiation in the field.

Locating an individual in the field was achieved by tuning in the receiver to the approximate position on the dial, which had been noted when testing the transmitters and turning the gain to maximum, at which point the pulse of the tag could hopefully be heard. Direction finding was poor at maximum gain, but as the animal was approached, the signal became stronger and the gain could be reduced, improving the directional strength of the signal. By following the same procedure, the animal could be located to within less than half 0.5m.

On most occasions, the snakes were left undisturbed, which meant a compromise on absolute accuracy, although it was often possible to see or judge the position of the animal from a distance. Disturbance to the animals was noted for assessment of the effect of disturbance on their patterns of movement. The range of the implanted tags varied between 30 and 200 metres, depending on habitat, topography and weather and it was often necessary to spend several hours locating a very mobile individual.

The tags used were of two types. Those used in the first year were type SS-1 single battery tags with an external whip antenna which were taped to the tail of the snake as shown in figure 2.4. Similar tags had been successfully used in studies of sand lizards (Dent,1986) and smooth snakes (Gent,1988). In this study, it was apparent that the external tags caused some behavioural change to the snakes, and on one occasion, a snake was completely immobilised by the antenna, which had become knotted round a tuft of grass. There was also some minor damage to the scales on the tail of

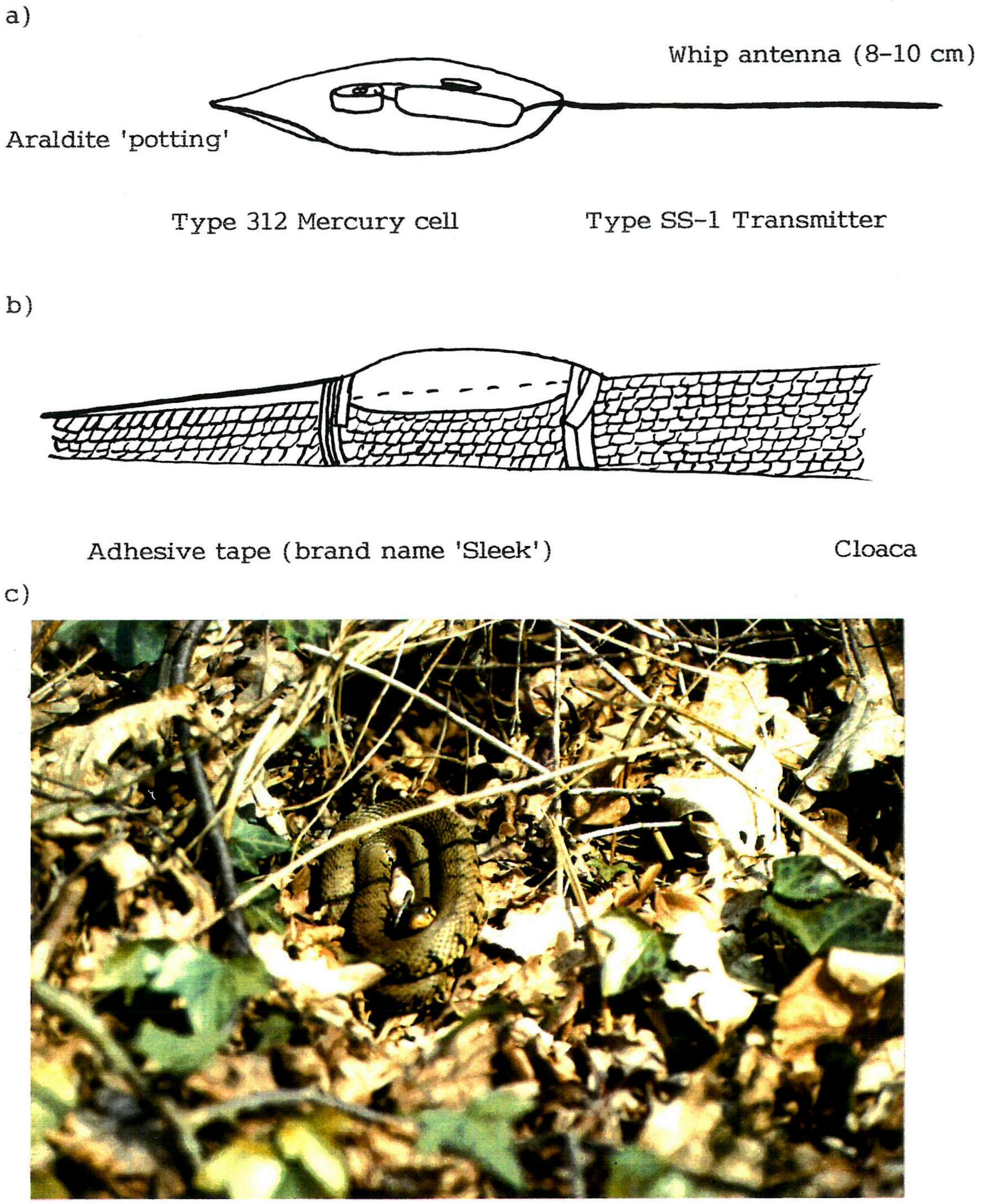


Fig 2.4 Attachment of external tags to grass snakes

a) Structure of the tag.

b) Attachment to the snake.

c) Snake with tag <u>in situ</u>.

some of the snakes. On balance, the method was not considered to be suitable for the purposes of the study. The tags used in the second and third field seasons were type SS-2 twin battery tags with a small loop antenna which were surgically implanted into the snakes. A series of photographs showing the surgical procedure is presented in figures 2.5 to 2.9.

2.4.2 Choice of animals

The criteria for choice of animals suitable for implanting were size, condition and sex. Primarily, the animals had to be the required sex and each snake had to be large enough to contain the tag easily. Occasionally animals that were thin or had an excessive infestation of parasites were captured. Particularly bad mite infestations were manifest as a cluster of mites visible around the eyes of the snake. Mites could also be seen moving on the scales of most snakes and if many were seen, the snake was either treated and released, or treated before surgery. A small solid domestic fly killer block placed in the tank of captive snakes for 24 hours either reduced or eliminated the infestation without causing the snake apparent harm.

A small female was tagged with an external tag in 1987, but rarely moved and lost weight, so the tag was removed. Tables showing details of the snakes used, length of the tracking period and ultimate fate of the animals are shown in Tables 2.1 and 2.2.

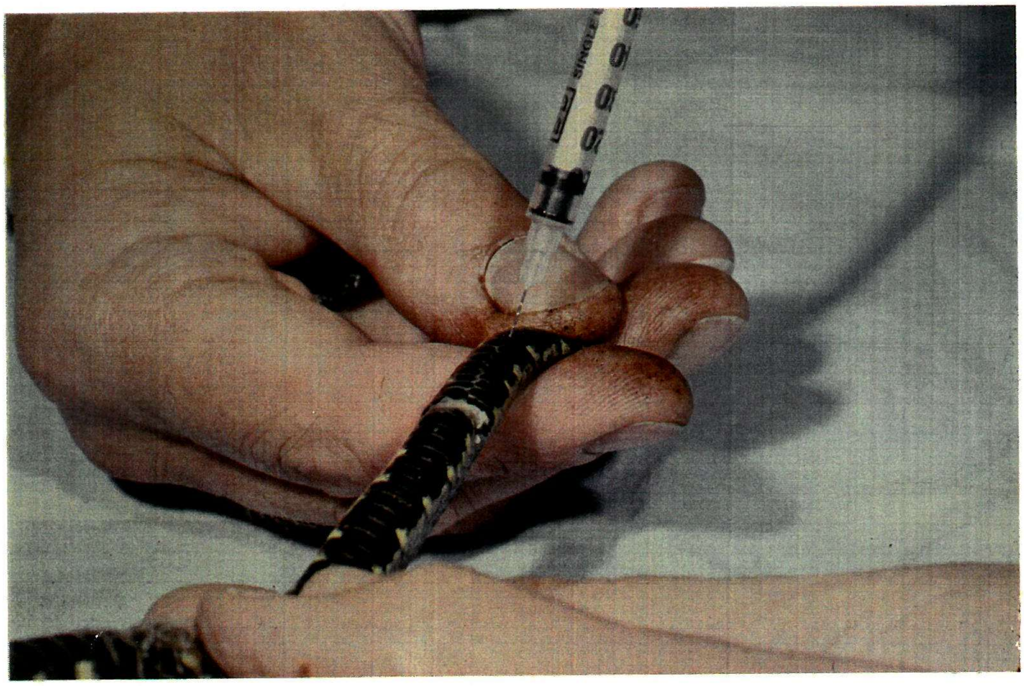


Figure 2.5 Intravenous injection of anaesthetic.

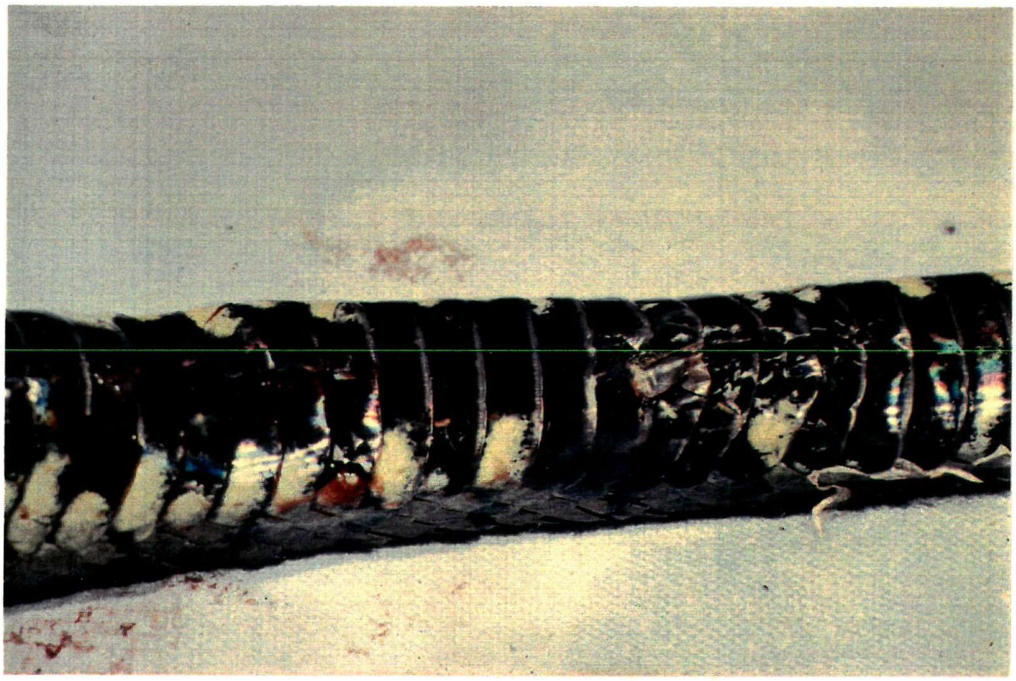


Figure 2.6 Incision of the ventral surface anterior of the vent. The visible scar is from a previous tag implant and apart from superficial damage to scales, has healed well.

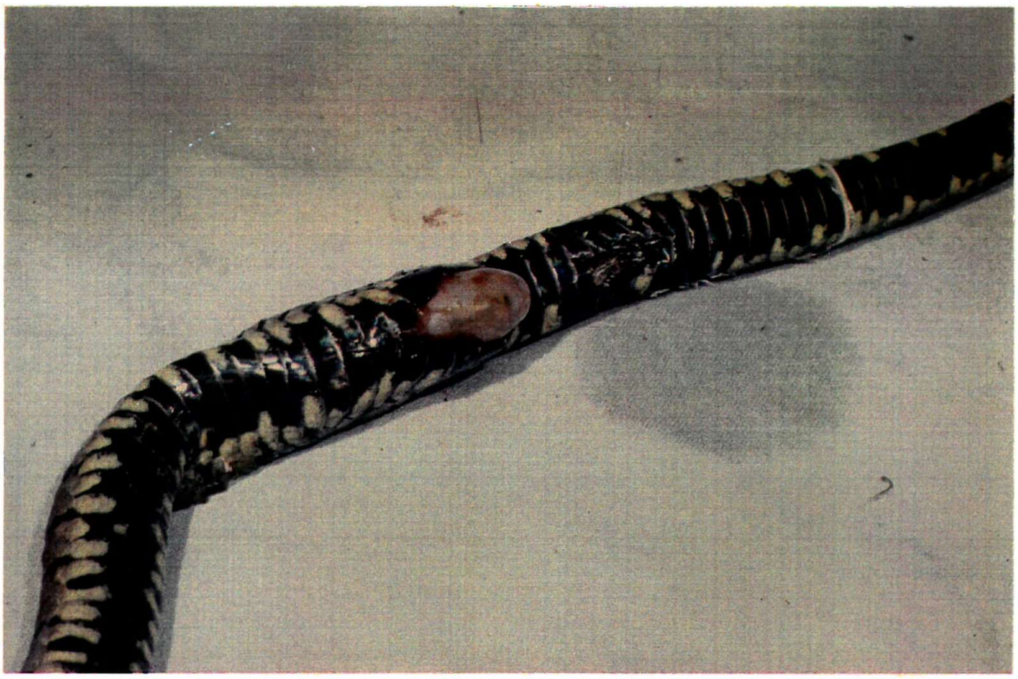


Figure 2.7 Insertion of the tag into the peritoneal cavity.

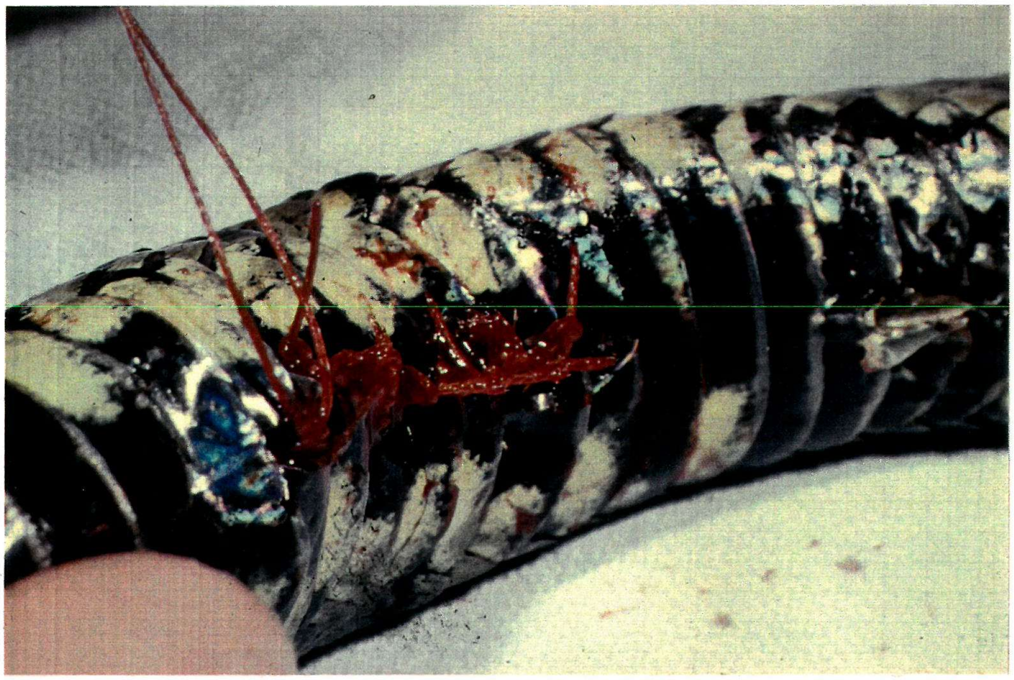


Figure 2.8 Suturing the incision.

Figure 2.9 Spraying with 'Opsite to minimise the chance of infection.

Snake No.	Sex	Duration (days)	Fate of animal
C 2	M	23	Released back to field.
C 3	M	25	Released back to field.
C 4	F	17	Escaped; tag fell off.
C 5	F	58	Released back to field.
C 6	M	6	Escaped; tag fell off.
C 9	F	16	Escaped; snake sloughed.
C 10	F	17	Escaped; tag fell off.
C 12	F	6	Escaped; tag fell off.
B 1	M	18	Released back to field.
B 3	M	14	Escaped; tag fell off.
B 4	M	16	Released back to field.
F 1	F	38	Released back to field.

Table 2.1 Tracking period and ultimate fate of snakes fitted with external tags.

2.4.3 Licences

A Home Office licence valid for 5 years was obtained for the implant work in 1988 and a Nature Conservancy Council licence (Ref SA:16:89) for all the work in 1988 and 1989. Rules therein were strictly observed.

Home Office inspectors visited the animal house where post-surgery convalescence of the snakes took place on one occasion and were wholly satisfied with the procedures taken and adherence to the Animals (Scientific Procedures) Act, 1986. An annual report detailing procedures for each preceding year was duly completed and returned in accordance with their instructions.

The Nature Conservancy Council (NCC) Licence permitted implantation of radio transmitters into grass snakes. The NCC funded purchase of transmitters (Contract No: HF3-03-208[76]) to the value of £420. An annual report and details of animals that died during the research were submitted as requested.

2.4.4 Surgical techniques

The anaesthesia of the snakes and implantation of the transmitters was carried out by a Member of the Royal College of Veterinary Surgeons and was achieved in a way that was considered to minimise the disturbance and distress to the animals. The snakes were kept at room temperature for several days before surgery and allowed to bask under 60W bulbs. They were provided with water but not food and were briefly inspected beforehand for obvious signs of illness or parasitism. Only healthy animals were used. Anaesthetic was given in the form of 1ml/kg bodyweight Saffan (alphaxalone and alphadolone acetate, Glaxovet Ltd) intravenously into the ventral caudal vein 2-3cm posterior of the vent and the snakes considered unconscious when they could no longer turn over when inverted, usually after approximately 10 minutes. An incision 3-5 scutes long was made in the ventral surface some 5cm anterior of the vent and the transmitter package inserted into the peritoneum.

The incision was immediately closed with 6-8 stitches using Dexon 1.5 metric biodegradable suture. The wound was finally coated with Opsite wound dressing (Smith and Nephew) and each snake monitored to ensure normal breathing until recovery from the anaesthetic. Such recovery was indicated by increased body movement and commencement of tongue flicking and normally took between 10 and twenty minutes. The animals rapidly regained apparently normal behaviour as indicated primarily by an extreme dislike of being handled, at which point they were placed in a tank and provided with cover, water and a basking lamp warm enough to allow normal thermoregulation. The whole process initially took approximately 35 minutes, but this was reduced to 20 minutes with practice.

Few problems were encountered with the surgical procedure, although one fatality occurred less than one hour after anaesthesia. In this instance, the snake failed to make a satisfactory recovery from the anaesthetic. All the other animals made rapid and apparently full recoveries. It is very important that the snake is fully unconscious when surgery is attempted; such a condition is best indicated by an inability to right the head when inverted and by a lack of reaction when the tail is pinched hard; occasionally, there was a slight reaction when the incision was made, in which case a local spray

Snake No.	Sex	Duration (days)	Fate of animal
111	M	135	Killed by predator.[1]
141	M	41	Unknown.[2]
181	M	71	Died in captivity.
1161	M	40	Killed by dog or fox.
11	M	94	Released back to field.
21	M	26	Unknown.[2]
31	M	52	Unknown.[2]
41	M	26	Released back to field.
51	M	33	Released back to field.
122	F	193	Killed by predator.[1]
172	F	56	Killed by predator.[1]
192	F	167	Released back to field.
12	F	313	Released back to field.
22	F	13	Unknown.[2]
32	F	88	Released back to field.
42	F	7	Died in the field.[3]

1. Tag found, but no sign of the snake. The tags were damaged in each case, although close examination failed to reveal what by.

2. Failure to find the snake. Could have been caused by tag failure, predation involving destruction or removal of the tag or long distance migration by the tagged animal.

3. Gravid when implanted. Although in apparent good health when released to the field, the tag prevented movement of the eggs through the cloacal vent and created a pressure necrosis from which the animal died.

Table 2.2 Tracking period and ultimate fate of implanted snakes.

anaesthetic was applied which eliminated the problem. Breathing rate and heart rate are rapid and regular at this time and are easily observed. The anaesthetic is effective for a short time only and surgery must be carried out immediately the animal is ready. Recovery from the anaesthetic is very rapid on occasion and this could potentially lead to problems if surgery is unfinished. Two supplementary doses of Saffan were given to one female animal in accordance with the recommendations of the manufacturer, without ill effect.

2.4.5 Care and release of implanted snakes

For the period following surgery, the snakes were kept singly in fish tanks which had been sterilised and fitted with lids. They were provided with fresh water daily, cover and basking lamps which provided an ambient daytime temperature of up to 25°C and a night temperature of 16-18 degrees°C. Ambient light and basking lamps were controlled by time switches which were set to approximate field conditions at the time. The last two snakes to be implanted were provided with frogs to eat but these were ignored and were removed after 36 hours. The snakes were disturbed as little as possible and after a week to 10 days were inspected by a veterinary surgeon for signs of infection or discomfort before being passed fit for release to the wild, at which point they were no longer bound by the provisions of the Animals (Scientific Procedures) Act 1986. The animals were released at point of capture in late evening to allow time to settie before the active period the following day.

2.4.6 Re-implantation of tagged animals

Four snakes (three females and one male) had second tags fitted at the time the first was removed. One died after surgery (see above), but the other three made full and complete recoveries. The use of longer life batteries eliminates the need for this procedure, since the snakes can then potentially be followed for a full season with just one implant.

2.5 Mapping

In order for the radio-tracking fixes and subsequent analysis to be conducted as accurately as possible, it was necessary to give careful consideration to the method of mapping the study site. Initially, a local planning map and high resolution Ordnance Survey maps were examined, but found to be out of date, insufficiently accurate or lacking in detail, so it was decided to map the site during the course of each field season; this was done as follows.

In the first instance, a major feature (a field boundary) somewhere near the estimated centre of snake activity was mapped, using a 30m tape and prismatic compass. This was then drawn onto a 1:1250 map. Adjoining features could be appended onto this base as necessary, dependant on the activity of the snakes. Major boundaries and features were mapped regardless of snake activity, both to complete the map, and to facilitate future habitat analyses. Specific features, such as path junctions, fallen trees, gates etc. were marked on the map as cornerstones from which subsequent mapping and snake fixes could be easily achieved. In this way, a fix could be mapped with minimum effort and maximum accuracy.

Errors in mapping were made evident when plotting by the first and last plots of enclosed habitats (eg. field boundaries) to meet. The maximum error known to have occurred was in a field with a boundary of 1100m and a maximum width of 290m; the error was approximately 15m, which represented 1.4% of the perimeter and 5.2% of the maximum width. Using this method, maximum errors were usually less than 2% and very often nil. Errors were minimised by remapping unacceptable inaccuracies and by measuring snake movements directly if they were less than 30m. The mapping process was highly labour intensive and was kept to a minimum, especially in the third field season. The master map was drawn onto tracing paper which was overlaid onto a grid which enabled fixes to be calculated to the nearest metre.

In the first two field seasons, maps of the movement of each individual snake were overlaid onto the base map and distances and bearings of movement calculated by measurement with ruler and protractor. By the third field season however, a computer program (Ranges IV, Biotrack, Wareham) was available which calculated this information and it was necessary only to input the grid reference of each location, thus eliminating the need to draw the range of each snake.

2.6 Body temperature recording

Of the 12 radio tags used throughout the course of this research, four were fitted with thermistors which made the tags pulse at different rates according to temperature. These intervals were calibrated in a water bath before the tags were implanted and it then became possible to remotely sense body temperature to an accuracy of +/- 0.5°C. The tags were also calibrated on removal from the snakes to ensure that battery drain and consequent drop in pulse rate was considered when calculating body temperatures.

Body temperature readings were taken at every fix of a tagged animal; these fixes spanned the entire active phase from dawn until dusk. Furthermore, with use of an interval timer and tape recorder it was possible to log the temperature of stationary animals for periods of up to several days. A more detailed methodology of this can be found in the chapter on thermal ecology.

2.7 Weather data

Weather data was collected in a number of ways both on and near to the study site at Chilworth. Weather summary sheets were purchased from the Southampton Weather Centre which showed for each day maximum and minimum temperatures, grass temperature at 9 am, soil temperature at 30 and 100 cm, total rainfall, rainfall between 6 am and 6 pm and its duration and finally the number of sunshine hours. The data was recorded at Mayflower Park in Southampton, approximately four miles south of the Chilworth site. Although this recording station is nearly at sea level and Chilworth area is between 50-80m above sea level, the data were considered acceptably accurate as a general indicator of conditions at the study site.

Owing to the continual malfunction and breakdown of the specialised weather recording equipment at Chilworth, data collection there was less comprehensive than had been planned. No windspeed and direction data was obtained except for short periods of a few hours before the machine failed. Gross radiation data too was seriously curtailed by the breakdown of both the solarimeter and the logger and the unavailability of portable loggers. However in the final field season, a solarimeter loaned by the Met Office was set up with a Grant logger to provide radiation data consisting of averaged readings every fifteen minutes for a period of two months. A home made temperature logger set up in a Stevenson screen and recorded air temperature in the screen and substrate temperature at a depth of 1 cm.

2.8 Laboratory work

Several experiments were carried out in an artificial indoor environment which had been purpose built for the study of snakes. It comprised an arena of 2.2 x 1.7 metres with a Panasonic (Model WV-1550/B) video camera positioned 2 metres from the ground pointing down at the arena and focused to include the entire floor surface of the arena. The recorder (Model NVto include the entire floor surface of the arena. The recorder (Model NV-8050, with timelapse facility) and television were in a separate room , so the snakes could be viewed without disturbance. Main ambient light consisted of 5 ft 'Truelight' strips; these and other domestic bulbs were controlled by time switches to mimic required light conditions. Basking lamps were provided and also controlled by time switch. Infra-red lamps were left on at all times during video experiments so that any nocturnal activity could be observed.

2.9 Data analysis

Most of the data handling and analysis was achieved using IBM and compatibles running a variety of programs. Raw data was kept in a Lotus 123 spreadsheet from where it could be examined, manipulated and exported directly for statistical analysis by Statgraphics v2.1 . Graphs and charts were drawn using Statgraphics, Symphony, Harvard Presentation Graphics and Lotus Freelance. Grant data loggers were unloaded using a program supplied specifically for that purpose and the data could be imported directly into the spreadsheet for subsequent analysis. The thesis was prepared and typed using PC Outline and Word Perfect v5.1.

Chapter Three
Ranging Behaviour

3.1 Introduction

The concept of home range has no generally accepted definition; Gregory et al (1987) noted six different terms used for the definition of home range. Jewell (1966) defined home range as "...the area over which an animal normally travels in pursuit of its routine activities." It should not be confused with territory, which is an area defended to some extent against intruders, particularly conspecifics, but is rather the area in which an animal spends the bulk of or all of its time. In this work, Jewell's definition has been accepted and the term 'home range' will be used will be used to define the area covered by each snake over a stated period of time, but will exclude short excursions made by individuals, for instance when foraging in an area not normally used by them.

Home range calculation can explain a great deal about the general ecology of an individual, population or species. The movement of grass snakes from one location to another throughout the season involves the expenditure of energy and may expose individuals to an increased risk of predation; it is reasonable therefore to assume that movements are made for reasons which can be explained by some facet of the ecology of that animal. This tenet applies to the behaviour of both individuals and populations. Brown & Parker (1976) showed that a population of Coluber constrictor (Colubridae) migrated over 0.5km from a communal over-wintering den to a summer area and in the same study referred to an individual female who used the same migration route and summer range over two consecutive years. Use of separate summer and winter areas has been shown to occur in several snake species including the colubrids Storeria dekayi (Noble and Clausen, 1936) and Thamnophis sirtalis (Gregory & Stewart, 1975) and Vipera berus Viperidae (Prestt, 1971).

Events connected with reproduction have also been shown to have an effect on the ranging behaviour of reptiles. The search for mates will clearly influence the behaviour of breeding individuals. For example, Madsen (1984) observed increased movement in male grass snakes, N.natrix, during the breeding season, and Viitanen (1967) and Prestt (1971) both reported extensive and frequent movements by male adders V.berus at this time. However, changes in the ranging behaviour of females have been connected with reproductive condition in a variety of studies; Shine (1979) reported that females of five out of six elapid species studied aggregated when gravid. Similarly, Reinert & Zappalorti (1988) found that the ranges of male and non-gravid female Crotalus horridus Viperidae had constantly shifting activity areas with low overlap, whereas the ranges of gravid females were more static, closer to the over-wintering site and maintained a higher degree of overlap.

The search for egg-laying sites (Madsen, 1984; Natrix natrix), the effects of feeding (Fitch & Shirer, 1971; Crotalus horridus) and the search for food and a suitable habitat (Christian & Tracy, 1985; Conolophus pallidus Iguanidae) have also been demonstrated to influence the ranging behaviour of reptiles. It is evident that scrutiny of the movement patterns of a population of animals can elucidate information concerning the ecology of not only the population and individuals under investigation, but also of the ecology of the species.

It is apparent, even from the few examples outlined above, that there will be seasonal differences in the ranging behaviour of an animal. Clearly, an animal that is highly active during the breeding season may show more tenacity to a more frequently used or core area within it's range over part or all of the remainder of the annual cycle. Few previous reptile studies have attempted to examine this difference in ranging behaviour over time, although this is largely because the tracking periods of individuals has been relatively short and precluded time series analysis. Furthermore, conventional range analyses such as those outlined below, which are used in most home range studies fail to consider the sequence of locations and view ranges merely as the use of space by an individual over the tracking period. Brown & Parker (1976) and Madsen (1984) examined monthly ranges which revealed that the snakes they studied maintained several more or less distinct within-season ranges. This basic extension of a somewhat crude analysis introduces time as a component of range analysis and reveals much more detail about the structure of the range than analysis of space use alone. The technological advances made in the field of radio-tagging over recent years have resulted in smaller tags with an increased field life and further work in this area is now possible, even on small reptiles where miniaturisation of the tags is important.

Since the development of cheap miniature radio-transmitters and to some extent, before this time, much attention has been paid to home range analysis as a tool to help explain the distribution of animals. For the most part, this has been limited to descriptive work on the size, shape and range overlap of single species, with little thought being given to the biological relevance of the information thus obtained (eg. Barbour et al, 1969; Madsen, 1984). A search of the existing literature has revealed no reptile studies which examine the utilisation of space within a range; such information may be a useful indicator of habitat selection and may even expose a degree of range separation where the overlap component of the total range is high, as shown by Samuel et al (1985) in a study of tanagers.

Jenrich & Turner (1969) examined the use of conventional sampling data to estimate the area of an animal's home range and concluded that different methods are not directly comparable. Furthermore, until recently (Munger, 1984), no studies have even acknowledged the difference between ranges constructed by animals moving in a random fashion and animals that show tenacity to a site or are territorial, and have assumed that by merely joining the external points of a range to provide a determinate area, such an area can be meaningfully described. More recently though, home range analysis has advanced into a more sophisticated science, largely because changes in the way in which ranges are calculated have been developed with biological relevance in mind.

The various methods of analysis have been explained in detail elsewhere (Kenward, 1987) and it is not proposed to examine them in great detail here, but it is worth looking briefly at the methods that have been seriously considered for use in the present study, focusing on their strengths and weaknesses.

i). Convex polygon analysis: This involves drawing the smallest possible convex shape around all of the fixes in a range. It has the advantage of being simple and does give a broad representation of the area over which an animal has moved. It has been used in many home range studies, both on snakes and mammals (Brooks & Banks, 1971; Haroldson & Fritzell, 1984; Laundre & Keller, 1984 and many others). However, single outlying fixes can greatly increase the area of the polygon, thereby overestimating the true range of the animal. Furthermore, the computed range will include large areas over which the animal never travelled. This method of calculation is rather better suited to the ranges of animals which are territorial or have periodically shifting ranges and in these cases overlaid ranges can separate neatly.

ii). Harmonic mean analysis: Most animals do not use their entire range with equal intensity, focusing instead on one or more favoured areas. This method was developed (Dixon & Chapman, 1980) in attempt to remove the extreme effect of single outlying fixes and to examine range utilisation as well as mere size and shape. Rather than calculating the arithmetic mean of the fixes to calculate their geographic centre, it uses the reciprocal of all fixes (the harmonic mean), thus weighting outliers to a lesser extent. Having calculated the harmonic mean, isolines can be drawn about this centre (or centres) showing the percentage probability of finding the animal within a stated percentage area. Any percentage can be calculated, but the higher percentages are likely to be more useful and 50%, 70% and 90% are most commonly used. Several "centres" may be simultaneously shown within the same range using this method, which would be particularly relevant perhaps for either a raptor which may have both a nest site and one or more hunting areas or roosts, or an animal which has a summer and a winter site, such as the adder, Vipera berus (Prestt, 1971). The resulting isoline plots can be overlaid onto maps to provide a very impressive graphical representation of the calculated ranges. The percentage isolines shown by plots of the results can also provide explanations of range use as with Samuel's (1985) work on tanagers. Reinert & Zappalorti (1988) found a strong positive correlation between the length of time Crotalus horridus were tracked and the area within the 95% isopleth, indicating that the core area (ie. most used part of range) expanded with time. Disadvantages with the method are that "unrelated" fixes tend to influence the isolines, pulling them out of shape, and fixes can be omitted from the range area altogether. Worton (1987), in a comparison of range estimation methods, found the use of harmonic mean analysis unreliable.

Multinuclear cluster analysis: A further refinement of the previous method eliminates the effect of unrelated fixes by treating each identifiable cluster of fixes separately and at present appears to be the most biologically appropriate technique for multinuclear range analysis. Within range polygons are formed by taking each fix in turn and placing it mathematically in the same polygon of fixes as its' nearest neighbour. Kenward (pers. comm.) recommends this analysis for accurate range calculation, in preference to the more established harmonic mean method.

All three methods have application in the study of grass snake ranging behaviour. Observation of the snakes during this research tended to indicate that grass snakes did not hold territories, thus apparently making polygon analysis redundant, but such analysis is useful for two reasons. Firstly, it is the same method used by Madsen (1984) and the results can therefore stand direct comparison with his. Secondly, several ranges can be calculated for the same animal for different periods throughout the year and each of the ranges overlaid to examine possible patterns in area utilisation throughout the season. Such calculations could be made using the other methods, but the resulting maps would be very confused and difficult to interpret.

Harmonic mean analysis and multinuclear cluster analysis are both more applicable to range utilisation in grass snakes as they both allow adequately for analysis of home range areas with one or more favoured sites. Movement of the snakes was difficult to predict in practice, but all of the tagged animals returned to a previously visited site or sites, in some cases more than once; this is discussed in Chapter 6. Furthermore, it would be expected that activity at and around the overwintering site in early spring and late autumn and any migration to a summer site would be clearly shown, as such areas would show up on the plots as distinct cores, since there would be a large number of fixes (assuming one fix per day) in close proximity to each other and the multi-nuclear method of calculation would tend to group these separately. Both of the methods can show such range formations graphically.

The internal structure of home ranges can be clarified further by analysis of the utilisation distribution of a range (Haynes, 1949). This is allied to the concept of core areas within a range, and involves progressively calculating the reduced range area as outlying fixes are excluded. Assuming 100% of the fixes comprises 100% of the range, the method then calculates the percentage of the total area used by decreasing percentages of the total fixes. If core areas are well developed and surrounded by a few distant fixes, it would be expected that the slope of a plot of range area against the number of fixes used will initially be steep as outliers are excluded and the calculated range rapidly decreases in size. The two plots in Figure 3.1 show hypothetical examples of two different range types. The first shows the utilisation distribution plot of a range for an animal that has a den or nest which it leaves to forage in only a few areas and the second shows a plot for a range where each fix or location is equidistant from the next (ie. systematic block design).

Range overlap can explain to some extent the intraspecific interactions within a population and has been examined in a number of mammal, amphibian and lizard studies. Conspecifics whose ranges exhibit a low degree of

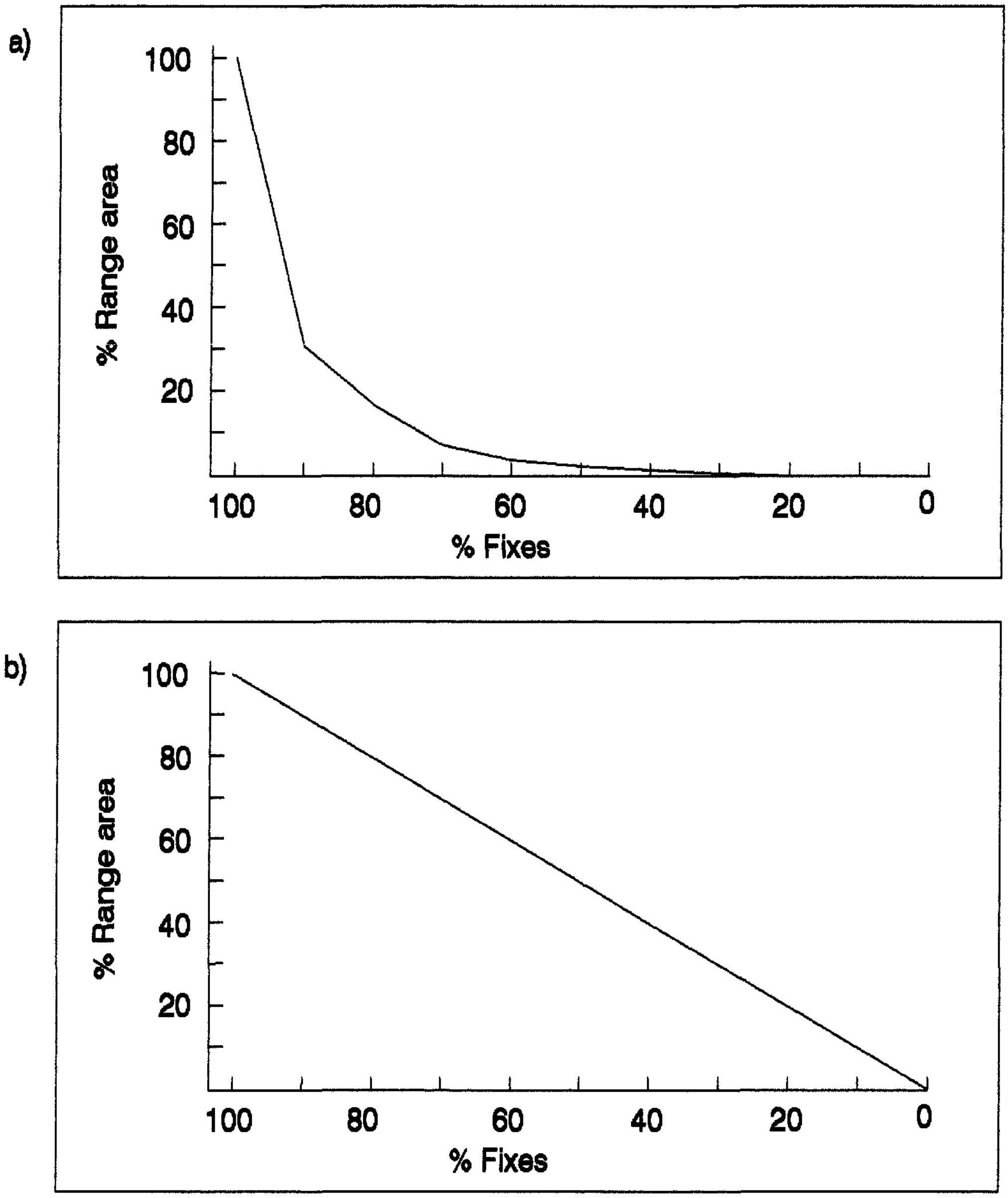


Figure 3.1 Models of two hypothetical utilisation distributions.

a) Plot of a range in which the radio-tracked animal has a den or nest, and a small number of foraging sites or habitually visited areas, from which it rarely strays. Note how 90% of the fixes are located in only 30% of the total range area and 50% of the fixes in perhaps 2-3% of the area.

b) Plot of a range in which locations (fixes) are equidistant over the entire range. Note how the percentage area used only decreases slowly as outlying fixes are excluded.

Utilisation distribution calculation is particularly suitable for use with multi-nuclear cluster range analyses as the latter already exclude areas not used by the radio-located animal.

overlap are presumably competing for some resource and maintaining a more or less exclusive territory in which to obtain that resource. Munger (1984) compared the observed overlap of Phrynosoma lizard ranges to the overlap of the same ranges placed randomly with respect to one another and showed that overlap between conspecifics was reduced, and suggested that competition for mates was a driving influence behind this behaviour. Similarly, Cloudsley-Thompson demonstrated that African geckoes, Tarentola annularis were always found alone behind artificial covers, suggesting either territoriality or an avoidance of occupied sites. A lack of both aggression and inter-sexual variation suggested that concealment was the driving influence for this behaviour and not direct competition for resources. No data could be found in published literature for the overlap of snake ranges.

Such behaviour may only be evident for part of the annual cycle of a species; Prestt (1971), in a study of Vipera berus in Southern England, showed that both males and females occupied individual laying out areas immediately after spring emergence and that there was very little overlap between individual areas until breeding began.

Conversely, aggregation has been demonstrated in several snake species, particularly amongst both sexes together at communal overwintering sites (Prestt, 1971, Vipera berus; Brown & Parker, 1976, Coluber constrictor; Madsen, 1984 and pers. obs., Natrix natrix) and amongst gravid females (Gregory, 1975, several species; Madsen, 1984 and pers. obs., N. natrix).

The purpose of this chapter is to analyse the use of space by free ranging grass snakes. Home ranges have been calculated and compared between both sexes and individuals. The internal structure of ranges and site tenacity of individuals has been examined. Monthly ranges have been calculated to examine any changes in ranging behaviour over the course of a season and finally, the range overlap of the radiotracked snakes has been investigated to examine for the presence of intraspecific influences on ranging behaviour in the species.

3.2 Methods

3.2.1 Data collection

Of sixteen individuals tagged in 1988 and 1989, one died after 7 days, one was lost after 13 days and two were caught at a different site and introduced into Chilworth. The remaining twelve have been used in the calculations for this chapter. The tracking period varied from 24 to 313 days and involved six snakes in 1988 and seven in 1989. In addition, one female was tagged late in 1988, overwintered with the tag in situ and followed throughout the subsequent season.

Although all of the snakes were usually located more than once each day, only the night-time location of each individual has been used in calculating the range and the utilisation distribution. The number of fixes taken during each day varied depending on the weather, the number of animals being tracked, the nature of the research at the time and the activity of the snakes on each day. However, snakes were always located at the end of each day and early the following day, so the overnight location was always known.

When a snake was located, great care was taken not to disturb it, even if that meant not seeing it and thus foregoing the collection of some data; this was not always possible and any disturbance was recorded so that analysis could be carried out to examine any effect this may have had on the movement of the animals. The location of each snake was established by measuring the distance and bearing from the snake to a known mapped point. In this way the position of the animal could be subsequently recorded onto a map to an accuracy of one metre.

Independence of consecutive fixes has proved to be a major problem when collecting data for home range and habitat use analyses and it is important to collect such data methodically. Independence requires that the location of each fix is not influenced by the previous fix. For instance, a day spent recording many fixes for the same snake will bias the range utilisation analyses, as closely grouped locations will be shown as a separate nucleus. In this case, the snake may have only spent a short time in that particular area, which could in theory form part of a larger nucleus or in the case of a moving snake, merely be part of a 'corridor', as the snake moves from one nucleus to another. Unrecorded or missing data will have a similar effect. In theory, the requirement for independence is satisfied if each fix is distant enough in time for the snake to have made a significant movement (relocation), even if the snake did not do so. The data presented below represent one fix per animal per day, taken at the end of the day at the night refuge. The use of one fix per day is acceptable because the 24 hour period between fixes is long enough to allow the animal to move to a different area, but eliminates the possibility of including brief excursions away from the normal area.

3.2.2 Range analysis

In this study, two methods were used for the calculation of the ranges of tagged grass snakes: convex polygon analysis was chosen for a number of reasons: firstly, it is simple and provides a good quantitative and graphical representation of home range; secondly, the results obtained can be compared with other studies which have used the same method; finally, for management and conservation purposes, it is important to know the size of the entire area over which an animal moves, even if only a small part of that range is used intensively.

Multi-nuclear cluster analysis was used in preference to harmonic mean analysis because it was felt to be more accurate in estimating the area of ranges than the latter. Nuclei within a range are shown as separate convex polygons within a total polygon and are more likely to exclude areas not visited by an individual. The method is not perfect since two or more apparently distinct clusters which contain a common fix will inevitably be grouped into one cluster or 'core' area. This notwithstanding, the areas delineated by the method are more likely to be accurate representations of the use of space within a range than those derived from harmonic mean analysis and for this reason, if for no other, the method is to be preferred.

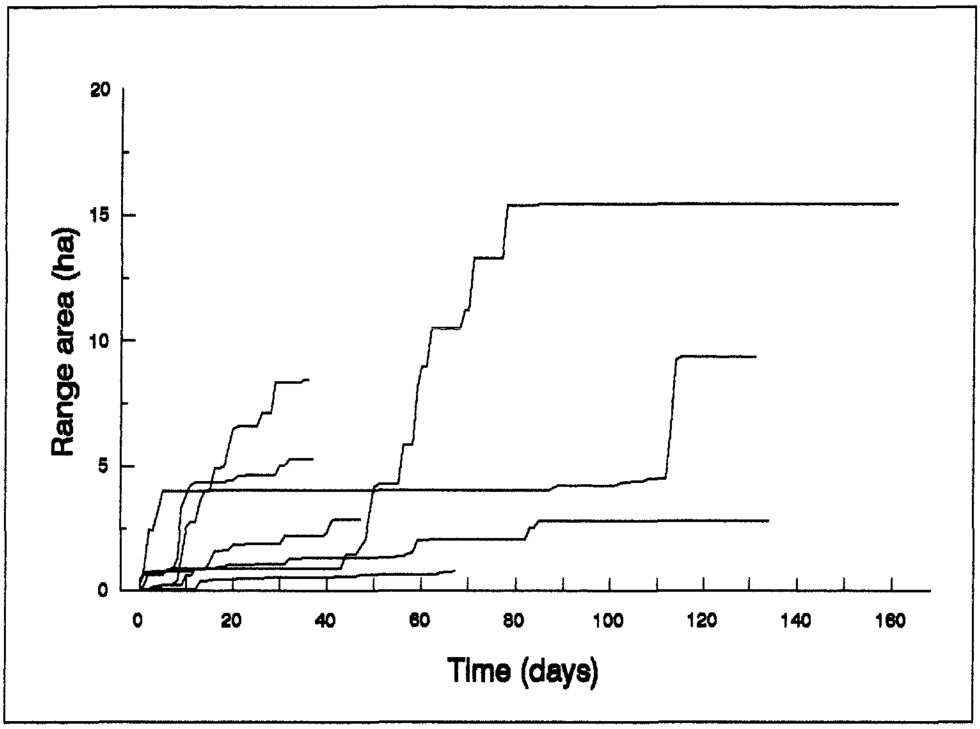
Analyses were performed using the "Ranges IV" program (Biotrack, Wareham), a purpose built movement and habitat analysis package. Only one location per day was used in an effort to eliminate increases in range size caused by brief forays outside the "core" area. In this way, the area with the densest fixes will be the area in which the animal is most likely to be found.

3.2.3 Range and utilisation distribution

The purpose of these analyses is to examine not only range size, but to explore the use of space within the observed ranges. In order to achieve this, the total range has been calculated for each snake for the entire period over which they were tracked, using both of the methods outlined. The convex polygons plotted show the maximum area over which the snakes moved during this period and provide a simple index of vagility over this time. Further investigation of the use of this range is provided by multi-nuclear analysis, which reduces this area into smaller polygons which illustrate quantitatively how the snakes use the total range.

Further examination of range use explores how the extent of movement varies over time and uses only convex polygon analysis. If the snakes use space to a varying degree over the course of a season, it may be expected that observed ranges will be smaller during times of reduced activity. The interval over which to measure such ranges can either be predetermined or can have some relevance to the biology of the animal. Madsen (1984), in his study of Natrix natrix used calendar months as units for dividing the season, although Kenward (pers. comm.) rightly states that this method pays little regard to the biology of the snake and he favoured instead either dividing the season into ecologically relevant periods (e.g. pre-mating, post-mating, oviposition, etc.) or choosing a time that is commensurate with the use of distinct within-range areas or periods of intensive movement by the snake such that if range size is plotted against time, one or more asymptotes will be exposed; such periods could in practice prove to be more or less analogous to the formation of nuclei shown by multi-nuclear analysis. Rose (1982) used this method in a study of Sceloporus virgatus and showed that 80% of home range was exposed after 18 sightings of the lizard. Figure 3.2 shows plots of range size over time for N. natrix at Chilworth in 1988 and 1989 and although asymptotes can clearly be seen, there is great variation in the time these take to occur for each individual. Use of these for calculating within-season range formation is therefore rejected.

The other biologically relevant method is also difficult to use because of the uncertainty of and variation as to exactly when ecologically 'relevant' periods begin and end. Emergence, mating and oviposition all take place over a period of weeks within both the species and within a population (pers obs); for instance emergence in New Forest grass snakes may have commenced 2-3 weeks before the Chilworth population as sightings of emerged grass snakes were reported before Chilworth snakes in 1987, 1988 and 1989 (Noble, pers comm; pers obs) and mating was observed at Chilworth over a period ranging from 7th April (1988) to June 11th (1989). A possible mating also occurred on 25th August, 1988 (Yapp, pers comm) although when caught, a cloacal



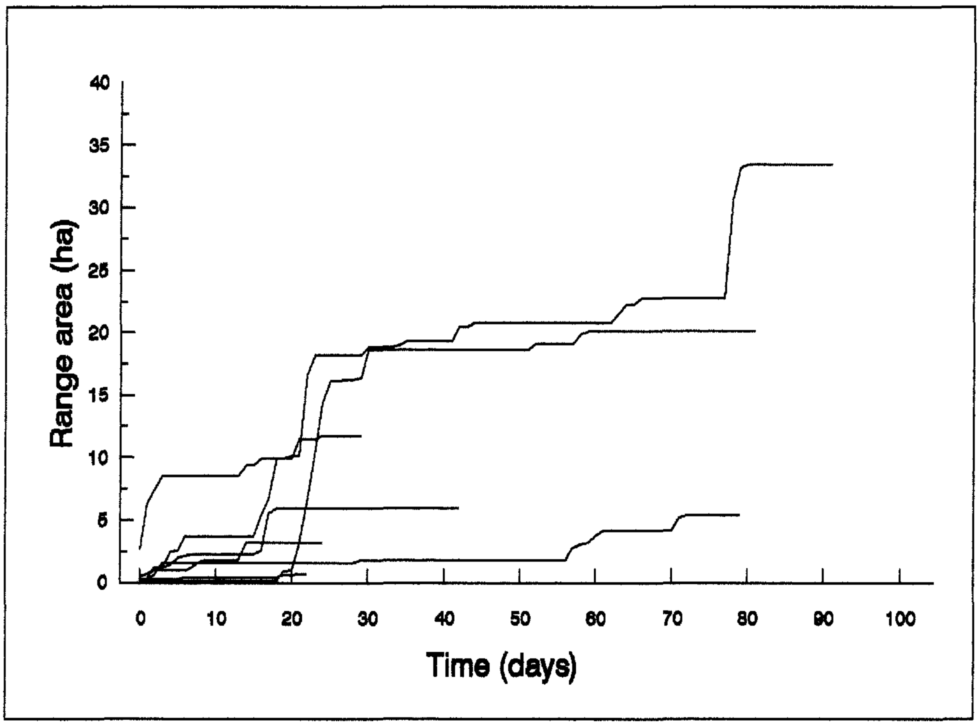


Figure 3.2 Plots showing the increase in calculated range size (minimum convex polygons), as consecutive daily fixes were included. Each graph shows similar plots for each individual radiotracked.
a) 1988
b) 1989

smear taken of the female showed no evidence of sperm. The beginning and end of events such as the emergence and breeding periods are difficult to detect in the field except in the broadest sense. Furthermore, no radio-tracked females bred during either 1988 or 1989. This makes accurate division of the season into ecologically relevant periods somewhat difficult and therefore this method too was rejected. Although the use of time lacks ecological relevance, it will be used in this study; the method is simple, objective and has substantive relevance to the management and conservation of the species by workers in the field. Analysis of movement data (see Chapter 4) meant that it was still possible to examine the relationship of movement over a season in an ecologically relevant context. Calendar months will be used and data that does not cover a full months tracking for each individual snake will be excluded. This length of time is considered long enough to minimise or eliminate the effects of abiotic variables that have an effect on the vagility of the snake, particularly periods of low temperature, during which mobility is much reduced.

Because of differences in the weather between 1988 and 1989, some of the data for the two years will be examined separately. The hot, dry summer of 1989 contrasts sharply with the cooler, wetter summer of the previous year and caused changes in movement and habitat use that were evident in the field. This will be examined in further detail in Chapter 4 of this thesis.

3.2.4 Range overlap

Overlap analysis was carried out on both total and monthly ranges in this study for all snakes and all months for which a full set of data had been obtained. Total and monthly overlap matrices were first calculated using minimum convex polygon analysis to provide a gross evaluation of the distribution of the snakes during a season and 100% multi-nuclear cluster overlaps were subsequently calculated to examine possible changes in ranging behaviour through time.

3.3 Results

3.3.1 Range size

Multiple convex polygon (MCP) and four multi-nuclear convex polygon (MNCP) range size calculations for radio-tagged snakes are shown in Table 3.1 and maps showing the areas in Figures 3.3 & 3.4.

(a)

Snake	n	MCP	100% MNCP	95% MNCP	90% MNCP	70% MNCP
111	135	8.60	0.95	0.13	0.02	0.00
141	41	4.68	1.72	0.07	0.06	0.00
181	71	0.61	0.13	0.03	0.02	0.00
1161	40	7.45	3.68	0.41	0.01	0.00
122	165	2.39	1.83	0.02	0.00	0.00
172	51	2.52	0.76	0.08	0.06	0.00
192	167	14.53	3.52	0.74	0.12	0.00

(b)

Snake	n	MCP	100% MNCP	95% MNCP	90% MNCP	70% MNCP
21	26	0.54	.09	0.07	0.00	0.00
31	52	5.85	1.11	0.03	0.02	0.00
51	33	11.69	11.69	1.11	1.02	0.00
12	123	33.49	10.20	0.61	0.12	0.00
32	82	5.3	5.30	1.66	0.32	0.03

Table 3.1 Length of tracking period in days (n), minimum convex polygon (MCP)and four multi-nuclear polygon (MNCP) areas (ha) for implanted snakes.
(a) 1988
(b) 1989.

There was no significant correlation between MCP area and the length of the tracking period for 1988 (r^2= 0.44, n=7, p>0.05) or 1989 (r^2=0.63, n=5, p>0.05). Nor was there a significant correlation between the length of the tracking period and the 100% multi-nuclear areas (MNCP's) area for either year (1988: r^2= 0.16, n=7, p>0.05; 1989: r^2= 0.41, n=5, p>0.05). When the data were combined there was no significant correlation ($r^2= 0.04$, $n=12$, $p>0.05$). The MCP areas for each of the two years were not significantly different when tested with a Mann-Whitney procedure ($U=0.487$, $n_1=7$, $n_2=5$, $p>05$); nor were the 100% MNCP areas significantly different ($U=0.974$, $n_1=7$, $n_2=5$, $p>05$). It is possible therefore, that some assumptions can be made which refer to data from both years.

The following maps (figures 3.3 [a]-[g] & 3.4 [a]-[e]) illustrate Chilworth study site showing the MCP and 100% MNCP ranges of all implanted snakes resident at the site. The shaded areas of the maps show areas calculated by the Multi-nuclear Convex Polygon (100%) method. These, together with the area within the dotted lines constitute the Minimum Convex Polygon.

Key

Dw	Deciduous wood
Cw	Coniferous wood
Mw	Mixed wood
Gg	Grazed grassland
Ug	Ungrazed grassland
Mg	Managed grassland
W	Wet grassland
Fg	Formal garden
P	Pond
A	Arable land (cereals)
C	Cultivated (tree nursery)
S	Stream
B	Built environment
━	Roads
●	Overwintering sites. All known sites are shown on the maps, but note that they do not necessarily refer to the snake ranges plotted.

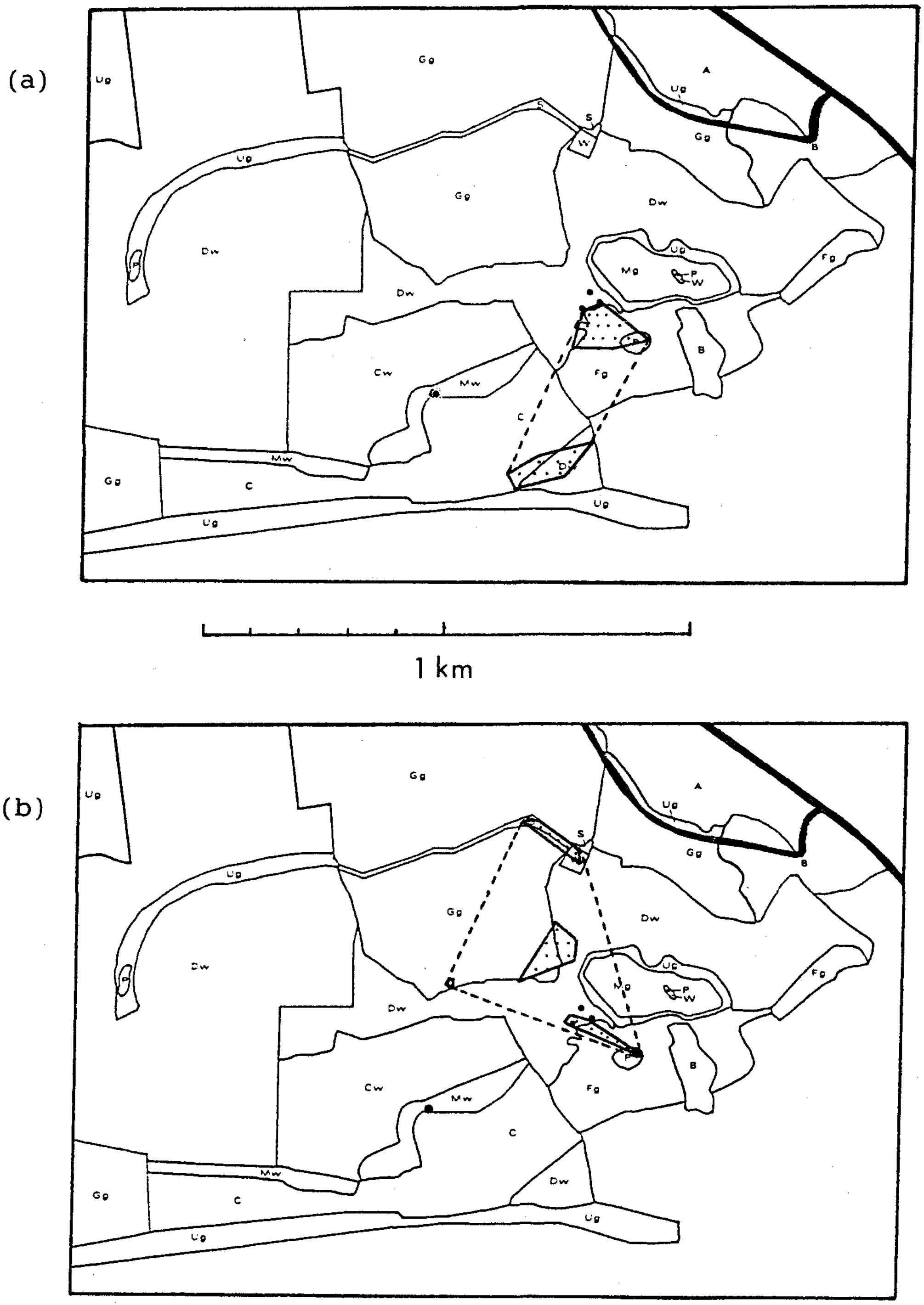


Figure 3. 3 MCP and MNCP ranges for implanted snakes.

Year: 1988
(a) 141
(b) 111

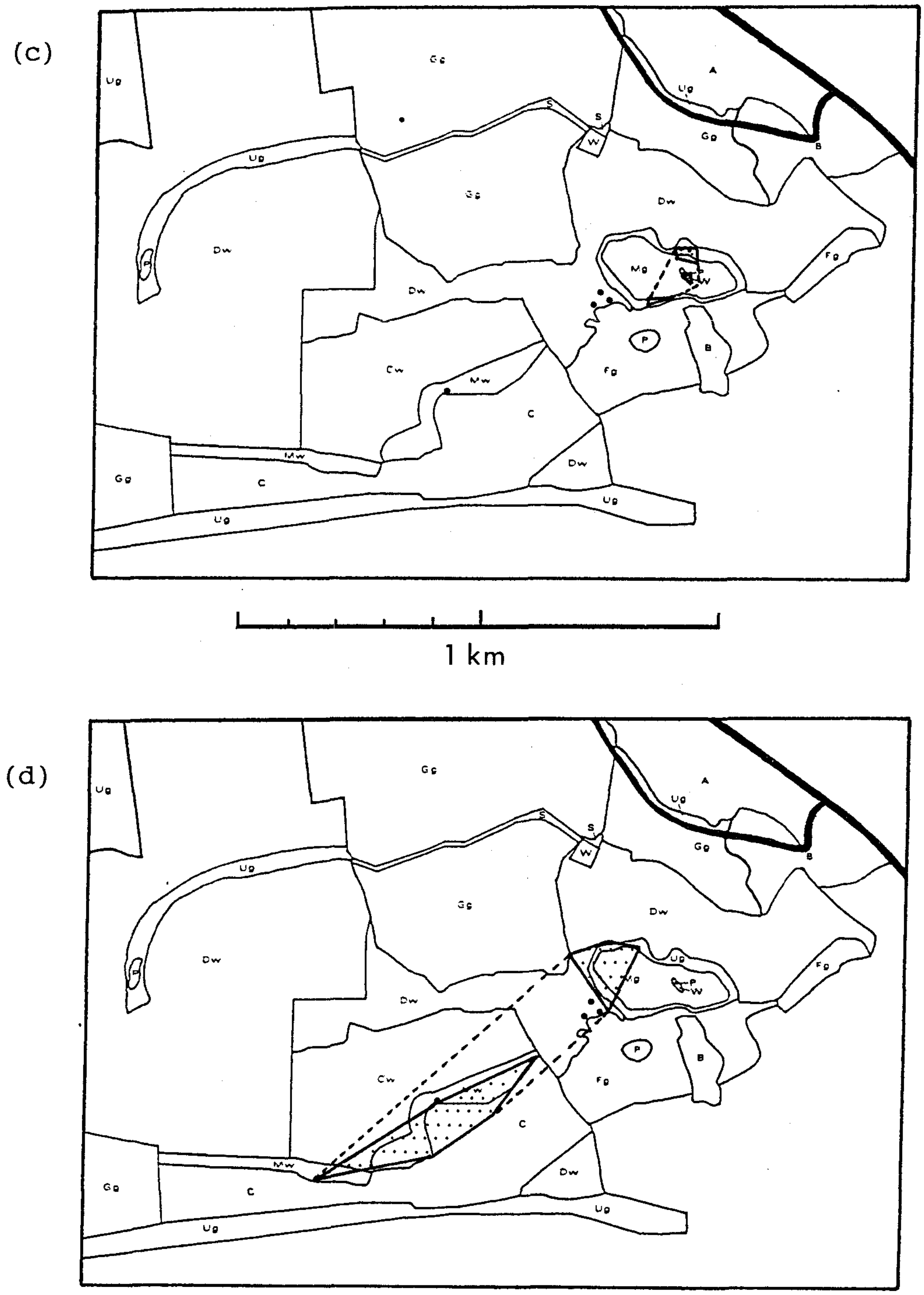


Figure 3.3 MCP and MNCP ranges for implanted snakes.

Year: 1988
(c) 181
(d) 1161

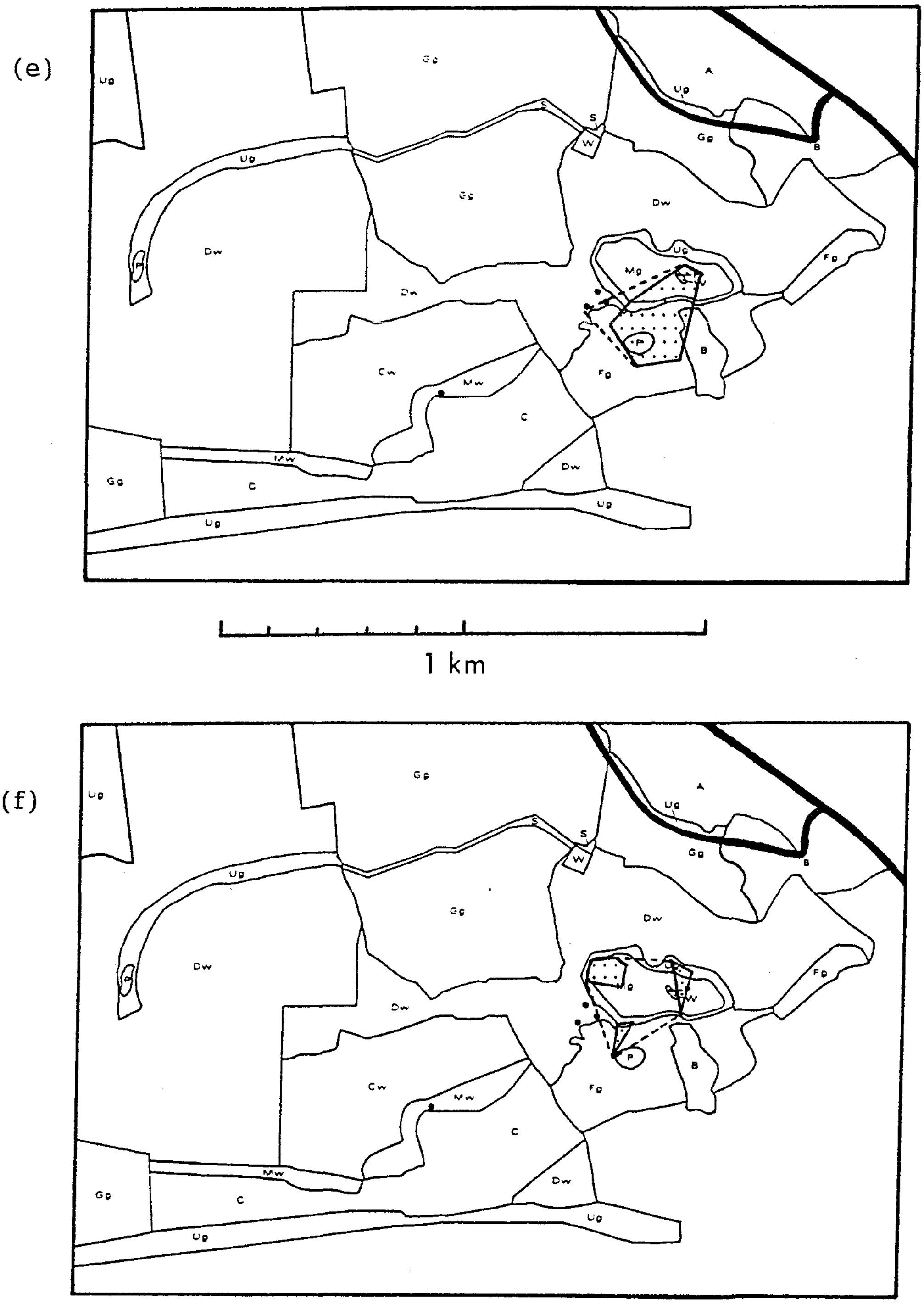


Figure 3.3 MCP and MNCP ranges for implanted snakes.

Year: 1988
(e) 122
(f) 172

(g)

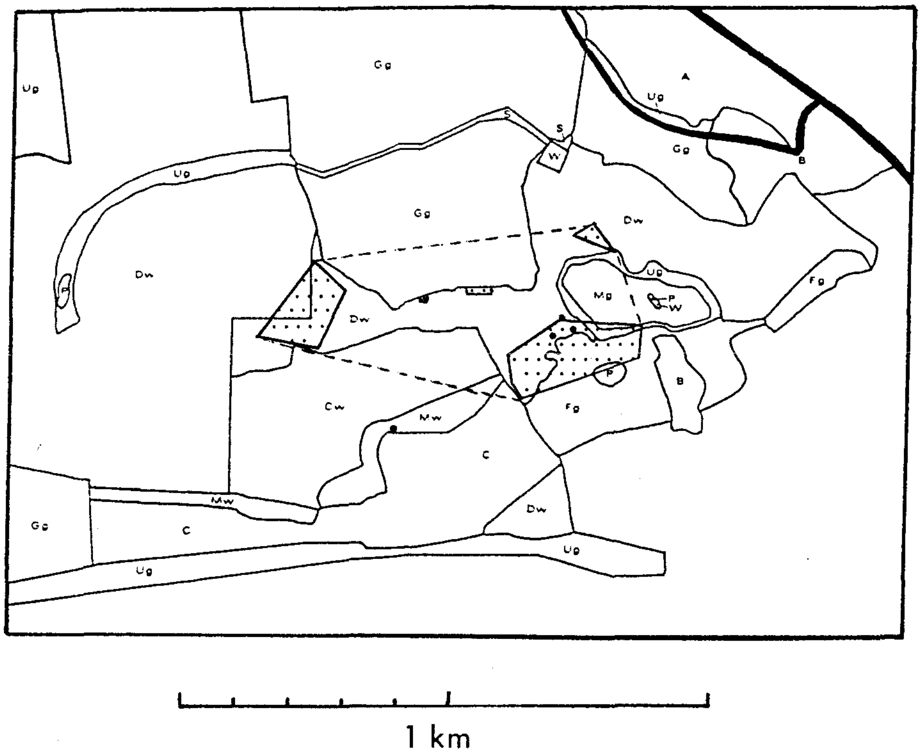


Figure 3.3 MCP and MNCP ranges for implanted snake.

Year: 1988
(g) 192

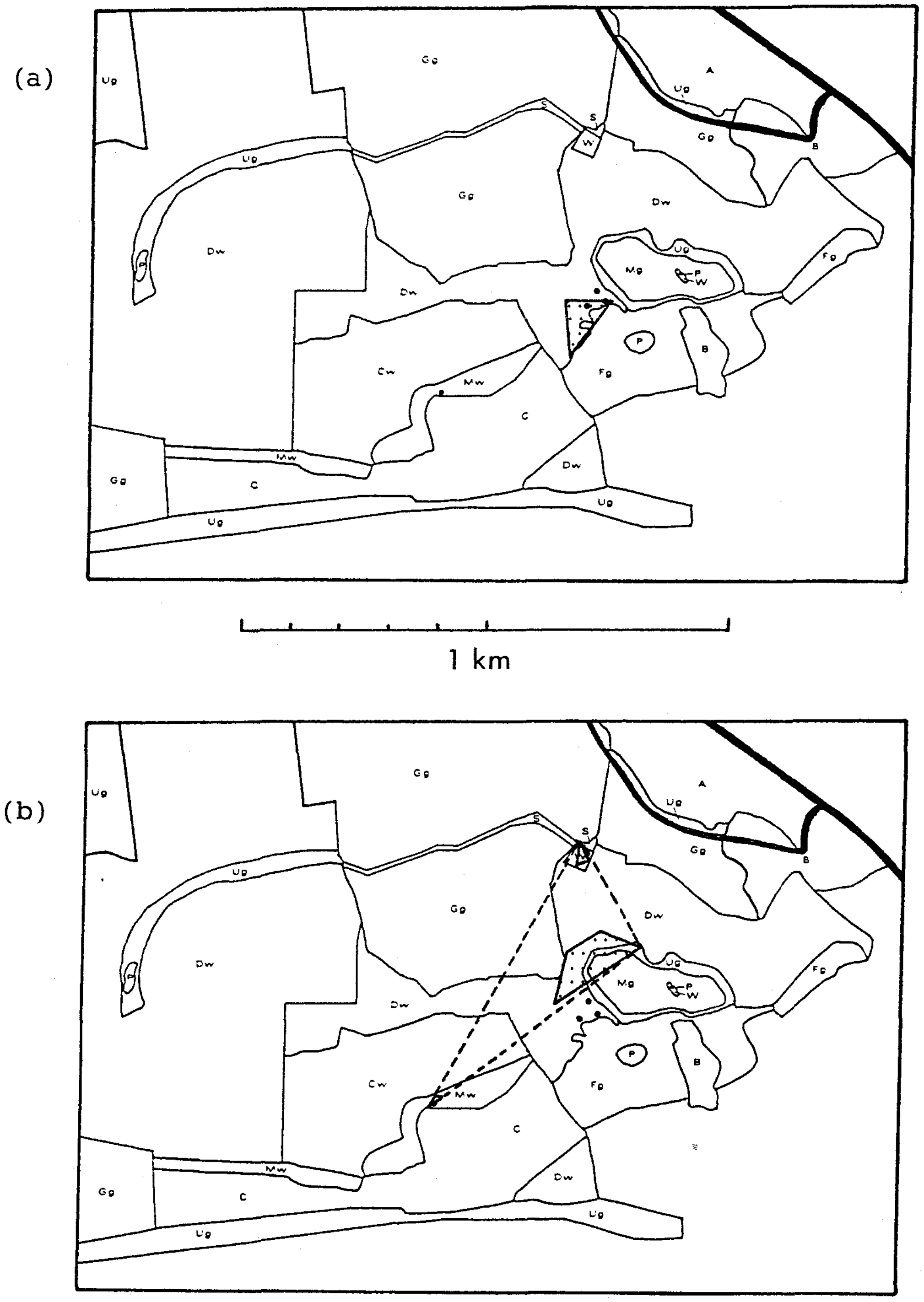


Figure 3. 4 MCP and MNCP ranges for implanted snakes.

Year: 1989
(a) 21
(b) 31

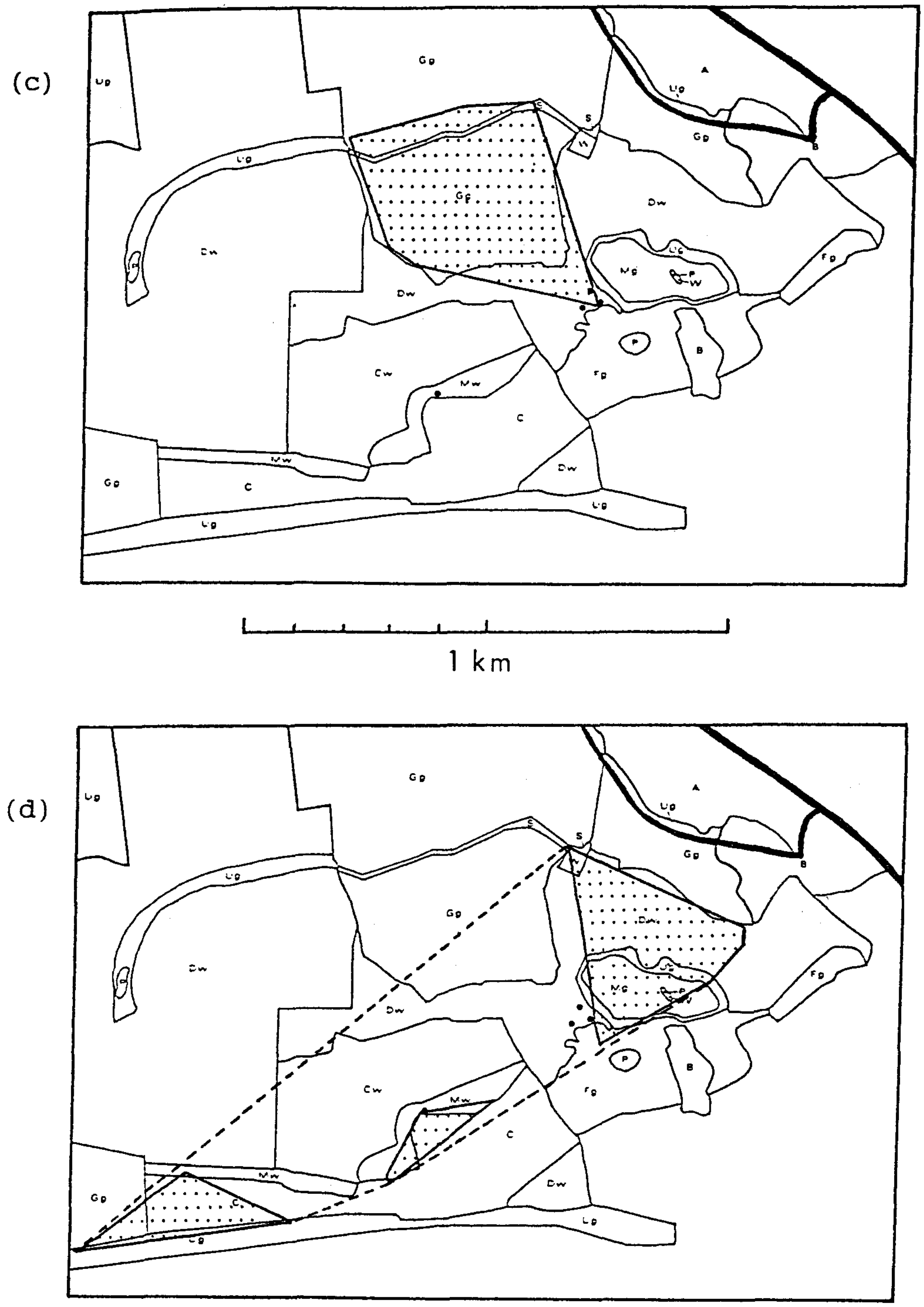


Figure 3.4 MCP and MNCP ranges for implanted snakes.

Year: 1989
(c) 51
(d) 12

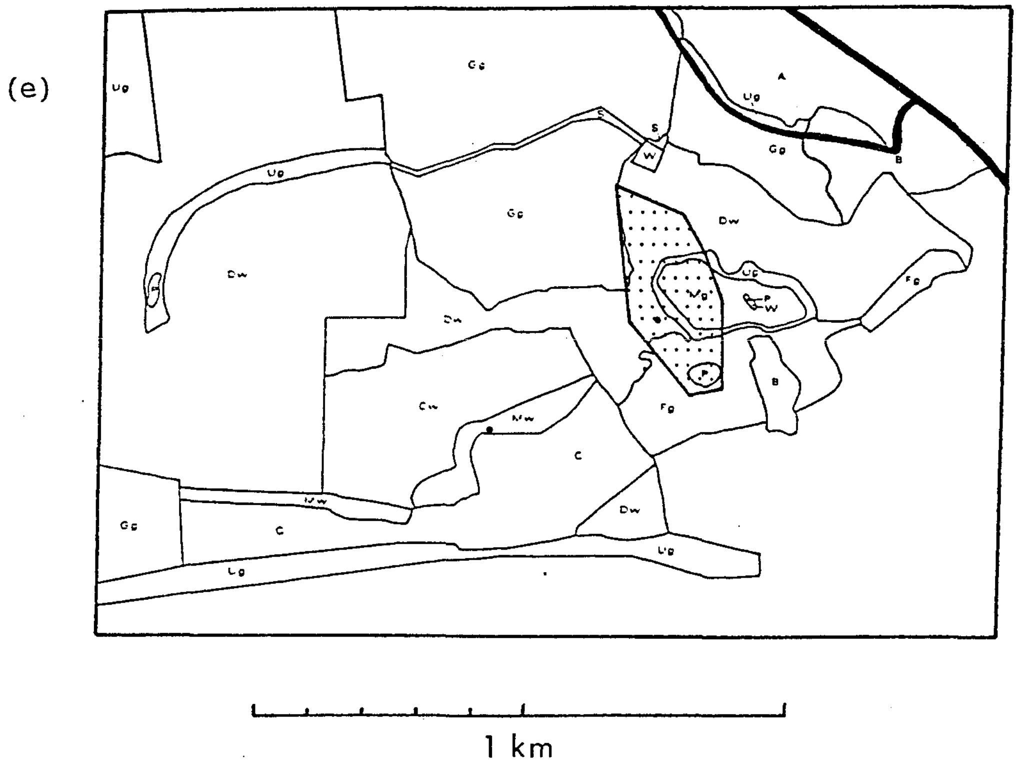


Figure 3. 4 MCP and MNCP ranges for implanted snake.

Year: 1989
(e) 32

The great variation in the MCP size between individuals both between and within year and sex categories follows no apparent pattern. The snout-vent lengths and weights are shown in table 3.2; these were analysed in turn to test for a significant correlation between either MCP or MNCP and the weight or length of either females or males (1988 & 1989 data combined); the results are shown in table 3.3.

(a)

Snake	S.V.L. (cm)	Weight (g)
111	54	73
141	48	76
181	60	107
1161	46	97
122	77	160
172	78	172
192	73	123

(b)

Snake	S.V.L. (cm)	Weight (g)
21	49	73
31	52	84
51	62	107
12	77	192
32	79	183

Table 3.2 Weight and snout-vent length of tagged snakes.
(a) 1988 (b) 1989

Male MCP/SVL	$r=0.23$, $n=7$, $p>0.05$.
Male MNCP/SVL	$r=0.47$, $n=7$, $p>0.05$.
Female MCP/SVL	$r=0.28$, $n=5$, $p>0.05$.
Female MNCP/SVL	$r=0.05$, $n=5$, $p>0.05$.
Male MCP/weight	$r=0.21$, $n=7$, $p>0.05$.
Male MNCP/weight	$r=0.02$, $n=7$, $p>0.05$.
Female MCP/weight	$r=0.24$, $n=5$, $p>0.05$.
Female MNCP/weight	$r=0.49$, $n=5$, $p>0.05$.

Table 3.3 Correlation co-efficients of MCP and 100% MNCP with snout-vent length and weight of tagged snakes.

The size of male and female MCP and 100% MNCP ranges were not significantly different from each other when the two years were combined (U=0.487; n1=7; n2=5; p>0.05 and U=0.974; n1=7; n2=5; p>0.05 respectively).

The other point worthy of consideration from these analyses concerns the nuclei or core areas shown by the multi-nuclear technique. Not only are the number of clusters in each range of interest, but the position of these clusters relative to each other and with relevance to the nature of the habitat and to time.

Statistical analysis of core areas is difficult both because of the small sample size and because ranges were calculated for individuals over different times of the year and two separate seasons; however, some general observations are note-worthy. Furthermore, the MNCP method, although valuable, fails to consider time and is thus a purely mathematical interpretation of the data. What follows is a brief examination of the data, using 100% MNCP's and field notes and observations taken during the research, with particular emphasis on patterns that have been identified.

Of the 12 ranges analysed here, 9 of the 100% MNCP's lie in part directly over a known overwintering site. This would be expected of snakes that initially emerged at these sites and remained there until movement began in spring. However, snakes 1161, 51 and 32 were caught and tagged in August, June and May respectively and their overwintering sites are not known. The remaining three animals all had core areas that were close to known overwintering sites.

Seven animals were caught and tagged at an overwintering site in early spring; the snakes were torpid and easily caught and it was assumed that they were at or very close to their own winter refuge. Of these seven, six (111, 141,122, 192, 31 and 12) left the site during spring and did not return (except in one case in passing) throughout the active period. Snakes 111 and 192 returned in autumn, and were presumably preparing to overwinter at the site; snake 192 was again captured early the following year at the same site. Snake 111 was killed by a predator at this site and 122 suffered a similar fate whilst apparently moving in the direction of the overwintering site late in autumn.

The number of nucleii (core areas) was small in all cases. Snakes 111 and 192 had four and five respectively, including in each case one that was a single location at which the snakes sheltered from cool and rainy weather conditions and in the case of snake 192, one series of nearby locations that were used while the snake was sloughing and consequently relatively inactive (see Chapter 4: Movement and activity). Excluding these special cases, the number of nucleii was three in six cases, two in a further three cases and one in the remaining three. In the instances where more than one nucleus is evident, 100% of the observations were made in areas markedly smaller than the MCP for each individual (see table 3.1). Further analysis of this 'utilisation distribution' is presented below. In the three instances where the 100% MNCP equals the MCP, two were of male snakes that were tagged over relatively short periods of 26 and 33 days and one was of a female that was tagged throughout May, June and July of 1989.

In every case except one of the three exceptions referred to above, the nucleii of the tagged snakes were areas in which other snakes were seen during 1988 and 1989, although not necessarily at the same time. In most cases, these other snakes were grass snakes although adders, V. berus were also much in evidence. Even from the maps of the tagged animals (Figs. 3.3 & 3.4), it is clear that some areas are apparently favoured by the snakes, whilst others are rarely, if ever visited.

As an adjunct to the data collected from the snakes which were implanted with tags, several were fitted with external tags at Chilworth in 1987. The tracking period for these was necessarily limited by the battery life of the tags and the potential damage that could be done to the snake by leaving the tags in situ for extended periods. Multi-nuclear analysis would reveal little except that the snakes move and is clearly inappropriate. Caution must also be excercised when making observations that pool data from implanted and externally fitted tags. Eight snakes were externally tagged and details of the snakes, tracking periods and observed ranges are shown in Table 3.4.

Snake	Sex	Duration (days)	Range (ha)
C 2	M	23	15.88
C 3	M	25	11.96
C 4	F	17	1.20
C 5	F	58	27.75
C 6	M	6	0.01
C 9	F	16	3.31
C 10	F	17	1.44
C12	F	6	0.03

Table 3.4 Tracking location and Minimum Convex Polygon area of externally tagged snakes in 1987.

No statistically significant difference was found between the MCP areas for externally tagged snakes and those of implanted snakes from either year (1988: $U=0.289$, $n_1=8$, $n_2=7$, $p>0.05$; 1989: $U=0.289$, $n_1=8$, $n_2=7$, $p>0.05$).

3.3.2 Utilisation Distribution

The utilisation distribution plots for implanted snakes are shown in Figure 3.5. As outlying fixes are progressively excluded from the analysis, the range area reduces markedly, until effectively reaching zero after exclusion of some 30% of fixes. An animal that used its' range with equal intensity would have a shallow decline that approached zero with a small percentage of fixes remaining. The notably steep decline in the initial stages of outlier exclusion indicate that most fixes of every individual are to be found within a very small area. This is more remarkable since the 100% area is the already reduced MNCP area, which itself identifies core areas. The 95% and 90% areas (Table 3.1) were tested using a one sided Wilcoxon Signed Ranks test against 95% and 90% of the 100% MNCP area and were found to be significantly smaller (90%: $n=12$, $T^+=3.12$, $p<0.001$; 95%: $n=12$, $T^+=2.86$, $n=12$, $p<0.01$). The data shown in Table 3.1 shows utilisation distribution data numerically by area down to the 70% level and it is clear that the percentage chance of finding a snake within a very small area is very high.

3.3.3 Monthly ranges

The monthly ranges (MCP) of all implanted snakes for which at least one full months data was collected are shown in Table 3.5 (a)-(b) and maps of the four snakes tagged for the longest periods in Figures 3.6 (a)-(d).

The small sample size prevented extensive statistical analysis, but a plot of median monthly range size (sex and year data pooled) is shown in Figure 3.7. The graph suggests that ranges are largest in May and reduce as the season progresses. The sample size for April is low because tagged dir snakes were not generally ready for release at this time. However, both of the snakes (one male, one female) tracked at this time showed very limited movement and remained close to their emergence sites. No snakes were ever caught away from the two overwintering sites until several weeks after the emergence period had started; the very low range figure shown for April is therefore almost certainly an accurate representation.

The maps shown in Figures 3.6 (a)-(d) demonstrate that monthly ranges for each individual demonstrate a great deal of overlap. Furthermore,

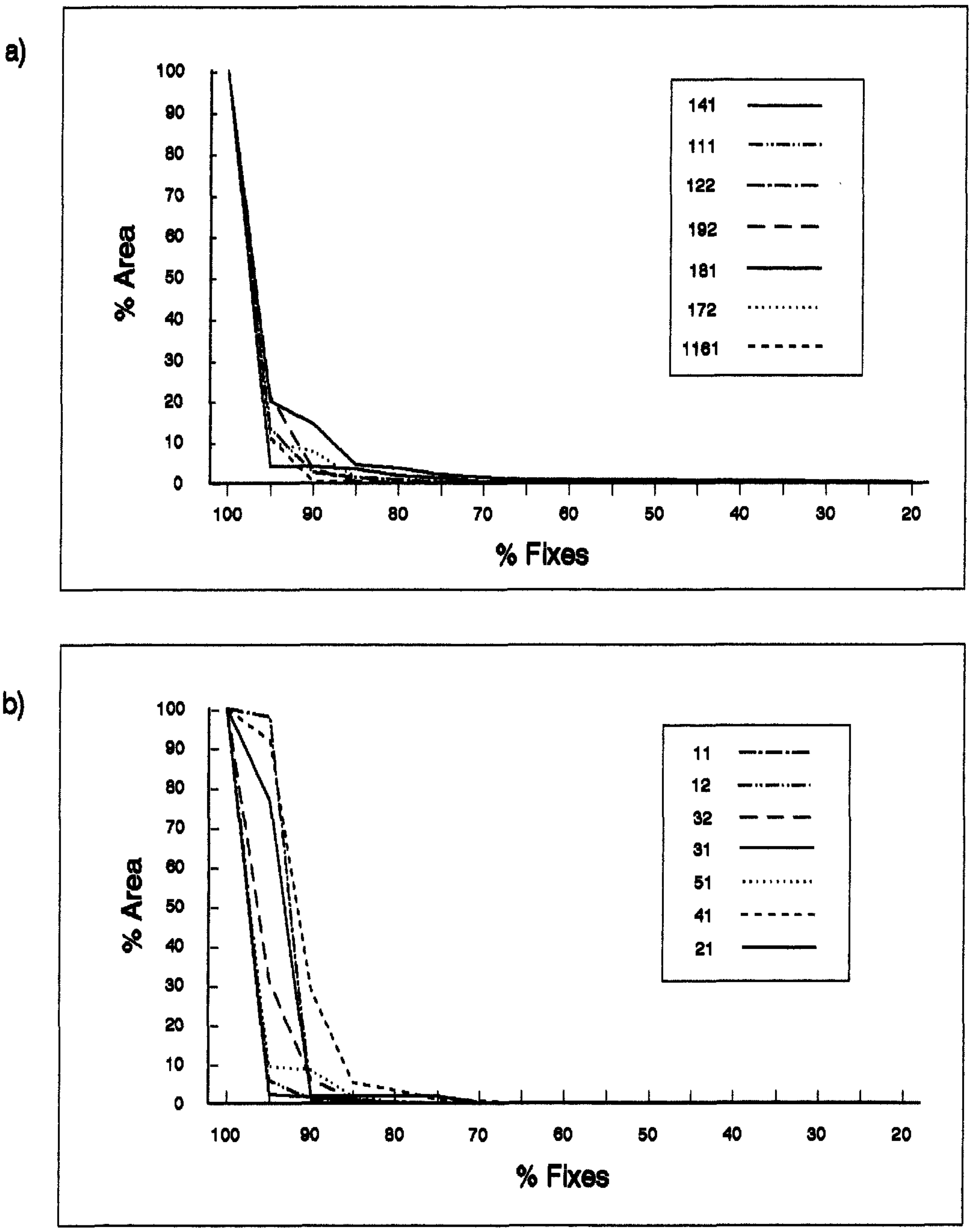


Figure 3.5 Plots of the utilisation distribution of tagged snakes.
a) 1988
b) 1989 (includes plots for 2 introduced snakes).

Snake	Apr	May	Jun	Jul	Aug	Sep
111	-	3.39	0.11	1.23	2.0	0.88
141	-	4.07	-	-	-	-
181	-	0.36	0.12	0.2	-	-
122	0.12	0.19	0.29	0.0	0.38	0.0
172	-	-	0.97	-	-	-
192	-	0.67	2.84	11.35	0.69	0.35

Table 3.5 (a) Monthly ranges (MCP) of implanted snakes (1988).

Snake	Apr	May	Jun	Jul
32	-	1.48	0.51	-
12	0.00	18.82	5.83	6.61
31	-	5.69	-	-

Table 3.5 (b) Monthly ranges (MCP) of implanted snakes (1989).

certain areas appear to form a more or less central 'zone' about which the animals base their movements. The western half of the managed meadow and the adjacent woodland, just northeast of one of the over-wintering sites was used by several individuals at various times throughout the year. Field observations showed that the unmanaged edges of the meadow were very frequently used by grass snakes and the meadow was often crossed from the southern to the northern edge by both tagged snakes and by other individuals observed in the field.

Three snakes (111, 192, 122) were all apparently preparing to overwinter at the same site as the previous year; all three were tagged until October, when snakes 111 and 122 were predated and snake 192 was removed from the field to have the tag removed.

Figure 3.6 (a-d) The following two pages show maps of Chilworth showing the monthly MCP ranges of four implanted snakes for periods of between 3-6 months from April to September.

Key

Dw	Deciduous wood
Cw	Coniferous wood
Mw	Mixed wood
Gg	Grazed grassland
Ug	Ungrazed grassland
Mg	Managed grassland
W	Wet grassland
Fg	Formal garden
P	Pond
A	Arable land (cereals)
C	Cultivated (tree nursery)
S	Stream
B	Built environment
╱	Roads
H	Overwintering sites. The site marked in each case relates specifically to the mapped individual.

Key to ranges

April —··—··—··—··—	May ———————	June ·····················
July — — — — — — — — — — ·	August —·—·—·—·—·—·—·—	September ·································

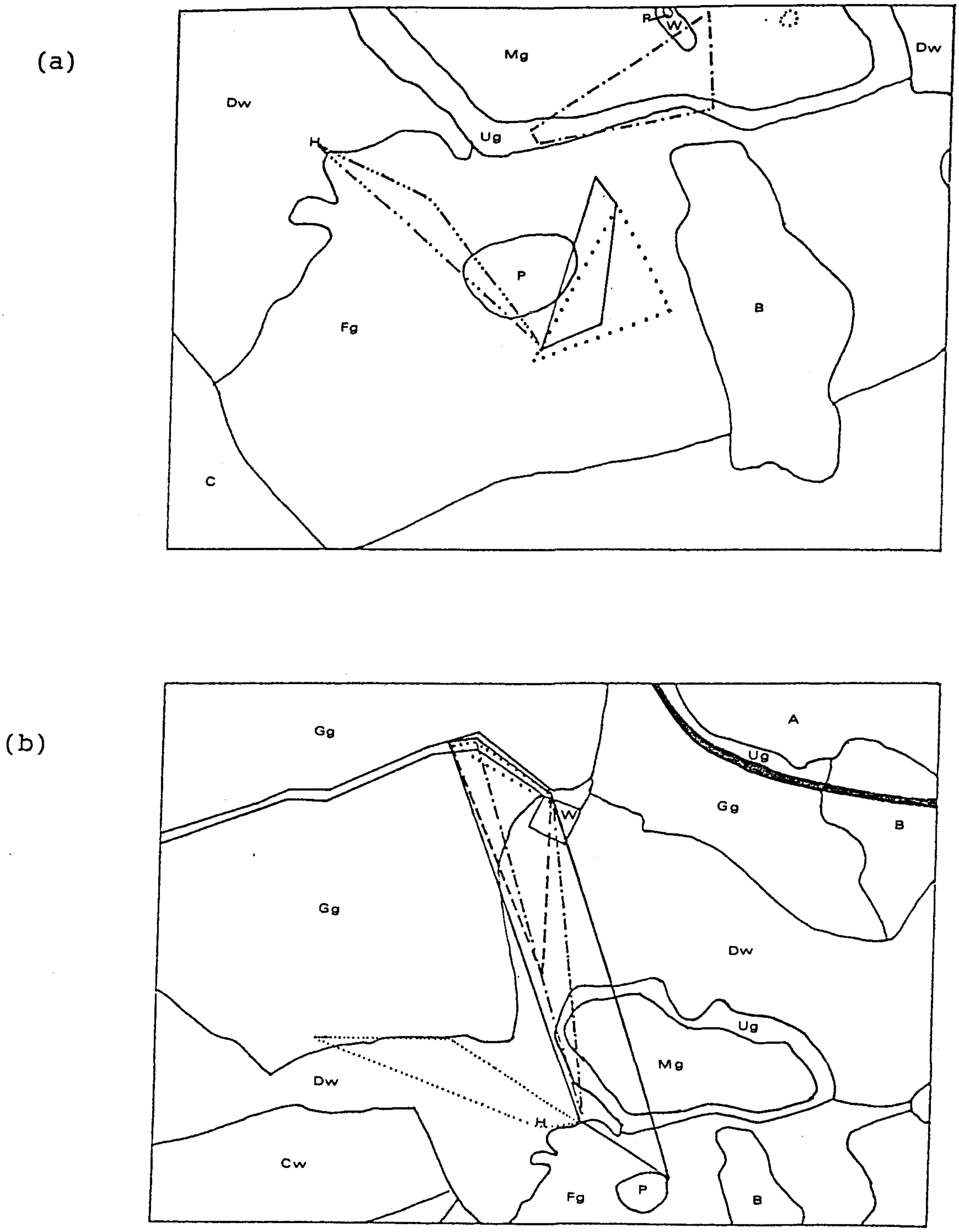


Figure 3.6 Monthly ranges (MCP's) of implanted snakes.
(a) 122 (1988)
(b) 111 (1988)

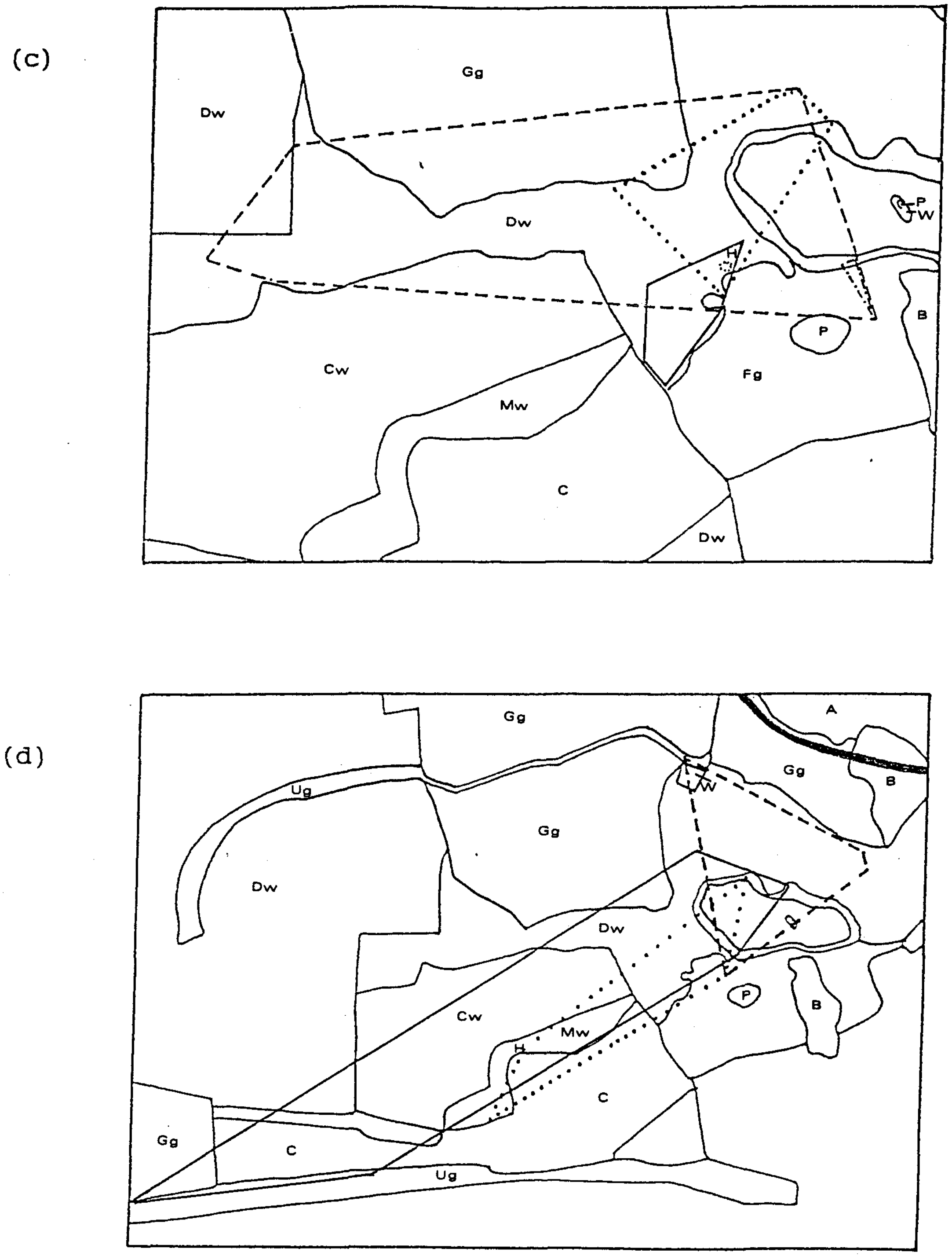


Figure 3.6 Monthly ranges (MCP's) of implanted snakes.
(c) 192 (1988)
(d) 12 (1989)

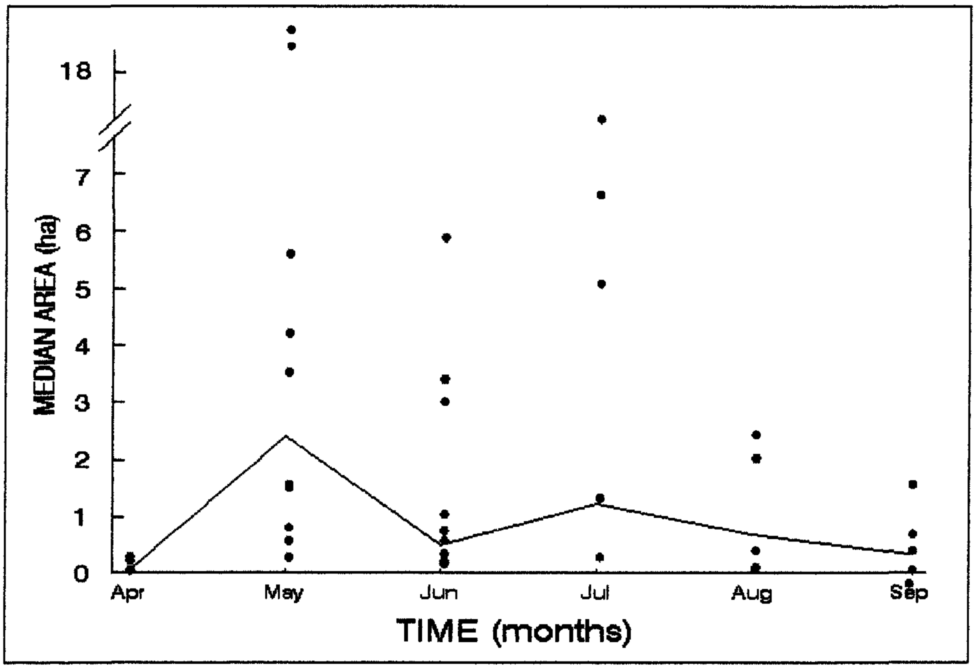


Figure 3.7 Plot of median monthly ranges (MCP's) of 11 tagged snakes. Markers show ranges of individual snakes.

3.3.4 Range overlap

Overlap matrices for the MCP ranges for 1988 and 1989 are shown in Table 3.6. It is evident that there is considerable overlap of ranges; however the mechanisms behind this are less clear. If the snakes are using common areas, which is true in part at least, (ie. overwintering sites), then the overlap could be merely random. It is probable that the snakes made use of specific types of habitat such as hedges and woodland edges. This being so, a high correlation may be expected between range size and degree of overlap on other ranges and this was indeed the case. Data for 1988 and 1989 were analysed separately and pooled and in each case range overlap showed a very high correlation with size of MCP range (1988: $r=0.933$, $n=7$, $p<0.001$; 1989: $r=0.972$, $n=5$, $p<0.0001$; both years: $r=0.96$, $n=12$, $p<0.0001$).

The situation though is complex for a number of reasons: firstly, an unknown number of other grass snakes were active in the area and interaction with these animals cannot be quantified; secondly, a high correlation is still possible even with animals positively interacting with each other, thirdly the MCP method includes large areas never visited by snakes and finally, because the method used ignores time.

(a)

	141	1161	172	192	111	122	181
141	-	2.5	3.4	24.0	5.2	14.0	0.0
1161	11.8	-	9.1	53.4	25.2	1.2	0.0
172	6.1	26.9	-	64.2	42.6	39.9	24.2
192	8.2	28.5	11.0	-	36.0	8.0	0.6
111	3.1	22.1	12.7	59.5	-	7.2	0.1
122	27.0	3.0	42.0	45.6	25.1	-	11.9
181	0.0	0.0	99.3	13.8	0.8	46.1	-

(b)

	21	51	32	12	31
21	-	1.8	75.4	99.4	0.0
51	0.0	-	9.5	43.5	18.9
32	8.1	22.2	-	83.0	39.0
12	1.9	15.1	13.4	-	18.5
31		37.3	34.6	100	-

Table 3.6 Range (MCP) overlap matrices for tagged snakes. Range areas in rows are overlapped by those in columns. The data shown represents the range of each snake for its' entire tracking period.
(a) 1988
(b) 1989

Matrices of core areas (100% MNCP) for 1988 and 1989 are shown in Table 3.7. Overlap percentages are noticeably lower, although still significant. Further analysis is difficult because of deficiencies in the MNCP calculation method. Although a single map of core areas for all animals for each year is not presented here, it is evident from the series of maps shown in Figures 3.3 & 3.4 that considerable overlap takes place in 'common' areas as stated previously. This is likely to be a result of habitat selection (eg. for prey abundance or for concealment and thermoregulation) rather than the maximisation of intraspecific interactions. A matrix of 90% MNCP core areas showed overlap in only 25% of ranges and it should be remembered that time was not included in the analysis, so spatial 'overlap' may have occured at different times of the year.

(a)

	141	1161	172	192	111	122	181
141	-	0.1	4.1	57.1	10.7	17.3	0.0
1161	0.0	-	10.4	1.1	0.0	0.0	0.0
172	8.8	51.1	-	20.8	4.26	23.6	11.2
192	28.5	2.0	5.0	-	7.0	16.5	0.6
111	20.1	0.5	3.5	22.7	-	8.4	0.0
122	16.1	0.0	10.1	31.6	4.5	-	1.7
181	0.0	0.0	61.8	9.8	0.0	18.0	-

(b)

	21	51	32	12	31
21	-	11.0	76.7	8.5	0.0
51	0.0	-	9.5	0.2	3.1
32	1.8	21.2	-	38.1	20.3
12	0.3	0.3	19.9	-	5.9
31	0.0	32.1	95.7	49.6	-

Table 3.7 Range (100% MNCP) overlap matrices for tagged snakes. Range areas in rows are overlapped by those in columns (a) 1988; (b) 1989).

3.4 Discussion

3.4.1 Range calculation and methodology

Researchers who embark on the measurement of the home range of an animal are faced with three fundamental problems. The first of these is the definition of home range and the suitability of a particular definition for the animal under investigation. Implicit in most definitions of home range is the concept of a home base which makes up the 'centre' of an area in which an animal moves and the assumption that an animal will move within a relatively stable area around that centre (Tiebout & Cary, 1987). As these authors state, definitions such as these are not appropriate for many snake species.

The second problem is that of time and the period over which to measure home range (see Gregory et al, 1987). Many home range studies have been of relatively short duration and most have been less than one season, particularly those using telemetry as a means of locating animals. Furthermore, if an animal uses two completely different areas in subsequent years, what then is the home range? It may be that home range becomes stable after only a short period and that an animal will cover its' entire range after only a short time (eg. Rose, 1982) and that the range size can be accurately estimated after only relatively few locations. The plots in Figure 3.2 suggest that this is not the case for Natrix natrix, as range size often continued to increase with time in an unpredictable manner.

The third problem is the range calculation method. Each method has limitations which lead to an inaccurate calculation of the area used by an animal. The most popular method and one that is used in this study (Minimum Convex Polygons) over-estimates the area used by an animal, by including large areas that an animal never visited. Correction factors have been used (Jenrich & Turner, 1969) in some studies (eg. Reinert & Kodrich, 1982; Goddard, 1984) in an attempt to compensate for the variation in sample sizes, but this seems to be inappropriate for snake studies, where the relationship between sample size and range size is variable. Multi-nuclear methods (Harmonic Mean and Cluster analysis) circumvent the problem of unused areas, but take no account of the order of locations and inevitably group together nuclei with a common location. As a result of these and other problems connected with data collection methods, comparison between studies is often inappropriate.

It is contended here that the first two of these problems are of little importance and that the objective of a study such as this (to study the

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It is contended here that the first two of these problems are of little importance and that the objective of a study such as this (to study the observed in this study. It is likely that this is because of the different habitats in which the studies were carried out. Madsen's study area consisted of open, grazed fields surrounded by stone fences (in which the snakes were usually located), whilst the habitat at Chilworth consisted on the whole of less open habitat, with much denser ground cover. The linearity of Madsen's habitat would inevitably lead to the formation of larger ranges, assuming an equal degree of activity of his snakes with those in this study.

Multi-nuclear Cluster analysis of the ranges (Table 3.1) showed that the areas actually used (as opposed to traversed) by the snakes were much smaller than the MCP area. The 100% Multi-nuclear Cluster Polygons (MNCP) include every fix, including outliers and in all but two cases, reduced the measured (MCP) range significantly. As outlying fixes are progressively excluded, the calculated range area reduces dramatically in all but one case until at the 70% area (ie. the area in which 70% of fixes are to be found) is smaller than the resolution of the mapping technique, and will equal $1m^2$ for each remaining different location. The plots of utilisation distribution show this clearly (Figure 3.5).

The reduction in MNCP areas is significantly more pronounced than would be expected by chance; what this shows is that the vast majority of the calculated home range areas are completely unused or used only transitorily. Snakes often stayed in one place for considerable periods (up to three weeks) and for a number of reasons. Firstly, they rarely moved during rain or on cool overcast days, presumably because a high body temperature would be difficult to reach (see Chapter 5). Secondly, during the period before sloughing or after feeding, little or no movement took place (see Chapter 4). Thirdly, movements around the overwintering sites during spring and autumn were usually limited. On other occasions, no reason could be readily identified why an individual became sedentary, although if a snake has no reason to move, selection will clearly favour those who neither waste energy nor risk predation.

Snakes often returned to a previously used area and refuge rapidly and more or less directly and the distances involved were sometimes large (up to 350m in one day). This phenomenon has been reported for several species of snake, notably the garter snake, Thamnophis sirtalis (Fitch & Shirer, 1971) and the adder, Vipera berus (Prestt, 1971; pers obs). The use of favoured areas presumably confers benefits such as opportunities for concealment and may also have advantages such as escape from predators (Stickel & Cope, 1947; Prestt, 1971) and improved thermal opportunities (Chelazzi and Calzolai, 1986).

Prestt (1971), Gregory and Stewart (1975) and Brown & Parker (1976) have reported the use of distinct summer and winter ranges for V. berus, T. Sirtalis and Coluber constrictor respectively and there was some evidence of such behaviour by snakes in this study, although it was not evident in every individual. Snakes 111, 141 and 181 both left their overwintering site and moved over 200m in one day to new sites at which they remained, in one case (111) for most of the rest of the active season. Snake 31 may also have shown such behaviour, but was lost shortly after moving. All of these snakes were male and all were radiotracked from the beginning of the active season at their overwintering sites. The overwintering site ranges and subsequent 'new areas' can be seen on the range maps in Figure 3.3. This apparent pattern was confounded by male snakes that were radiotracked only during the middle and latter part of the season. These snakes did not show tenure to any particular site and ranged widely. No data was available for these animals up to the autumn submergence period as one was killed by a dog or fox (1161) and in 1989, fieldwork was terminated at the end of July.

These observations differ from the other studies mentioned in that the 'summer ranges' of the animals observed in this study were distinct from each other, whereas both T. sirtalis, C. constrictor and V. berus populations moved to a communal summer area some distance from the overwintering site (V. berus, 500m and 1200m (two sites); C. constrictor 663m to 781m (females and males) and T. sirtalis, 10.7km (both sexes). The observed seasonal movements by N.natrix were considerably smaller, averaging 200m.

It would appear that such seasonal movements are made by snakes in search of food resources, as feeding only takes place in the summer areas. However, in this study, the main food source of grass snakes, the toad Bufo bufo, was apparently widespread over the study area and two snakes were observed feeding at an overwintering site and several more that had recently eaten were observed in this area. Of the seven snakes that were initially tagged and released at the overwintering sites, only one (192) returned there during the middle part of the season except in passing, although other grass snakes were occasionally observed in these areas. Of three snakes which were tagged for almost the whole of the 1988 season, two returned in the autumn (111 and 192) and one was moving in that direction when it was killed by a predator (122). It would appear from this that the same overwintering sites are used from year to year. Snake 192 was subsequently caught in spring 1989 at the overwintering site.

Female snakes showed less site tenure than did the males. Although females left the overwintering site at approximately the same time as males, there was no apparent movement to a summer area. However, the 100% MNCP ranges each contained only a small number of nuclei for all snakes, regardless of sex. Furthermore, since there was no difference between sexes in the 100% MNCP range areas, the observed differences in ranging behaviour are difficult to quantify and could potentially be coincidental.

During the course of the study, grass snakes (tagged or untagged) were only rarely seen together away from the overwintering sites although grass snakes and adders were observed basking on top of one another. This differs from the observations of Phelps (1978), who reported observing mating grass snakes away from summer sites. On the few occasions that grass snakes were found together, the reason appeared to be because the habitat offered a particularly good thermal environment. On one occasion, three grass snakes were found under one piece of tin; on another, two tagged snakes spent several days in the same tree stump (see Chapter 5) and at a known egg-laying site (not at Chilworth), five snakes, including two males were found under a plastic sheet on a compost heap.

It is possible, therefore, that summer dispersal could be a mechanism for minimising intraspecific interactions and thereby maximising the availability of resources. This possibility is investigated in Chapter 7.

3.4.3 Monthly ranges

Few obvious patterns emerged from the calculated monthly ranges, although the small sample sizes in some months mean that assumptions about the data set must be cautious. Figure 3.7 plots the median monthly ranges, which show pronounced peaks of range size in May and July. These peaks are extended if means are plotted as some very large ranges are included in the calculation.

The plot of monthly ranges (Figure 3.7) shows a peak of range size (MCP) in May as the snakes dispersed from the overwintering sites. These ranges are large because they include both the overwintering site and the areas to which the snakes moved. Table 3.5 shows that individual snakes tended to cover large areas during this time but in June ranged much less widely. The reduction in June range areas not only marked the end of the spring 'migration' away from the overwintering sites, but a contributory factor could have been that the snakes first sloughed and fed during this period and both of these activities led to a reduction in movement and therefore ranging (see Chapter 4).

Ranging in July was variable between the six snakes tagged, ranging between 0-11.35 ha (both female snakes). During July in both seasons, snakes were actively foraging and the variation in range size may have been connected to the availability of food. The largest range observed during this time (192: 11.35 ha) was of a snake that had been active in coniferous woodland and food resources may have been scarce in such a habitat. The large range was caused almost exclusively by a single large uni-directional movement of approximately 350m made to a previously used refuge. Movements during this period also tended to be in the direction of the overwintering sites and by September, two of the three tagged snakes (111 and 192) had returned to their previous winter refuge and the other was less than 100m away.

No clear patterns of range shifting are shown by the mapped plots of monthly ranges shown for four snakes in Figure 3.5. On the contrary, monthly ranges show a high degree of overlap for all four individuals, whereas similar plots drawn by Madsen (1984) showed that monthly ranges were more separate and followed a broadly circular pattern away from the winter refuge in spring and back to it in autumn. It may be that the pattern recorded by Madsen was largely caused by the linear nature of the habitats used by the snakes in his study (ie. snakes could often move only in one of two directions if they were to avoid exposure to predators). In the present work, the greater diversity of the habitat meant that snakes could move in virtually any direction and find at least one of several required resources and that this led to the greater overlap of ranges observed.

3.4.4 Range overlap

Overlap of ranges between snakes was variable in both years. The high correlation of range size and degree of overlap between other ranges suggests that overlap was more a function of range size than a consequence of intraspecific interaction. The exclusion of untagged snakes also means that these results exclude a significant number of other potential range overlaps and the exclusion of time from the analyses further confounds the results.

The overlaps recorded however show that individual snakes do not disperse to discrete areas in the summer and this fact is reinforced by the multi-nuclear nature of their annual ranges. Feeding is a fundamental reason for movement in an active forager such as N. natrix and as the food resource at Chilworth was apparently widely distributed (recently fed snakes were seen at many locations at the site) and itself mobile at the individual level, the maintenance of territories would have no obvious advantage, except perhaps a knowledge of the area. Field observations showed that grass snakes at the site were frequently in the near vicinity of conspecifics, although only on very few occasions did these snakes potentially interact away from the overwintering sites. A satisfactory computation of range overlap could in any case only be achieved if all snakes in the area were regularly located.

Observations from this study have varied widely from the studies by Phelps (1978) and Madsen (1984) on the same species. Phelps recorded 'erratic movement' in his study on heathland grass snakes in the New Forest and this was observed at Chilworth. Madsen identified a pattern in the ranging behaviour of his snakes, but there was nevertheless a large variation of ranging behaviour within his study.

The probable reason for the diversity of the observations recorded is that the snakes respond to the suitability of the habitat and do not follow some intrinsic pattern of seasonal movement. Habitats in this and the other two studies have been significantly different and direct comparison may therefore be invalid. All three of the studies have shown that overwintering sites are used in successive years, that movement away from these areas during the summer is not uni-directional and that the snakes maintain a home range to some degree, although whether the same summer areas are used from year to year is not known. A further extension of a study such as this, to track snakes in successive seasons would be a useful addition.

Chapter Four

Movement patterns

4.1 Introduction

The spatial movement patterns of an animal reflect many aspects of its ecology and for this reason many studies have been carried out into the movement of snakes. The costs of movement in terms of energy expenditure and increased risk from predators presumably mean that snakes will only move when the potential benefits from such action are likely to outweigh incurred costs (Huey & Pianka, 1981). In practice, with such secretive animals, work in this area can be difficult and it is only since small, cheap radiotracking equipment has become available that detailed studies have been widely carried out. As a consequence of this, most of the work that has been published on activity patterns in snakes has focused on seasonal patterns (Barbour et al,1969; Brown and Parker, 1976; Madsen, 1984 and many others), with rather fewer including work on diel patterns (eg. Moore, 1978; Gannon & Secoy, 1985).

Many long term snake studies have identified seasonal patterns of movement in snakes and shown these to be linked to known events in the annual life-cycle of the animals. Such patterns are manifest across a wide range of species from several families. Seasonal migration has been shown to occur in several species as populations move from winter refuges to summer feeding areas. Most notable among these is the red-sided garter snake Thamnophis sirtalis parietalis, a population of which migrated up to 18km from winter den to spring site and returned in the autumn (Gregory, 1974; Gregory & Stweart, 1975). Other observations of seasonal migration include the rattlesnakes Crotalus atrox, 1-2km (Landreth, 1973) and Crotalus viridis lutosus, 0.9-1.2km (Hirth et al, 1969) and several other species, eg. Masticophis taeniatus, 1.5-3.6km (Hirth, et al, 1969) and Vipera berus, 0.5-1.2km (Prestt,1971).

Such movements are common, if less dramatic in many other species of snake. Some species have been shown to migrate more gradually away from the winter refuge over successive months until mid-season, when an equally gradual return was made to the winter refuge, eg. Reinert & Zappalorti (1988), Crotalus horridus; Madsen (1984), Natrix natrix.

Some snakes have shown even more restricted ranging behaviour, staying close to the winter refuge for the whole season, eg. Hirth, et al, (1969), Coluber constrictor mormon, Gannon & Secoy (1985), gravid Crotalus viridis viridis.

In most of the above cases, migration has been shown to be driven by habitat selection as prey are located some distance from the winter refuge areas. This hypothesis is reinforced by the fact that some species have been shown to change habitats in mid-season. Shine & Lambeck (1985) noted that the aquatic arafura filesnake Acrochordus arafurae used damp grassland in the wet season and migrated to billabongs in the dry season and Holman & Hill (1961) recorded a large scale migration of Natrix sipedon pivtiventris during a drought which had dried up the population's normal habitat. Shine (1979) suggested that the mild Australian winter allows elapid snakes to overwinter in shallow burrows close to the summer sites, which is why communal overwintering and seasonal migration are virtually absent in this family of snakes.

Reproduction may also initiate a noticeable change in movement in both male and female snakes. Male adders, V. berus (Prestt, 1971) and grass snakes, N. natrix (Madsen, 1984) both showed increased movement during the search for mates; gravid female adders, conversely, are relatively inactive (Prestt, 1971), as are oviparous females until immediately before oviposition, when activity increases during the search for a suitable egg-laying site (Madsen (1984), N. natrix; Parker & Brown (1972), Masticophis taeniatus taeniatus.

Ecdysis may also have an effect on the vagility of some snake species. Madsen (1984), N. natrix and Gent (1988), Coronella austriaca both noted reduced movement in the period before sloughing and Madsen also noted increased movement after sloughing as snakes increased the time spent foraging.

In addition to seasonal patterns of movement, many authors have noted daily activity patterns in snakes. The most fundamental question that has been addressed is the time of day that snakes are active, and this seems to be temperature dependent. Heckrotte (1962) noted that Thamnophis radix was diurnal at low temperatures, crepuscular at intermediate temperatures and nocturnal at high temperatures. Landreth (1973) observed that Crotalus atrox was active in the early and late part of the day during warm weather, but during the middle of the day in cooler weather; in very warm weather, the snake became nocturnal.

It would therefore be expected that in cool temperate climates such as that found in Britain, snakes would have a predominantly diurnal activity pattern, and this was indeed the case. During the course of this research, no grass snake was ever observed to change location during the night, even on nights when the ambient temperature was as high as daytime temperatures when snake movement may have been observed. Gaywood (pers comm) noted a similar diurnal pattern for all three British snakes.

The purpose of this chapter is to examine the temporal nature of spatial movement and how it relates to environmental variables and to intrinsic biotic variables such as digestive and slough condition and annual cycle.

4.2 Methods

The animals used in this part of the research were externally tagged snakes in 1987 and snakes that had been surgically implanted with transmitters in 1988 and 1989. The methods used for these procedures are explained in Chapter 2. All snakes used were released at the point of capture as soon as possible after the transmitters had been fitted. In the case of the external tags, this was usually the same day and several of these snakes were tagged in the field and released immediately.

The period over which each snake was radiotracked varied according to the type of transmitter used and to the ultimate fate of the snake in the field (see figures 2.4 and 2.5). A graphical summary of tracking periods is shown in figure 4.1. Fieldwork was terminated at the end of July, 1989.

All snakes were located at least once a day, late in the evening, so that their night refuge was always known. In addition to this, intensive radiotracking on most days was carried out to locate snakes at shorter intervals of between .25 and 4 hours. It proved impossible in practice to achieve this in a strictly methodical manner, as the snakes were highly mobile and it often took several hours to find an individual, even though it may have been located within the previous few hours. It was felt to be important not to lose snakes, particularly those that had been implanted with transmitters and the limited range of these tags often necessitated a time consuming search for a misplaced individual. Nevertheless, a large quantity of movement data was obtained from all hours of the day when snakes were active. The snakes were located using the procedure defined in Chapter 2, and could be located with absolute accuracy, although care was taken not to disturb snakes.

Analysis of variance of the distances moved in each of the three years showed that there was no significant difference in the magnitude of daily movement distances between the three years ($p>.05$), so data from all three years (ie. external and implanted tags) has been combined where appropriate.

4.2.1 Annual movement patterns

Movement per day was analyzed as part of an examination of the annual patterns of grass snake vagility. The distances between successive night refugia were calculated and plotted to provide a graphical representation of

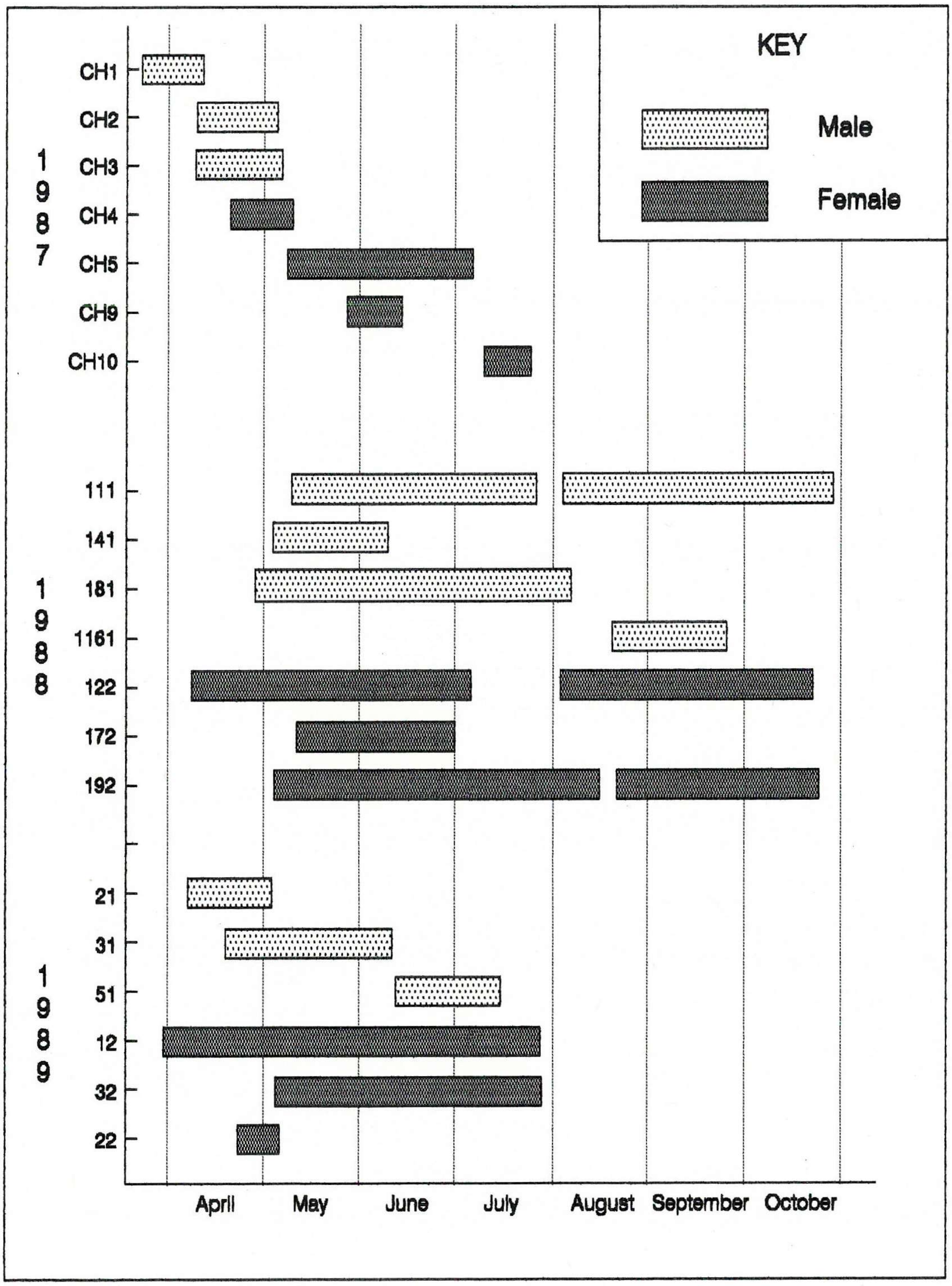


Figure 4.1 Details all snakes used for the collection of movement data, showing the periods over which they were tracked.

snake movements. Such measurements are undoubtedly a conservative estimate of snake mobility as they provide only a 24 hour relocation distance and fail to consider activity within each 24 hour period; however they do provide an overall index of snake movement.

It had been the intention to combine the movement data from each year to provide a single graph for each sex which would show a seasonal pattern of movement, but when the graphs for 1988 and 1989 were plotted separately, the patterns were obviously different and it was decided not to combine the data. The two years are therefore discussed independently.

4.2.2 Rate of movement

The rate of movement was calculated by dividing the distance travelled between two successive locations by the time interval in hours. Only locations less than three hours, but more than one hour apart were used. The value obtained was assigned to the one hour block into which the mid-point of the interval fell. For example, a snake that was recorded as having travelled 65m between 11.30 and 1.15 had moved at a rate of 65m/1.75hrs = 37.1m hr^{-1} and this was assigned to the block 12.00-13.00 hrs.

The mean of the figures obtained were subdivided into sex, month and year and plotted in two ways. The first showed the mean of all movements for each group and the second showed the mean of all observations in which movement was noted.

4.2.3 Daily movement patterns

The relative frequency of movement observations in hourly intervals was plotted in a series of monthly bar charts for 1988 and 1989, using data from implanted snakes. This was calculated using all pairs of observations less than three hours, but more than one hour apart. Snakes which recorded a change in location of less than one metre (the resolution of the location technique) were assumed not to have moved.

4.2.4 Movement and body temperature

The thermal ecology of the grass snake will be discussed in Chapter 5 of this thesis and although the relationship between the movement and body temperature of moving snakes is examined there, the data presented relied on the use of logging equipment for remote recording and thereby weighted the observations heavily towards stationary animals. The analyses below represent observations made at spot locations during the course of routine radiotracking.

Throughout the research programme, effort was made to avoid disturbance to snakes during radio-location. This meant that it was often difficult to determine whether a snake was moving or not. If an individual was moving constantly at the time it was located, it was not necessary to observe the animal in order to ascertain that it was not stationary, but snakes which were moving slowly or intermittently were not usually disturbed and some data on moving snakes was thereby forfeited. However, the body temperatures (Tb) of snakes that were known to be moving were obtained on 163 occasions. In order to maintain consistency no data was used in the following analyses that accrued from continuous monitoring of snakes.

The frequency of observed body temperatures of snakes that were moving when located was plotted. The body temperature data was then subdivided into observations made under different categories of cloud cover (CC), air temperature (Ta) and substrate temperature (Ts) and analysed using a Kruskall-Wallis one-way analysis of variance to examine the effects of those three variables on the Tb of the snakes. These variables were divided into subjective categories: Cloud cover was subdivided into 0-25, 26-75 and >75%; Ta into 0-10, 10-20 and >20°C and Ts into <15, 15-25 and >25°C. The assumption was that any variable which affected Tb would also affect to some degree the willingness or ability of the snakes to move. Conversely, any variable that had no effect on Tb had either had, or was having, no influence on the movement of the snakes.

4.2.5 The effects of ecdysis on movement

The exuviae of implanted snakes were found on eight occasions in which the daily movement of these snakes before and after exuviation was known. Mean daily movement was calculated for a subjective 21 day period (10 days before and ten days after sloughing) which was chosen to include the periods when snake movement was likely to have been significantly influenced by their physical condition. It includes the period before sloughing when the eyes of the snakes were 'milky' and the period afterwards when foraging or relocation to a more favoured site or habitat may have occurred. Mean daily movements before and after sloughing were compared using a Mann-Whitney U-test.

4.2.6 The effects of feeding on movement

The mean daily movements for ten day periods before and after feeding are plotted for six snakes. These periods were again subjectively chosen to include the period before eating when movements may have been increased by foraging and the period afterwards during which digestion occurred. Mean daily movements before and after ingestion were compared using a Mann-Whitney U-test.

4.3 Results

4.3.1 Annual movement patterns

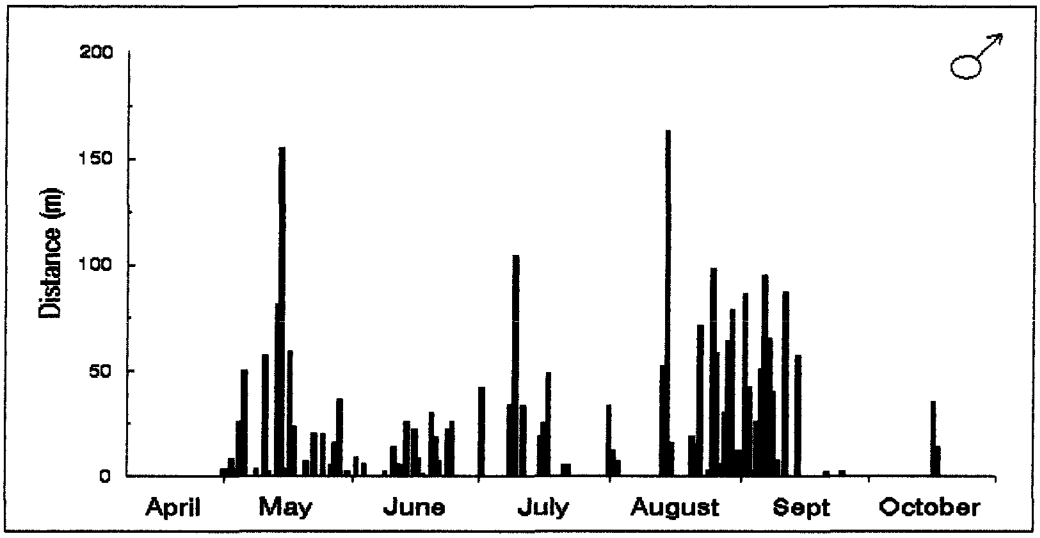
Bar graphs plotting mean daily (re-location) movement of male and female snakes for 1988 and 1989 are shown in figures 4.2 and 4.3. The annual pattern for each sex are noticeably different over each year; in 1988, males showed a peak of activity in May and another in August and September. In mid-season, activity was generally at a lower level and on many days, no movement was recorded. In 1989, however, this pattern was not repeated; although a small number of significant movements (ie. not merely wanderings around the overwintering site) were recorded in April and early May, the magnitude and frequency of movements remained much the same until the end of July. It is possible that a spring migration of the sort that appeared to occur in 1988 occurred again in 1989, although the peak of activity was much narrower in the latter year and the distances involved were not so great.

In 1988, female snakes moved regular, short distances until June and July, at which time the magnitude of the movements increased substantially. After this time, movements were short and infrequent. In 1989, a markedly different pattern developed as substantial movement away from the overwintering sites occurred in early May, followed by movements which were generally of a larger magnitude than those of the previous year. Again, there were many days on which no activity was recorded.

There was no significant difference between the frequency distributions of male and female daily movement distances when tested with a Kolmogorov-Smirnov two sample test (n_1=559; n_2=801; z=1.387; p>0.05) so a frequency distribution of both sexes combined is shown in Figure 4.4. The distribution is highly skewed and movement did not occur on 62.9% of days. Long distance movements were relatively infrequent.

4.3.2 Rate of movement

Figure 4.5 shows plots of the rate of movement (m/hr) of snakes over successive months during 1988 and 1989. Each plot shows both the mean of all observations and the mean of all observed movements greater than zero. In both years, movement rates of both sexes rose sharply in May from low levels in April and remained broadly constant for the remainder of each year, except for female snakes in July, which showed increased rates of movement, a)



b)

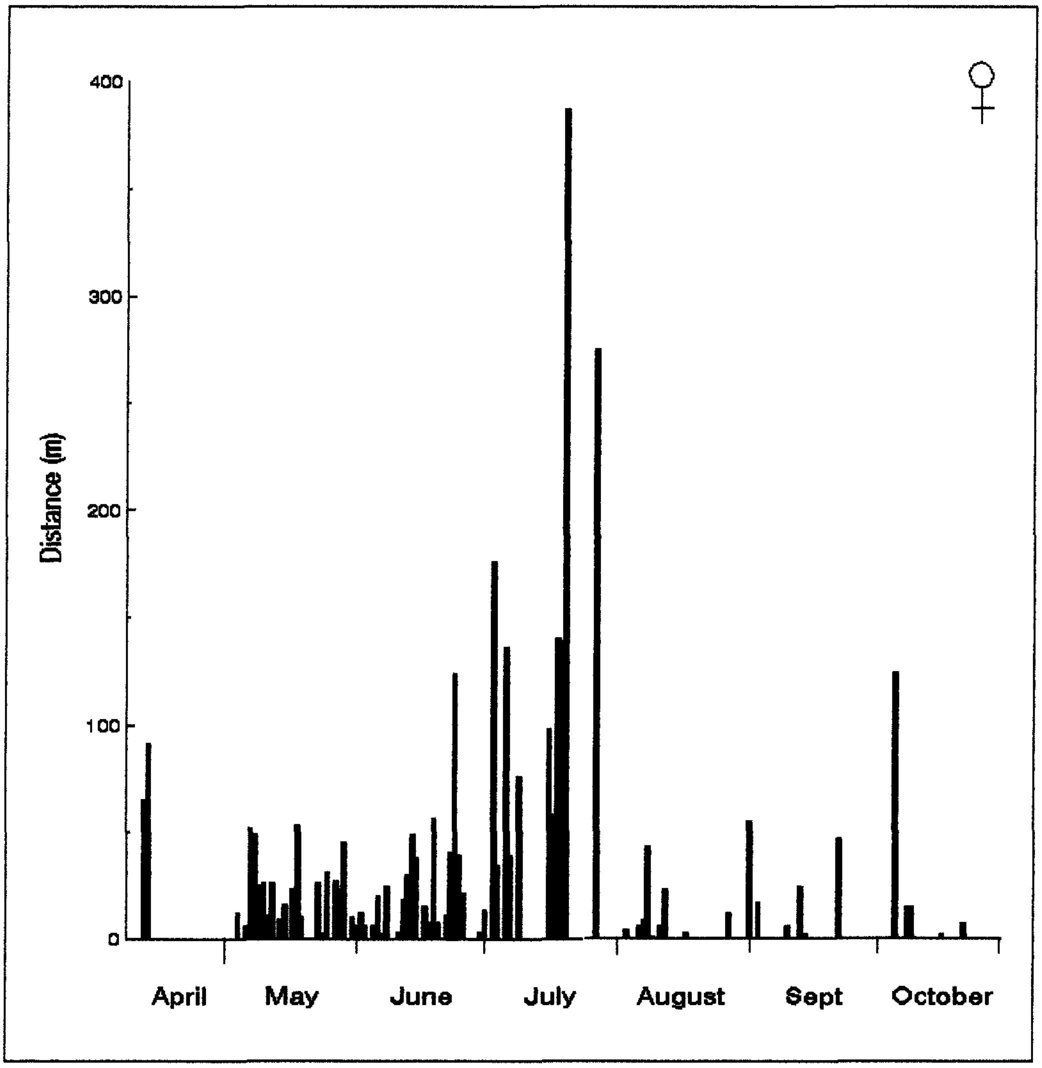
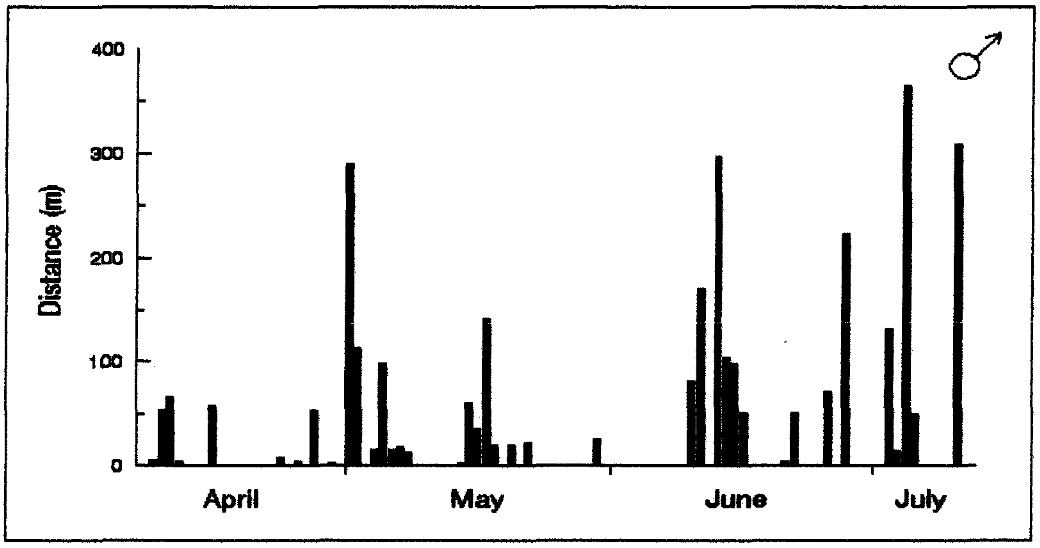


Figure 4.2 Annual mean daily (re-location) movement of radiotracked snakes throughout 1988. Each bar shows the mean data for one day. The sample size can be calculated from the tracking periods shown in Figure 4.1. a) males. b) females.

a)



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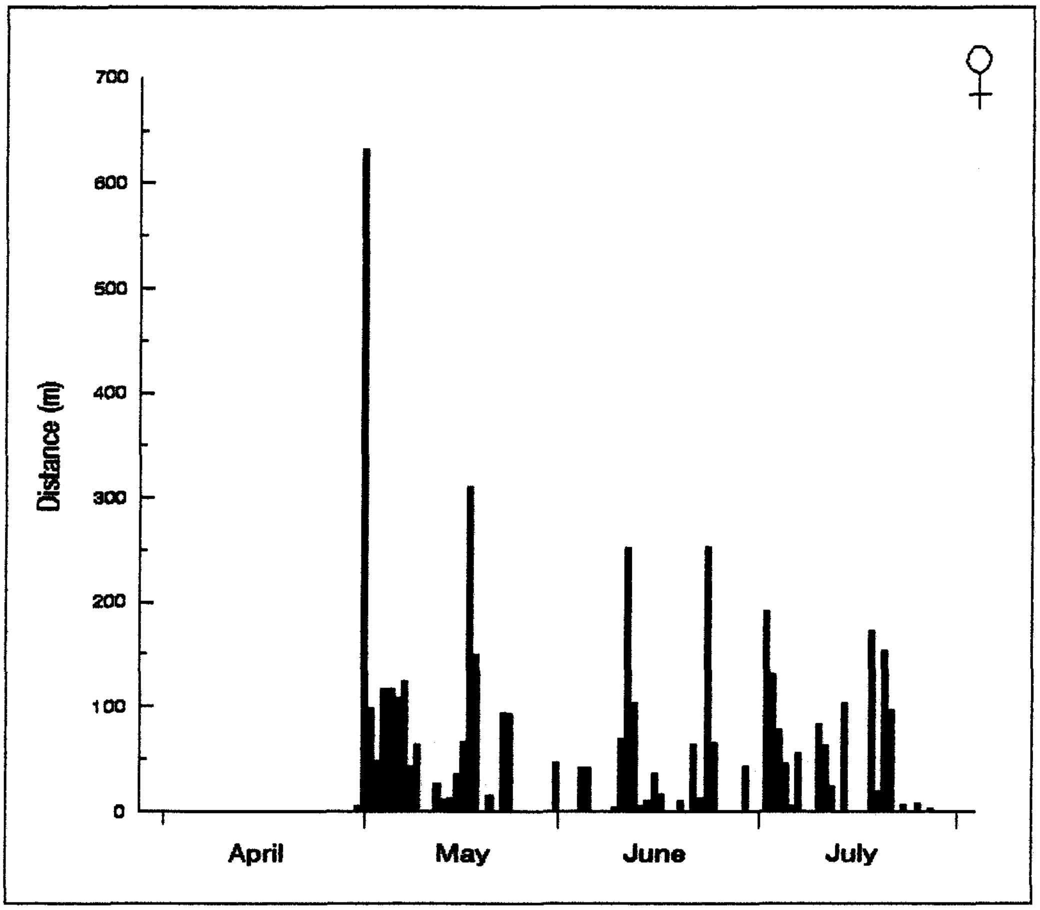


Figure 4.3 Annual mean daily (re-location) movement of radiotracked snakes throughout 1989. Each bar shows the mean data for one day. The sample size can be calculated from the tracking periods shown in Figure 4.1. a) males. b) females.

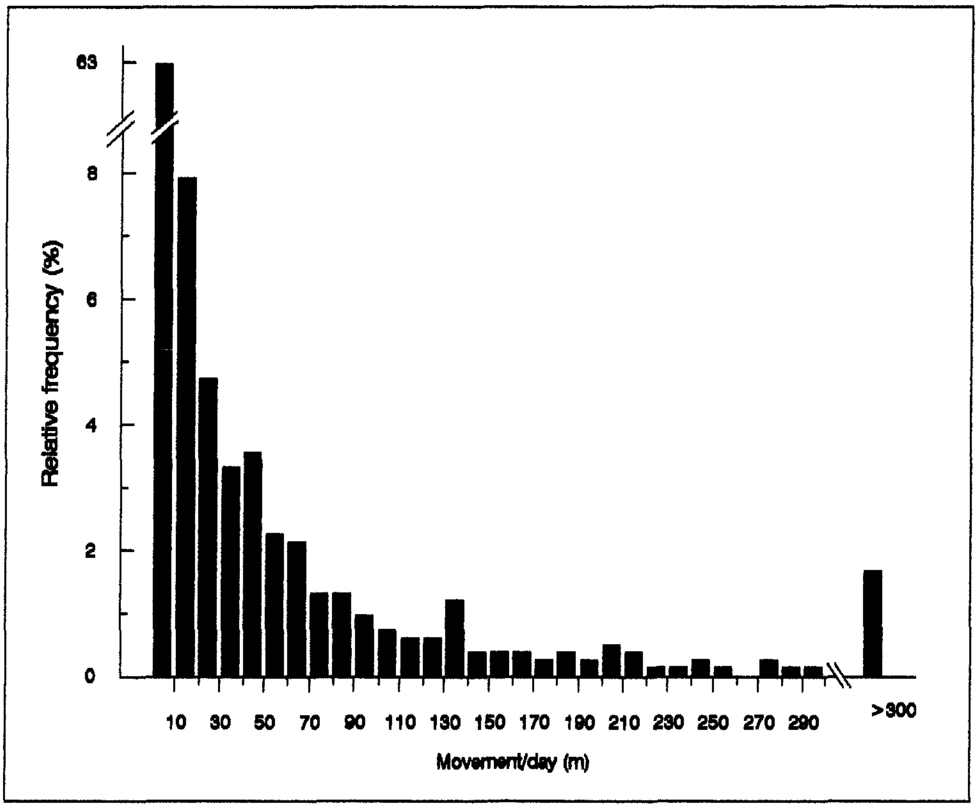


Figure 4.4 Frequency distribution of the daily (relocation) movement of all radiotracked snakes of both sexes for 1987-1989.

but moved less frequently, which meant that the mean movement rate of all observations (ie. including zero movement) continued to decline. A slight increase in movement rate was again observed in September.

4.3.3 Daily movement patterns

Calculation of mean movement rate at various times of day over each season would have meant reducing sample sizes to an unacceptably low level for many hours of the day, particularly in months when the snakes were relatively inactive. In order to further examine the daily activity of grass snakes over the season, the incidence of movement as opposed to non-movement was examined. Male and female data was pooled in order to maintain satisfactory sample sizes ($n_{min}=4$; $n_{max}=28$). All observations of movement over periods of less than three hours were included for analysis and the movement assigned to the hour of day into which the mid-point of the observation period fell. The results are shown in Figures 4.6 and 4.7.

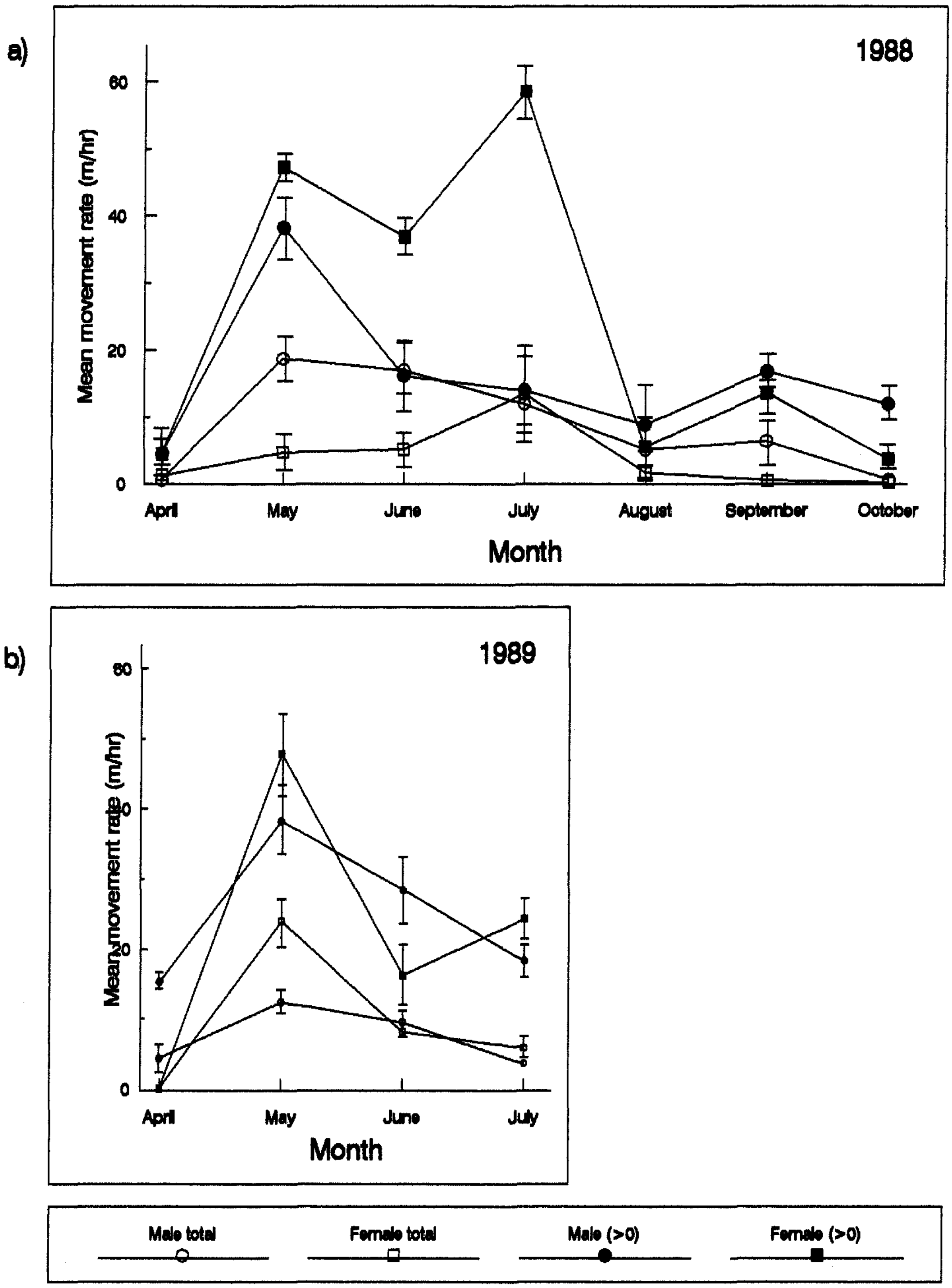


Figure 4.5 Mean monthly movement rate of male and female grass snakes throughout 1988 and up to July, 1989. The plots show the mean of all observations and the mean of all non-zero observations: a) 1988, n=840; b) 1989, n=620.

Activity periods ranged from 4 hours in April to a maximum of 11 hours in July and August. No snake was observed moving after 19.00 hrs, even though sample sizes at this time of day tended to be high as the location of night refugia was almost always sought as a priority. Snakes were occasionally observed moving before 9.00 hrs, but the mid-point of the observation period fell into later hourly divisions. No obvious diurnal pattern is evident and snakes showed a high incidence of movement frequency over most hours of the day, although movements were observed less frequently in earlier hours of the day in every month except June.

4.3.4 Movement and body temperature

A plot of the distribution of body temperatures of moving snakes is shown in Figure 4.8. The modal temperature is between 27-28°C and a definite peak is evident between 26-30°C. The distribution is skewed slightly to the left and approximately 10% of the recorded temperatures were higher than those which the snakes normally reached during basking (see Chapter 5).

Body temperature (Tb) readings were assigned to various categories (Table 4.1) and tested using Kruskall-Wallis chi-square and Mann-Whitney U-tests. No snakes were recorded moving when Ta was less than 10°C and Ts was less than 15°C. Tb was not significantly different within the two air temperature categories in which it was recorded ($U=0.267$, $n_1=107$, $n_2=57$, $p>0.05$). There was no significant difference between body temperatures recorded in the three substrate temperature categories or in the three cloud cover categories. (Ts: $\chi^2=5.586$, $n_1=9$, $n_2=59$, $n_3=95$, $p>0.05$; CC: $\chi^2=0.235$, $n_1=73$, $n_2=57$, $n_3=32$, $p>0.05$;).

Although the results show that whilst low air and substrate temperatures may have affected the ability of snakes to reach and maintain a body temperature that enabled movement , the body temperatures recorded at other times were not seemingly influenced by environmental variables, showing that snakes would move under a broad variety of conditions. This may also mean that snakes devote less time to precise thermoregulation whilst moving. This reinforces some of the observations of body temperature of moving snakes made in Chapter 5 and both sets of results are discussed in the following section.

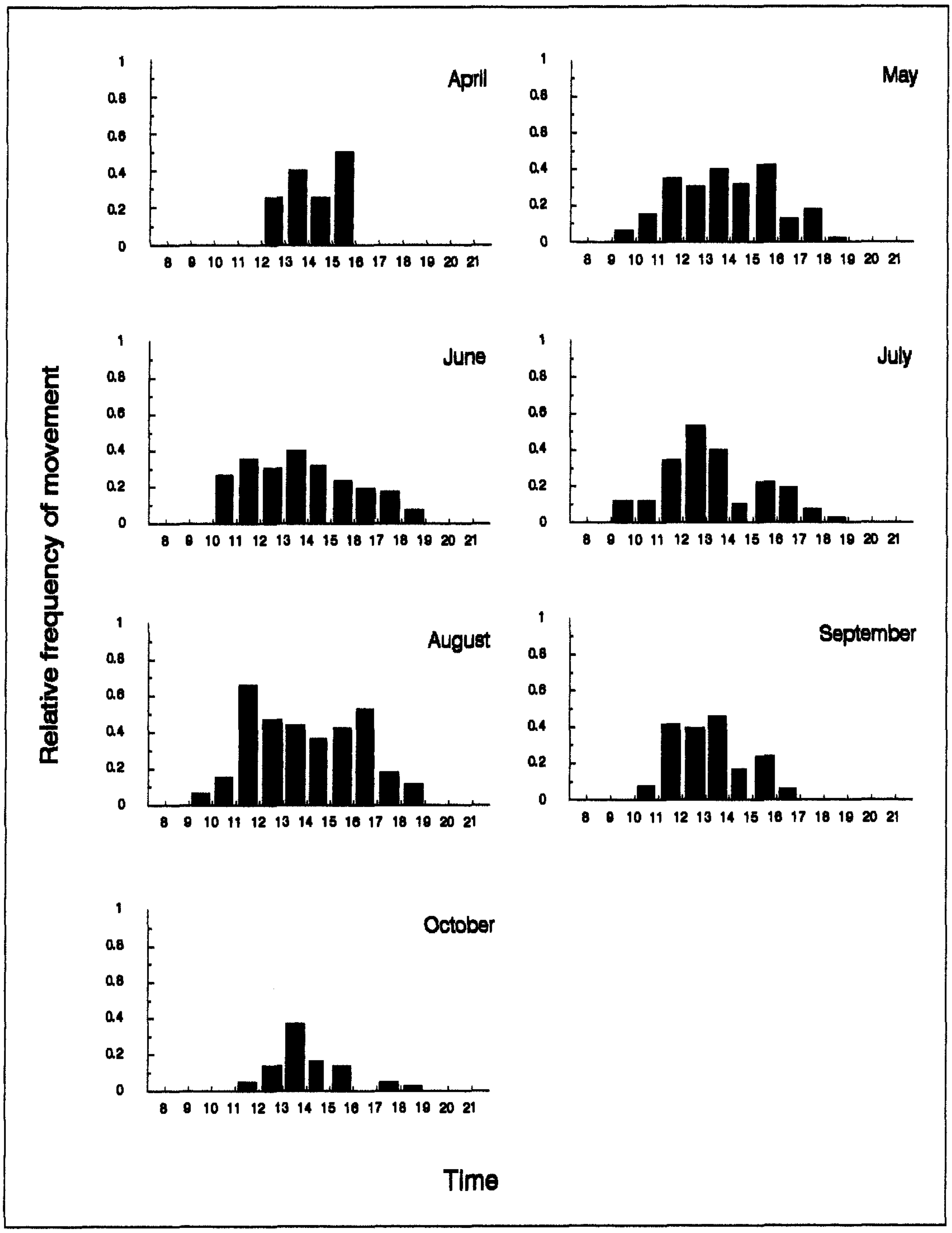


Figure 4.6 Relative frequency of grass snake movement (sexes combined) between 7.00 hrs and 21.00 hrs by month during 1988. Movements <1m are excluded (n_{min}=4; n_{max}=28).

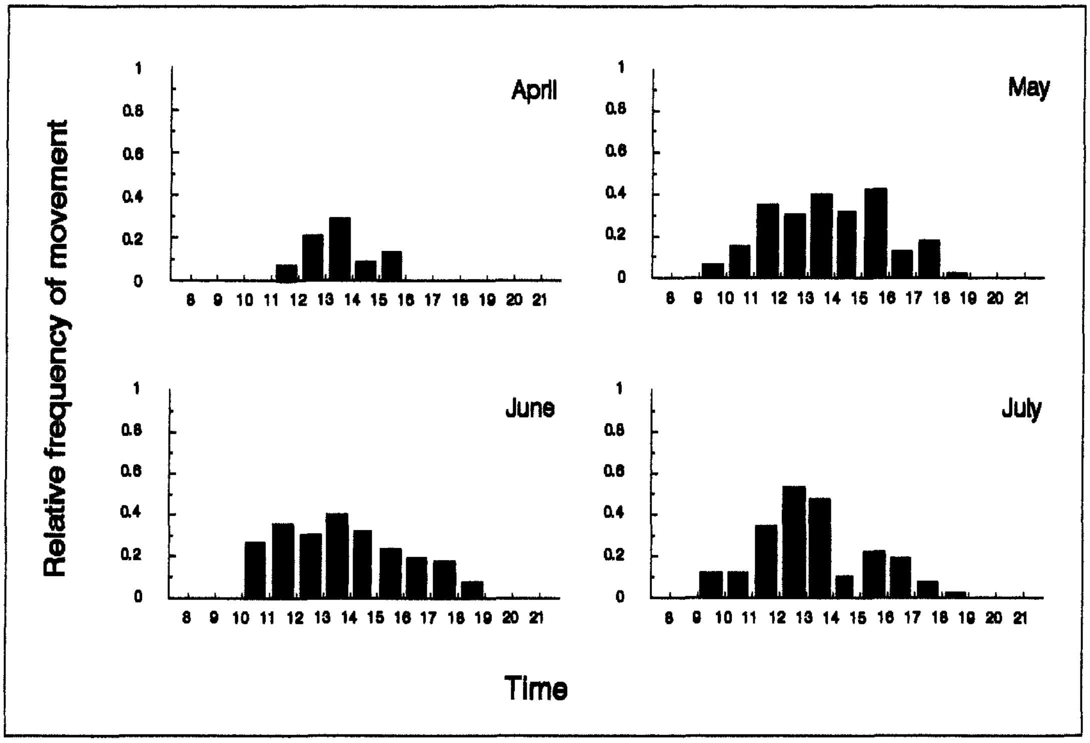


Figure 4.7 Relative frequency of grass snake movement (sexes combined) between 7.00 hrs and 21.00 hrs by month between April and July 1989. Movements <1m are excluded ($n_{min}=4$; $n_{max}=28$).

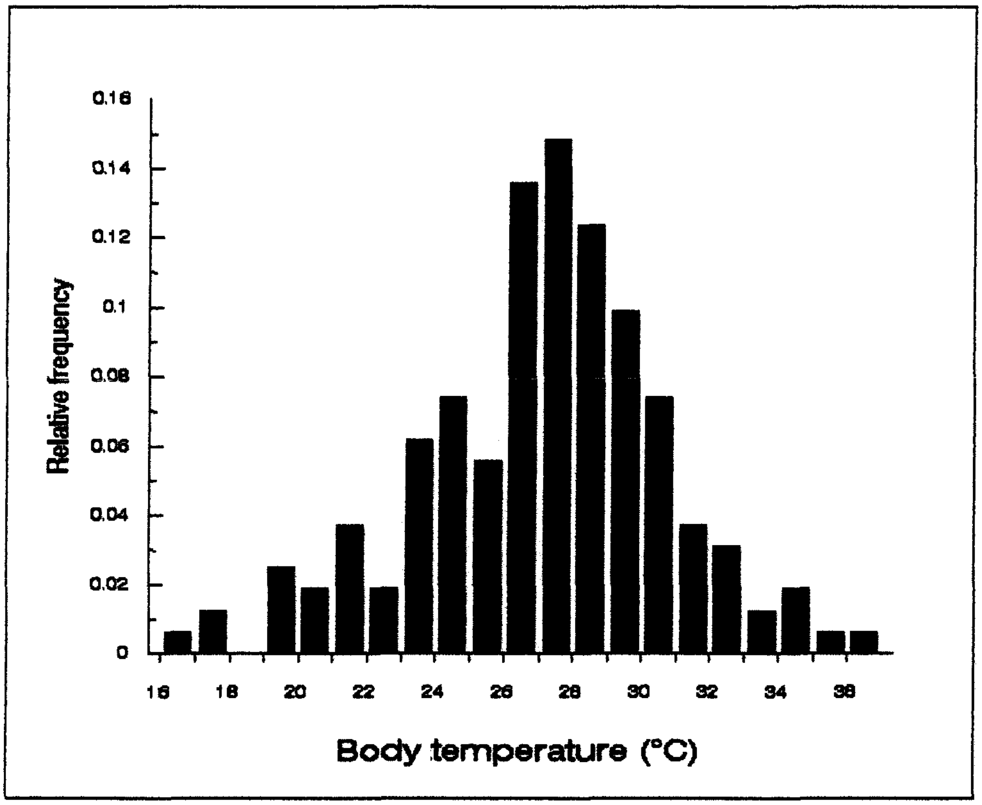


Figure 4.8 Distribution of body temperatures (point readings) of moving snakes (n=163).

4.3.5 The effects of ecdysis on movement

The exuviae of implanted snakes were found on eight occasions and the mean daily movement of these snakes during this period is shown in Figure 4.9. The intervals of ten days before and after sloughing which are plotted are subjective and have been chosen to include the periods when snake movement is likely to have been significantly influenced by their physical condition. It includes the period before sloughing when the eyes of the snakes were milky and the period afterwards when foraging or relocation to a more favoured site or habitat may have occurred. There was a significant difference in the observed movements during the 10 day periods before and after the days on which the snakes sloughed ($U=5.543$; $n_1=80$; $n_2=80$; $p<0.0001$).

It is clear from the bar graph that movement before sloughing is severely curtailed for several days. 'Milky' eyes were not always observed in the radio-tracked snakes, but observations of both captive and some tagged snakes showed that the eyes became 'milky' between 4-8 days before the skin was cast. This coincides with the period of restricted movement observed at this time. Movement immediately after sloughing was extensive and all of the observed snakes moved on either the same day or the day following loss of the skin.

Cloud %	Ts⇒ Ta⇓	<15°C	15-25°C	>25°C
0-25	0-10°C	-	-	-
	10-20°C	20.6 [1]	27.2 [11] (21.1-35.0)	28.0 [33] (21.9-33.2)
	>20°C	-	26.8 [10] (24.5-32.7)	27.9 [18] (26.3-34.8)
25-75	0-10°C	-	-	-
	10-20°C	26.5 [8] (19.7-29.9)	27.4 [14] (16.8-30.0)	29.8 [23] (22.4-31.6)
	>20°C	-	28.5 [8] (23.3-35.7)	25.3 [5] (17.4-32.1)
>75	0-10°C	-	-	-
	10-20°C	-	26.7 [10] (19.9-31.2)	26.4 [7] (18.2-32.3)
	>20°C	-	27.0 [6] (21.0-34.2)	24.8 [9] (17.7-36.3)

Table 4.1 Body temperatures of moving snakes under various environmental conditions. Median temperatures for each category are shown, with range in parentheses and sample size in square brackets. Hyphens represent categories for which no data was recorded. Data was collected only from radiotagged snakes in 1988 and 1989. Data from continuously logged snakes was not used.

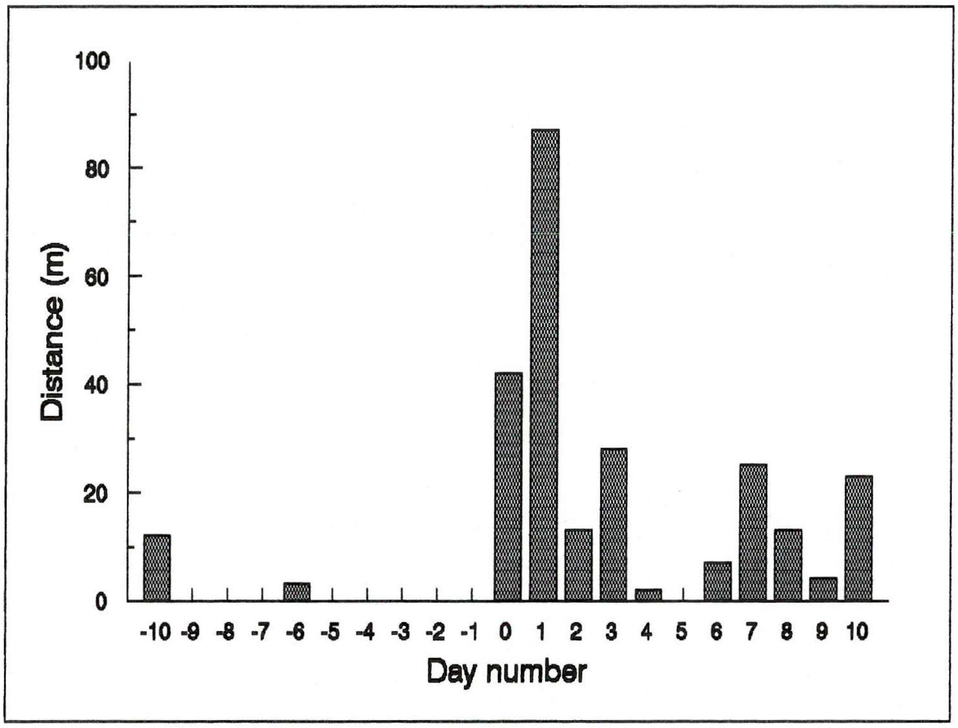


Figure 4.9 Mean daily movement of snakes in a ten day period before and after sloughing (n=8). Exuviation took place on day zero.

4.3.6 The effects of feeding on movement

On six occasions, tagged snakes were seen to have eaten large food items that caused bulging of the body and loss of normal streamlining (see Figure 1.4, p.7) Figure 4.10 shows the daily movement 10 days before and after feeding. It appears that for several days following intake of a substantial food item, movement is restricted while the snakes digest the food item. Over the 10 day periods before and after eating, there is a significant difference in the distances moved ($U=2.41$; $n_1=60$; $n_2=60$; $p<0.05$). The difference in movement is even more significant over a 7 day period before and after eating ($U=4.707$; $n_1=42$; $n_2=42$; $p<0.0001$).

Figure 4.11 shows observations made of both tagged and untagged snakes that contained a noticeable food bolus. The observations made were random and opportune, but provide an overall indication of the times of year at which grass snakes caught prey and by definition, the times of year at which they foraged.

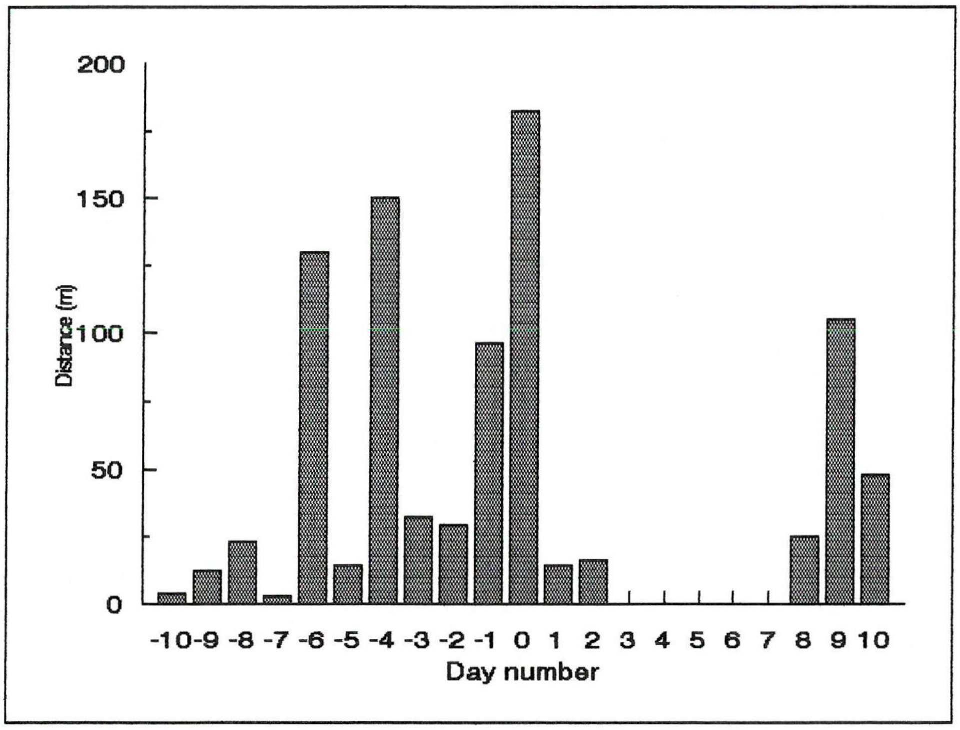


Figure 4.10 Mean daily movement of snakes in a ten day period before and after feeding (n=6). The prey item was consumed on day zero.

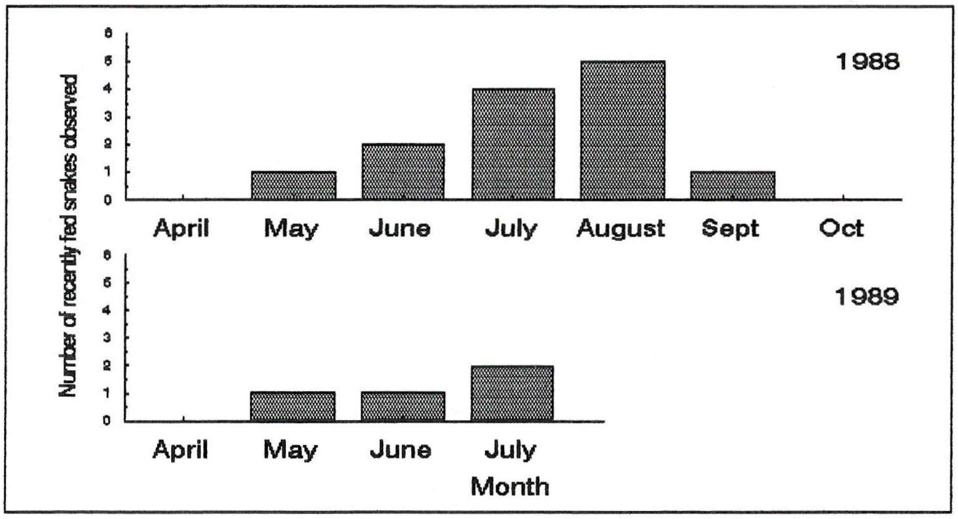


Figure 4.11 Number of snakes observed in the field which contained noticeable food boli.

4.4 Discussion

4.4.1 Annual movement patterns

The annual movement patterns shown in figures 4.2 & 4.3 show little consistency between years for either sex. There was evidence of increased movement in male snakes in late April and early May in both years, which represented movement away from the overwintering sites. Female activity also increased at this time as the snakes left the winter refuge area, but whereas the mean daily movement was small in 1988, both tagged females in 1989 made dramatically large migrations away from their respective refuges. In one case, the female had mated the previous evening and as the female had not left the overwintering site since emergence, it is possible that subsequent migration was motivated by mating. The other female was not seen with a male snake and the stimulus for migration would appear to be something other than sexual activity.

Male snakes also showed increased activity in spring as they left the winter refuges and the distances moved were sometimes large. Snakes in both years dispersed in various directions and there was no apparent movement towards a favoured or known single summer area as reported by Phelps (1978) and Madsen (1984) for the grass snake, although individuals sometimes appeared to make unidirectional movements over a period of two or three days to a site at which they remained for some time subsequently. This was discussed in Chapter 3.

Although mating opportunities may be higher at the winter refuge areas where there are a relatively high number of animals, there are a number of other factors which are likely to stimulate snakes of both sexes to move away in the spring. Of these, one of the most important is food. Following several months of winter torpor, food will be of particular importance, particularly in the case of females who will need increased nutrients to facilitate the development of eggs. The main food item of the grass snake, the toad Bufo bufo is active in April and May and the snakes may make a trade off between the probability of mating with the need for food. Gregory & Stewart (1975) observed that Thamnophis sirtalis migrated large distances from winter refugia to the summer site and stated that the presence of prey at the summer site stimulated such a migration. Although one snake in this study was observed consuming a toad at one of the two winter refugia (in July, 1988), toads were widespread throughout the study area, as the observation of snakes containing visible food boli confirmed, so the dispersal of the snakes in spring was consistent with hunting activity.

Even if snakes have not mated, a second reason for which to leave the winter refuge may involve basking behaviour and thermoregulation. Although both overwintering sites at Chilworth were south facing, the sun in April and May was relatively low in the sky and direct insolation was available for only part of the day. Clearly, a snake that is mobile can either move to a more exposed habitat or site, or move more locally to 'follow' the sun during the day.

One factor that may act as a restraint to spring migration away from overwintering sites is connected with predation. Immediately after spring emergence, the snakes were lethargic and their movements relatively sluggish for some time, even when warm. Snakes were noticeably easier to catch early in the season and must presumably have been extremely vulnerable to predators. The snakes at this time were in a familiar environment and the habitats offered cover and opportunity to bask and raise body temperature. Movement away from the winter refugia may have placed the snakes at an increased risk of predation at a time when burst speed and other defences were diminished. The initiation of spring movement may therefore be delayed until snakes have reached a physiological condition that will reduce the chance of predation.

Clearly the reasons for initiation of movement in spring are complex and specific observation of snakes at overwintering sites will be needed to further understand the reasons why snakes leave the overwintering areas.

Madsen (1984) observed a decrease in the vagility of gravid female grass snakes followed by a sharp increase during the period immediately before oviposition and attributed this to movement towards 'manure-hills' in which the eggs were laid. In this study, no tagged females subsequently developed eggs, although two were observed mating. The increase in female movements observed in 1988 in July, is therefore without apparent reason. However, although three females were tagged, the data represents observations made of only one, because one had recently been killed by a predator and the other had been removed for replacement of the transmitter. The female was not foraging at the time, but had made several rapid, large, unidirectional movements to a previously unvisited area and had then returned after several days to the same refuge. In 1989, no such large movements had been observed when fieldwork ceased at the end of July.

Female movement in the latter part of 1988 was much reduced. The snakes moved on fewer days than had been the case earlier in the year and foraging was observed less frequently. The slight increase in movement in early October was the result of females returning to their winter refuge site.

Although moderately active throughout the summer, the activity of the males peaked in late August and early September in 1988. In contrast to the sedentary females, foraging behaviour was evident at this time and both tagged and untagged male snakes were observed with food boli. Thus, in 1988, male and female foraging occurred at different times of the year. An explanation for this may lie in the fact that females may have less need for food later in the season if no egg development has taken place. Neither of the tagged females was observed with a food bolus after July of that year.

In October, 1988 a brief increase in movement can be observed in both male and female snakes. All movements recorded at this time were generally in the direction of the overwintering sites that each of the individuals had used the previous year. The three snakes from which the movements were recorded were the only individuals which were tagged for a whole season, and all had returned to their former overwintering site, suggesting that this may be true for all or most grass snakes. Snake 192 was found at the site the following spring, but the other two snakes were both killed by predators, so no conclusive evidence was available regarding the location of their winter refuge.

Seasonal movement patterns have been observed in a number of snake species (reviewed in Gibbons & Semlitsch, 1987) and although such patterns existed in this study, they were less pronounced than for many other species. One reason for this may be the nature of the British climate, which even in summer can often be wet or cool. Although seasonal, the weather in Britain is typical of temperate regions and is often cyclonic and unpredictable, unlike the weather in North America and Australia, where many other studies have been carried out. Anticyclones dominate the weather of most large land masses, leading to stable weather conditions for much of the year, which may make annual patterns of snake movement more easily discernable. In Britain, the variable weather may obscure patterns that could otherwise be clearly seen. Madsen's (1984) study of the grass snake showed more clearly defined movement patterns, but again, the Scandinavian weather is more greatly influenced by central Asian anticyclones than that of Britain, which leads to more predictable weather conditions.

4.4.2 Rate of movement

Although extensive movements were made by snakes of both sexes, movement was relatively infrequent and when movement did occur, distances tended to be short. Movements over 100m occurred on approximately 10% of daily observations and snakes did not move on nearly 63% of days. Infrequency of movement has been observed in a number of snake studies (eg. Barbour et al, 1969, Carphophis amoenus amoenus; Prestt, 1971, Vipera berus; Tiebout & Cary, 1987, Nerodia sipedon; Gent, 1988, Coronella austriaca).

Lack of movement by an individual meant that either emergence had not occurred or that the snake was basking. Snakes did not emerge on cool or wet days and activity was frequently restricted to basking on days when conditions were apparently suitable for a wide range of activities. Movement involves an energetic cost and probably places an individual at a greater risk from predators. Snakes will presumably, therefore, only move when the benefits of such action outweigh the costs, and as infrequent feeders, mid-season activity may be restricted to movement from one basking site to another, movement away from disturbance and possibly periodic relocation as a defence against predators.

The fact that snake movements were mainly small suggested that they were made for reasons other than foraging. However, the data shown only records one location per day and does not indicate total movement throughout a twenty-four hour period, and on a few occasions, snakes made very extensive movements, only to return to within a short distance of their previous night refuge.

The movement rates of both sexes followed a broadly similar pattern over both years. Male movement rates were highest during spring movement away from the winter refuge and declined to a more or less constant level throughout the rest of 1988 and to July, 1989. The rate showed a slight decline in August, 1988, which was surprising, as although the snakes were more or less sedentary in the first half of the month, they were very active in the latter half. In order to examine this further, all non-zero movements were plotted and the movement rate was still shown to be low. This indicates that active males moved only slowly, which may be more consistent with foraging behaviour than relocation. This is reinforced by the data in Figure 4.11, which shows that male grass snakes were more frequently observed with food boli during August, 1988 than at other times of the year. A broadly similar pattern was observed in 1989 until July, when fieldwork was terminated.

Female movement rates did not show a similar pattern to that of the males. In 1988, the movement rate remained high until July, although caution should be exercised when examining the July figure as it was calculated from only one snake, which made several large and rapid relocation movements at this time. The June movement rate (non-zero observations) was similar in both years and mean daily movements were of similar magnitude (see figure 4.3). The very low movement distances recorded by Madsen (1984) for gravid females were not seen in the non-gravid individuals in this study. The highest percentage of recently fed females were observed during June in both years, which suggests that movement at this time was directed towards foraging. It is possible that even non-gravid females may instinctively search out oviposition sites at this time of year, which may result in the higher movement rate observed in females.

The slight increase in movement rate recorded in September appeared to be associated with relocation movements back towards the winter refuges. Both males and females moved towards their previously used overwintering sites at this time and such movements appeared to be unidirectional and more purposeful than those observed of foraging animals.

Clearly, the reasons for movement will greatly influence the rates and frequency of observed activity and further work in this area would be more useful if such reasons could be identified with greater precision than they were in this study.

4.4.3 Daily movement patterns

The ectothermic nature of grass snakes dictates that they must reach and maintain a body temperature that facilitates activity, and the data shown in figures 4.6 & 4.7 reflects this. The active period was most extensive in mid-season, when warmer weather and longer days meant that higher body temperatures could be reached and maintained for longer periods.

The frequency of movement observations was more frequent in the middle part of the day in all months. In August, 1988 the weather was particularly warm and snakes would have risked overheating had they moved at the warmest time of day. This may account for the bimodal distribution of movement frequency observed during this month.

The snakes were entirely diurnal and frequently took refuge underground at night (pers. obs.). Such behaviour is typical of temperate snakes and neither of the other two British snakes are active at night (Prestt, 1971; Gent, 1988) although Gaywood (1990) observed some nocturnal activity in captive grass snakes held in an artificially warm environment. Gibbons & Semlitsch (1987) report a number of studies in which species show a diel activity pattern dependant on environmental temperatures. No nocturnal movement was observed in captive snakes during the laboratory study carried out for Chapter 7 of this thesis. Unfortunately, no studies have been carried out on the activity patterns of grass snakes in areas where night time temperatures are warmer than those in Britain, such as in southern Europe. Such studies, or further work on captive grass snakes could clearly be of value in explaining the diel rhythm of the species.

4.4.4 Movement and body temperature

The wide range of body temperatures over which snakes were observed to move suggests that precise thermoregulation is abandoned at these times. The modal temperature of moving snakes of between 27-28°C was approximately 3-4°C below the preferred Tb of 30-31°C recorded in stationary, basking snakes and was similar to the mean Tb of captive moving grass snakes recorded by Gaywood (1990) of 26.9°C in thermally unlimiting conditions and 22.4°C during thermally limiting conditions. Body temperatures in excess of this preferred maximum were also recorded in approximately 10% of cases, which suggests that snakes have little thermoregulatory ability whilst moving.

Snakes moving in warm sunshine in an open environment may risk overheating or disruption in the body's moisture balance. Conversely, snakes moving in a cool or shaded environment risk lowering body temperature to levels at which burst speed or prey catching ability become impaired. Madsen (1987) suggested that mating grass snakes were particularly vulnerable to predation by birds because they had not reached a body temperature at which defences such as burst speed were optimal.

Except in cases where snakes were disturbed and retreated at high speed for considerable distances (50m or more), observed snake movement was relatively slow and punctuated by brief pauses. The reason for these pauses may be to make small adjustments to body temperature which compensate for impreciseness in or lack of thermoregulation whilst moving. This is in accordance with observations made by Saint-Girons & Bradshaw (1981) who stated that foraging in a captive Pseudonaja affinis was interrupted by brief periods of thermoregulation. Gaywood (1990) also observed pauses in the movement of N. natrix during thermally unlimiting conditions (ie. warm), during which the snakes took cover from direct insolation, and stated that this was a common pattern of behaviour.

Studies by Wilson (1974) and Bennett et al (1975) have shown that the aerobic metabolic scope of members of three families of lizard are maximal at or near to the preferred body temperature of the lizards. Thus, at the preferred temperature, although movement may be supported by glycolysis, aerobic capacity is nonetheless high, which will facilitate the relatively short, rapid movements necessary to escape predators or catch prey.

Although safe and efficient movement by grass snakes would appear to be favoured by relatively high body temperatures, there were still many occasions on which the recorded Tb of moving animals was significantly lower than the modal temperature. As stated above, it would have been useful to attempt to identify the reasons for movement and then to examine Tb in the light of those reasons. For instance, whilst it may well be necessary for a snake foraging in a relatively open habitat to maintain a high Tb wherever possible, this may not be necessary for a snake foraging in a closed habitat such as dense woodland where the chances of predation may be lower, or for a snake making one short relocation movement on a day when high Tb's are not achievable.

The lack of significant difference in body temperatures recorded in moving snakes under a variety of weather conditions suggests that movement occurred regardless of those weather conditions. The snakes were apparently able to raise Tb to at least moderately high levels under a variety of environmental conditions by using behavioral thermoregulation or perhaps by choosing a suitable micro-habitat or microclimate. Gaywood (1990), reported that grass snakes were more likely to move under 'thermally unlimiting' conditions and this may have been the case in the present study. No snakes moved when the air temperature (Ta) was less than 10°C and conditions at this time may well have been representative of 'thermally limiting' conditions.

Again, the wide variation in recorded body temperatures also suggest that snakes do not thermoregulate with great precision whilst moving.

The plots shown in Figures 5.7 and 5.8 demonstrate that movement can be maintained for considerable periods at a wide range of body temperatures. Although movement at high Tb's may confer certain advantages on snakes, such as predator avoidance, it may often be the case that movement at low Tb's is a cost that is outweighed by the benefits obtained by movement. Examples of this would be movement by a cool snake to a warmer site or foraging by a snake in well concealed environment such as an overgrown ditch.

4.4.5 The effects of ecdysis on movement

Movement in snakes was significantly reduced during the 10 day period before ecdysis. Between 4-8 days before sloughing, the eyes of the snakes turned milky in appearance and the snakes became noticeably less alert (see Figure 1.3). This lassitude may have been due either to the inability to see properly or to a physiological change associated with sloughing, but in any case, coincided with a period of greatly reduced movement.

The inhibiting effect of sloughing on snake activity has been reported by several authors (e.g. Madsen, 1984). However it is not known whether movement was decreased or ceased because of an inability to see or react to potential predators with sufficient speed, or whether basking time increased to facilitate the process of ecdysis. Gent (1988) found no difference in the body temperatures of Coronella austriaca in the periods before and after sloughing, which suggests that movement is restricted because of the impaired physical condition of the snakes.

4.4.6 The effects of feeding on movement

Feeding also had a significant effect on the movement of the snakes. Extensive movements for several days before feeding were followed by several days of inactivity following feeding. The period of increased activity before feeding is undoubtedly connected with foraging, particularly on day zero, when the prey were taken. Distances here are likely to be gross underestimates since locations were only recorded periodically rather than continuously. The ingestion of large food items (see Figure 1.4), apart from causing possible discomfort and reduced burst speed, has been reported as resulting in greatly increased basking effort in the snake Constrictor constrictor (Regal, 1966). This was connected with probable accelerated enzyme production and mechanical functions and also with completion of digestion before putrefaction of ingested food could take place. In Regal's study, the snakes began moving again immediately following defecation.

In this study, snakes which were handled whilst containing a large food bolus invariably regurgitated their gut contents, which suggests that reduced mobility and therefore a diminished ability to escape from predators is a significant reason for a reduction in movement in the immediate post-feeding period.

Chapter Five
Thermal Ecology

5.1 Introduction

In common with other ectotherms, snake behaviour is constrained by abiotic environmental considerations. This has presented investigators with a wealth of opportunity for the study of snakes in a wide range of climatic regions and the last two decades in particular have proved productive in this area. Studies have been wide ranging and have involved both captive and free-ranging animals, the latter particularly during the last decade, when miniature temperature sensitive radio-transmitters have become available.

Initial interest was generated by the work of Cowles (1939, 1941) and Cowles and Bogert (1944) since when the research has followed three broad paths. Firstly are works directed predominantly towards the physiology of reptiles, such as critical maximum and minimum temperatures (eg. Greer, 1980), heat exchange and water relations (eg. Dmi'el & Borut, 1972; Dawson, 1975) and the relationship between temperature and metabolism (eg. Davies & Bennett, 1981; Bennett, 1982).

Secondly are works which examine temperature as a more or less stand alone variable, observing daily and seasonal body temperature patterns under a variety of environmental conditions and the 'preferred' body temperatures of the species under investigation (eg. Saint-Girons & Saint-Girons, 1956; Dewitt, 1967; Spellerberg & Phelps, 1975).

Finally, the vast majority of research has examined thermoregulation as a cause and effect of reptile behaviour. Such studies have taken place over periods ranging from a few days to several years and have explained a great deal about the way in which reptiles interact with their environment. Crowley (1985) demonstrated inter alia that sprint-running performance in the lizard Sceloporus undulatus was optimal at the same temperature range for both high elevation (cool) and low elevation (warm) environments. Heckrotte (1962) noted an increase in activity with temperature in the snake Thamnophis radix up to a maximum of 31°C, after which activity was reduced. Similarly, Paladino (1985) stated that there may be an optimal temperature for locomotion in ectotherms and that this may vary from species to species. Saint-Girons & Bradshaw (1981) observed alternating periods of thermoregulation and foraging in enclosed Pseudonaja affinis, suggesting that the snake overheated during forays and thermoregulated to maintain a lower temperature.

The relationship between temperature and digestion in ectotherms has also been investigated; Skoczylas (1970), in a study of Natrix natrix showed that digestion did not occur at 5°C, was slow at 15°C and optimal between 25-35°C. Greenwald & Kanter (1979) and Hailey & Davies (1987) report similar results for the snakes Elaphe guttata and Natrix maura respectively and Regal (1966) observed a thermophilic response by a number of captive lizards and snakes following feeding.

Thermoregulatory behaviour and temperature selection has also been shown to have an effect on rates of ecdysis (Semlitsch, 1978: Natrix spp.), striking and prey capture (Greenwald, 1974; gopher snakes), tongue flicking, as a measure of responsiveness to chemical stimuli (Cooper & Vitt, 1986; Eumeces laticeps) and to be affected by reproductive condition (Beuchat, 1986), ambient den temperature selection of overwintering snakes (Sexton & Hunt, 1980; Elaphe obsoleta and Coluber constrictor) and familiarity with the environment (Chelazzi & Calzolai, 1986; Testudo hermanni).

Although many investigators have carried out behavioral studies of radio-tagged snakes, most studies using thermally sensitive tags have used captive snakes in artificial environments (eg. DeWitt, 1967; Moore, 1978; Lillywhite, 1980; Gaywood, 1990), or chance observations of free-ranging snakes (eg. Fitch, 1965; Mushinsky et al, 1980; Gregory, 1984). Few studies have examined the thermal ecology of individual free-ranging snakes and the majority of these have involved tropical and sub-tropical snake species (Montgomery & Rand, 1978; Shine, 1979; Shine & Lambeck, 1985; Shine, 1987; Slip & Shine, 1988). However, De Bont et al (1986) force fed thermo-sensitive transmitters to smooth snakes (Coronella austriaca) and Petersen (1987) surgically implanted tags into garter snakes (Thamnophis elegans vagrans); both of these studies identified daily patterns of temperature fluctuation, an estimation of the 'preferred' temperature of the snakes and information regarding thermal criteria and the timing of morning emergence and evening submergence.

Correlation of the body temperature of ectotherms with a selection of recorded environmental variables is not straightforward and for this reason, several studies (Crawford et al, 1983; Petersen, 1987; Gaywood, 1990) have used the 'operative' temperature (Bakken & Gates, 1975), which was estimated by using physical models. Such models incorporate heat exchange through all routes and make some allowance for the inherent thermal qualities of the study animal, allowing the thermal environment to be effectively quantified in one simple variable (model temperature). Such an approach has clear advantages, but has limited value in a study of free-ranging animals, where it must be assumed that those animals are positively selecting their micro-environment, and where the model could be some distance from the experimental animals, thereby increasing the chances of receiving a different thermal input.

It is evident therefore that temperature and the way in which reptiles use thermal resources are central to their ecology, and a complete study of activity in grass snakes would be incomplete without an examination of the species' relationship with the thermal environment.

The use of a few known free-ranging individuals for the study of thermoregulation can expose a number of features of the behaviour of those individuals under a variety of field conditions. Such features include daily and seasonal patterns, the effects of different weather conditions on body temperature and snake behaviour and to a lesser extent, behavioral aspects of thermoregulation such as body posture and method of basking.

Development of thermally sensitive radio-tags was at an embryonic stage at the time of this research and the tags did not become available until midway through the first of the two seasons in which tags were implanted. A full year's data is shown, but is distributed over two seasons which were somewhat different in terms of weather. This will be made clear in the text where appropriate.

5.1.1 Aims of the research

The data presented in this chapter endeavour to explain the relationship between temperature and the various normal activities of the grass snake. The work examines various aspects of the thermal ecology of the species particularly as they relate to the activity of the animals in the field.

Much of the data does not lend itself to analyses of intraspecific variation in body temperature and associated behaviour and these are examined only where appropriate. The data were collected as part of a wider ranging study of the species, much of which relied on disturbing the animals as little as possible. As a consequence, much potential observational data was forfeited.

Despite their obvious value, no laboratory studies were carried out into the thermal ecology of the snake because the research was predominantly field based and laboratory studies would have made intensive use of limited equipment resources.

Two basic aspects of thermal ecology are considered: firstly the extent to which fundamental environmental factors influence body temperature and secondly, the subsequent behavioral response of the snakes to their fluctuating thermal condition.

5.2 Methods

Thermally sensitive transmitters were extensively tested and a design of a satisfactory standard suitable for long-term implantation in grass snakes became available in May, 1988 at which point one male and one female were implanted. The success of the tags enabled five further females and two further males to receive similar tags during 1988 and the following year. The volume of data collected varied over the two seasons depending on the availability of thermally sensitive transmitters and suitable snakes. However, data was collected for the periods of May to October, 1988 and April to July, 1989. Tracking periods for these animals are shown in Table 5.1.

1988		1989	
Snake	Tracking period (days)	Snake	Tracking period (days)
111	135	21	26
1161	40	22	10
122	76	32	82
172	51	12	123
192	69		

Table 5.1 Length of tracking periods using thermally sensitive radio-tags.

5.2.1 Data collection

Data presented in this chapter were accumulated in two ways: the first involved recording the body temperatures of tagged snakes on each occasion they were located; the second involved the use of recording equipment to log an individual's body temperature over periods of up to two days. Basic weather variables were logged on a routine basis and others were taken as point readings.

5.2.1.1 The thermally sensitive transmitters

Thermally sensitive transmitters (Model SS-2, Biotrack, Wareham) were capable of measuring body temperature to a theoretical accuracy of 0.1°C.

In practice, the pulse rate of the transmitters drifted slightly (the equivalent of approximately -0.5°C) after approximately two weeks of operation (Cresswell, pers comm; pers obs), but as the transmitter package was recalibrated on removal from the snakes, it was possible to allow for drift when converting pulse rates to temperatures. Thus, although a known accuracy of ±0.5°C was ensured, error in temperature calculation may have been as low as 0.1°C. The number of thermally sensitive transmitters that were available was limited, so no work was carried out to investigate the accuracy of the transmitters over a longer period, although Biotrack, the manufacturers of the equipment had test prototypes running continuously and were confident that drift was negligible after this initial period up until the time when battery power was becoming depleted (Cresswell, pers comm).

The design of the tags was broadly similar to those referred to elsewhere in this work, except that a thermistor was built into the circuit which caused the pulse rate of the transmitter to vary constantly with temperature. The range of the transmitters varied widely according to the pulse length of the signal and the habitat in which each animal was located, and was typically 50-100m. The transmitter and battery were sealed in epoxy resin and coated in paraffin wax to provide a waterproof, smooth and inert (bio-compatible) package suitable for implantation into the snakes.

The transmitters were calibrated by immersion in a water bath that was gradually heated from 2-40°C, recording the time taken for 25 pulse intervals (26 pulses) at 2-3°C intervals with a stop watch, and noting the water temperature at that time with a mercury thermometer of known accuracy. A calibration curve could then be drawn for each transmitter. Subsequent transmitter temperatures could be calculated by recording the interval of 25 pulses and reading the corresponding temperature from the graph.

The pulse rate of the transmitters was slow at low temperatures and became faster as temperature increased. The calibration curve of the transmitters at the end of each tracking period was very close to the curve at the time the package was implanted and a high degree of stability during the tracking period was assumed.

Two types of battery were used to power the transmitters. The initial tags supplied used two 1.2V mercury batteries with a field life of three months. Two transmitters used in late 1988 and 1989 used a larger 2.4V lithium battery which gave a potential field life in excess of one year. The latter produced a package which was considerably larger than the former, which limited its' use to large female snakes.

The temperature of the transmitter was assumed to correlate exactly to the temperature of the snake, although this may not always be the case. A time lag may exist between a change of snake temperature and the temperature of the tag. In practice, this appeared to be minimal, as on several ocassions both in the field and in the laboratory, recorded temperature was observed to change rapidly once a snake had moved into a different thermal environment.

More significantly, the body temperature of a snake can vary from one part of the body to another. For instance, a snake that basks partly in the open and partly under vegetation may show a considerable temperature gradient along its' body length, although Peterson (1987), reported no significant difference in the means and variance of oesophageal and cloacal temperatures or the means of body and cloacal temperatures. Furthermore, Webb & Heatwole (1971) reported that the head temperature of two uniformly heated species of python rose faster than temperatures over the rest of the body, so it would appear that in addition to a possible variable response to thermal microclimate, that the snakes themselves can to some extent influence the temperature distribution within their bodies.

5.2.1.2 Point readings

Snake temperature was always taken before approaching tagged animals in order to avoid disturbance. The snakes were then cautiously approached and activity and condition noted if possible. These readings were taken over random periods because up to six snakes were tagged at any one time and locating them could be very labour intensive, particularly when they were active or widely dispersed. Over the course of two seasons, data was collected from all hours of the day when the snakes were active. Several other variables including cloud cover (%), relative humidity (%) and time were also recorded at each location and a variety of others which are discussed elsewhere in this thesis.

Other point readings were taken from untagged moving and basking snakes encountered in the course of field work. Body temperatures were taken with a fast acting Schultheis type thermometer within fifteen seconds of catching snakes. This compensated to some extent for the lack of body temperature data obtained from moving tagged snakes. Such data was often not obtained in order not to disturb snakes and because it was often difficult to tell if a snake was basking or pausing whilst moving.

5.2.1.3 Automatic logging

Connection of a portable cassette tape recorder to the receiver allowed the pulses from the tags to be recorded; a home made timer plugged into the remote socket of the recorder allowed the tape to be switched on for a pre-set length of time at specified intervals. In most cases the recorder was set to run for twenty seconds every 15 minutes. This allowed a 24 hour period to be continuously recorded onto one side of a single tape. Most logged readings were taken at night, partly because the receiver was in more or less continuous use during the day and partly because remote logging was only possible if the snake stayed within range of the receiver. In order to conceal the equipment, it was necessary to place the antenna at or near ground level, which limited the range of the tags to only 10-15 metres. The tape recorder was tested before use to ensure that record and playback speeds were identical and long-life batteries used as these provided the least variable output.

5.2.1.4 Manual continuous logging

This was achieved by recording the body temperature of snakes manually in the field at fifteen minute intervals. It had the advantages that data could be obtained for moving animals and that more than one animal could be logged simultaneously although this was rarely achieved since two or more animals were rarely in range. Total recording periods using this method were shorter than those logged remotely and were typically of four to five hours duration.

5.2.1.5 Weather recording

In the first of the two seasons, a basic, home-made logger was used which recorded shade air (at 1m) and unshaded substrate (at 1cm depth) temperatures at hourly intervals to the nearest whole degree. The machine though was rather unreliable and on several occasions did not operate correctly and the data had to be abandoned. In mid-1988, a Grant Squirrel was made available which enabled readings to be made every 15 minutes with greater reliability. In June, 1989, the Meteorological Office at Bracknell, Berkshire kindly made available a solarimeter which could be connected to a Grant recorder which logged averaged readings over a preset period. The solarimeter was fixed to the top of a caravan and unshaded, thereby giving an accurate representation of total incoming solar radiation. In addition, a basic monthly weather data sheet was purchased from Southampton weather centre, which provided maximum and minimum temperatures, sunshine hours, rainfall amount and rainfall duration as a series of daily totals. Southampton weather centre is situated some five miles south of the study site, but the gross weather data was assumed to provide a satisfactory indication of the general weather at the Chilworth site.

Weather data was also collected in the field at the time of each snake observation. Relative humidity, the presence of rain and percentage cloud cover were all noted at each location. The latter was achieved by fitting a 4 cm hollow plastic tube with a cross hair and pointing it randomly at the sky twenty times at an angle of 45° or greater to the ground. Cloud cover was thus calculated to the nearest 5%. Air temperature data (at Im in shade) was also calculated at many locations but data from the remote temperature loggers was used to provide consistency. In any case, correlation of manual and logged air temperatures was very high ($r=.985$; $n=310$; $p>0.001$)

5.2.2 Data analysis

The use of regression analyses in the study of snake thermoregulation has been used by several workers (Petersen, 1982; Gent, 1988) in an attempt to show the relationship between body temperature and environmental variables. Since snake body temperatures do not fluctuate about a mean, but between upper and lower limits (see Huey, 1982), such a data set is unlikely to be normally distributed. Although much of the data presented here satisfies the criterion of independence, parametric regression techniques and statistical tests which assume normality are avoided.

Male and female data have been combined for some analyses as the data aims predominantly to show relative rather than absolute values (ie. no attempt has been made to examine critical maxima and minima or to precisely measure the extent and success of thermoregulation, as studied by Gaywood (1990) for all three native British snakes).

5.2.3 Relationship of body temperature with environmental variables

5.2.3.1 Air and substrate temperatures

A comparison of male and female body temperature was carried out using Mann-Whitney and two sample Kolmogorov-Smirnov tests. The relationship between body temperature/air temperature (Tb/Ta) and body temperature/substrate temperature (Tb/Ts) are examined graphically and using Spearman's rank correlation. Plots were drawn to represent the difference between Tb/Ta and Tb/Ts during basking, movement and concealment. Plots are shown of logged temperatures on days with generally different weather conditions.

5.2.3.2 Cloud cover

Median Tb was calculated for each of 21 categories of cloud cover. The data was sub-divided into male and female categories because of the apparent difference in male and female body temperatures and basking behaviour. Some of the data sets were therefore small and statistical analysis was only possible on some categories, in which the difference between male and female Tb was examined using Mann-Whitney tests.

5.2.2.3 Insolation

Logged data of simultaneous insolation and body temperature is presented to examine how insolation (independent of temperature) influences snake temperature.

5.2.4 Emergence, submergence and night temperatures

Logged data are examined to investigate criteria for morning emergence and evening retreat of individual snakes. Plots are shown of logged night time temperatures and these are discussed.

5.2.5 Thermophilic response to feeding

On two occasions, logged body temperatures were available for snakes before, during and after eating. Behaviour and body temperatures at these times are examined to investigate a possible thermophilic response to feeding.

5.2.6 Thermophilic response to sloughing

It was common for radiotracked snakes to remain in one location for several days and little attempt was made to observe them at these times for fear of disturbance. As a consequence, sloughing was usually only discovered after the event, when the shed skin was found at the location. Only one snake that was known to be in an inter-slough condition had a thermally sensitive transmitter and three days temperature are shown for this animal, one day before and two days after sloughing.

5.3 Results

5.3.1 Relationship of body temperature with environmental variables

Median body temperatures of all point readings (n=941) were 23.7°C (males) and 26.7°C (females). A Mann-Whitney test indicated that there was a significant difference between the two distributions (U=5.8; n1=372; n2=569; $p<0.001$). Frequency distributions of male and female body temperatures are shown in Figure 5.1. The most frequent temperatures recorded fell between 15-35°C and there is some indication that the distributions are bi-modal, with a lower frequency in the 27-29°C range. The female distribution is negatively skewed, whereas this skew is virtually absent from the male distribution. A two-sample Kolmogorov-Smirnov test indicated that the two distributions were significantly different ($D=0.236$; $n_1=372$; $n_2=569$; $p<0.001$).

Figure 5.2 shows scatter plots of Tb/Ta for males and females. Both sexes were able to raise Tb markedly even at low Ta. At Ta's of less than 14°C, Tb always exceeded Ta, but when Ta exceeded 15°C, Tb's lower than Ta were recorded in both sexes. Spearman's rank correlation of Ta/Tb was calculated for both sexes (males: $r_s=0.604$, n=372 $p<0.001$; females: $r_s=0.53$; n=569; $p<0.001$)

Figure 5.3 shows scatter plots of Tb/Ts for males and females. Both sexes, but particularly males frequently raised their body temperature to a level higher than that of the substrate. Spearman rank tests showed a significant correlation between Tb/Ts in both male snakes ($r_s=0.672$; n=84; $p<0.0001$) and females ($r_s=0.267$; n=149; $p<0.001$).

The maximum Tb observed was 37.1°C (females) and 34.6°C (males) and the minimum 8.2°C (females) and 8.4°C (males).

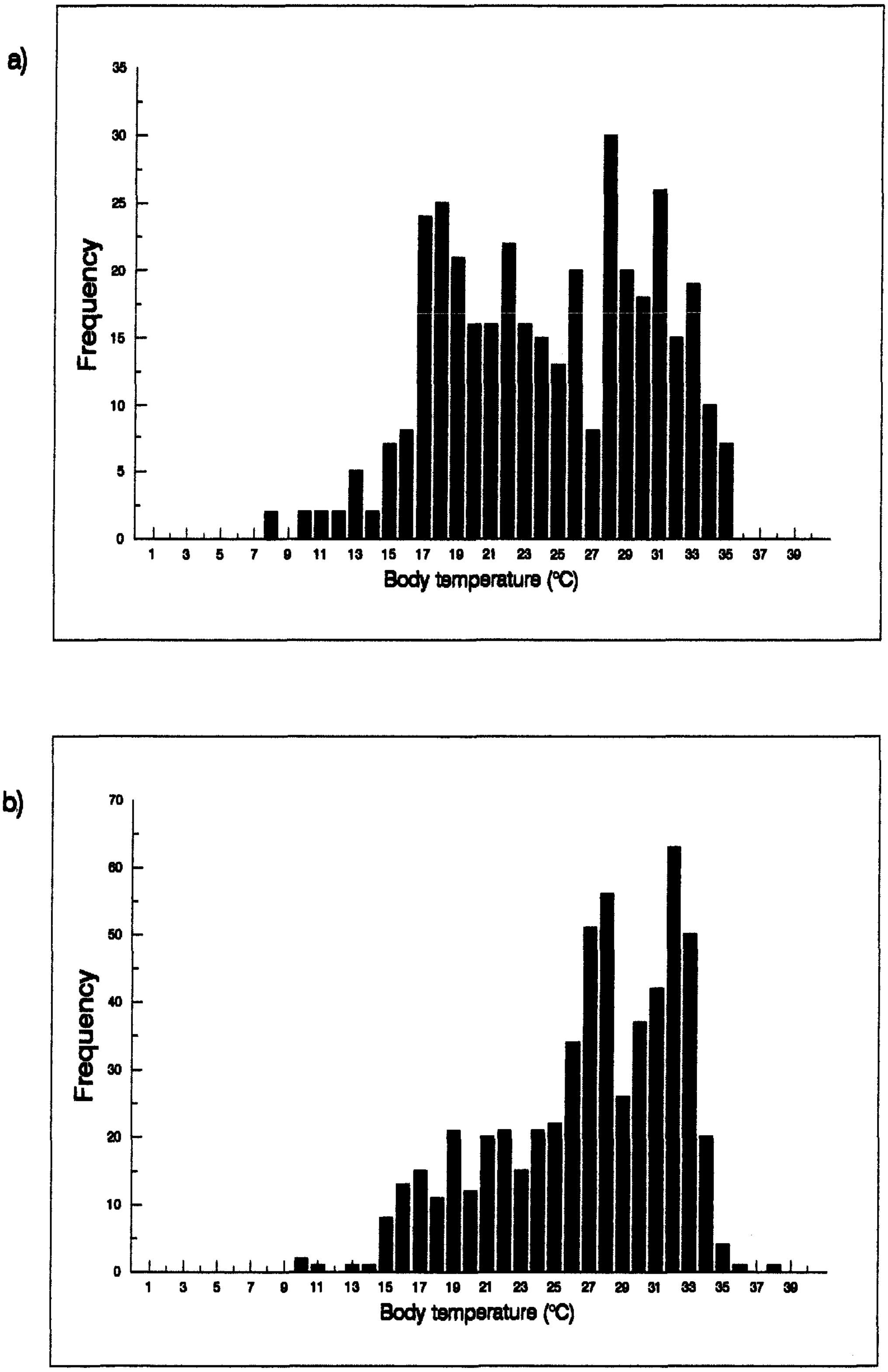


Figure 5.1 Frequency distributions of the body temperatures of male and female grass snakes, taken from point readings throughout 1988 and 1989.
a) Males (n=(372)
b) Females (n=569)

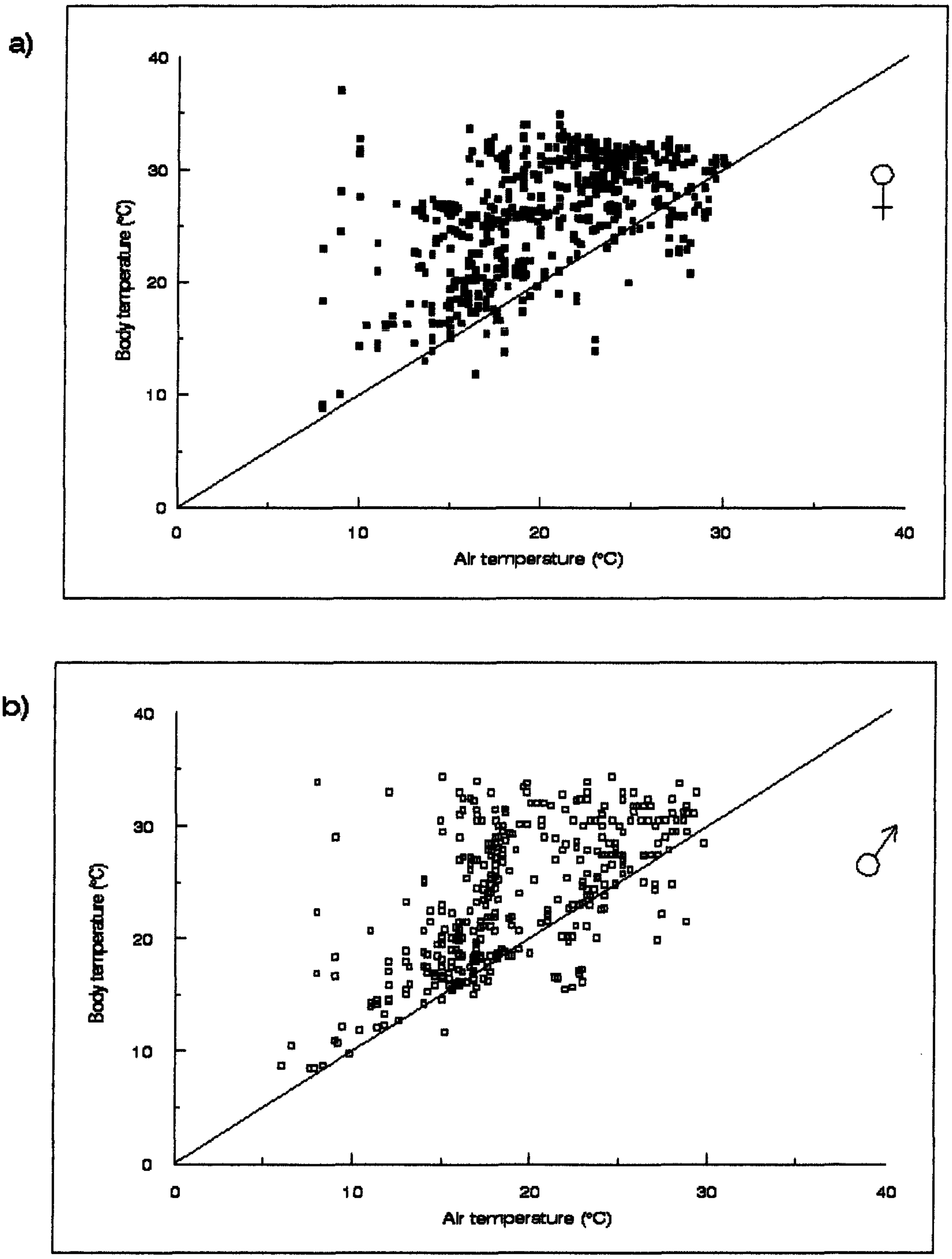
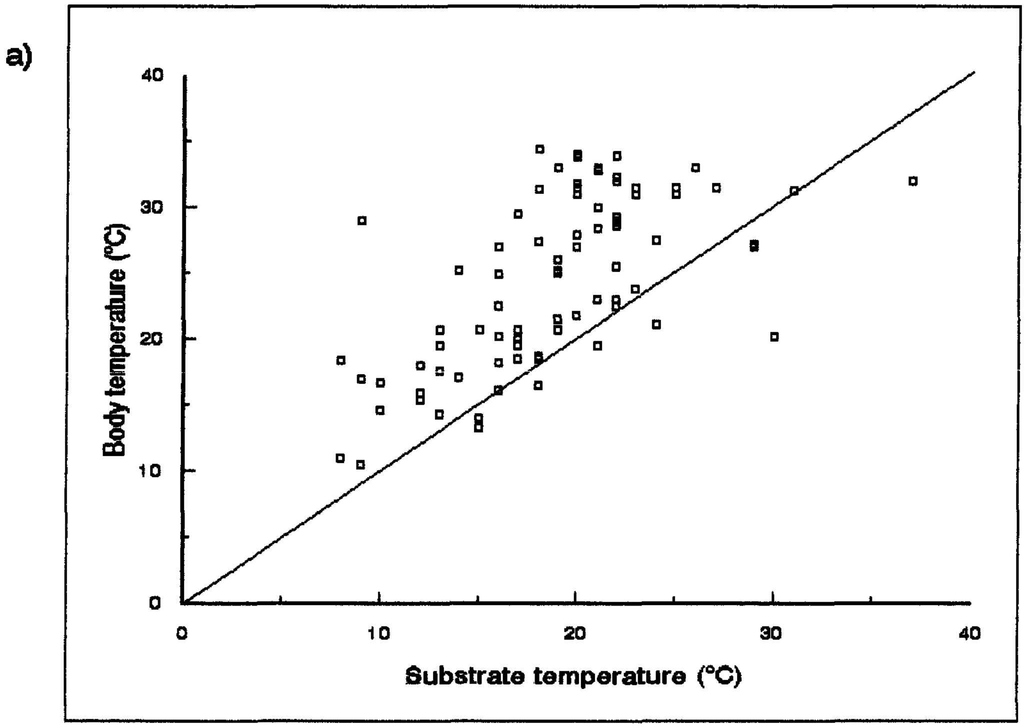


Figure 5.2 Scatter plot of grass snake body temperature (Tb) and shade air temperature (Ta), taken from point readings throughout 1988 and 1989. The fitted line shows Tb=Ta.
a) Females (n=569)
b) Males (n=(372)



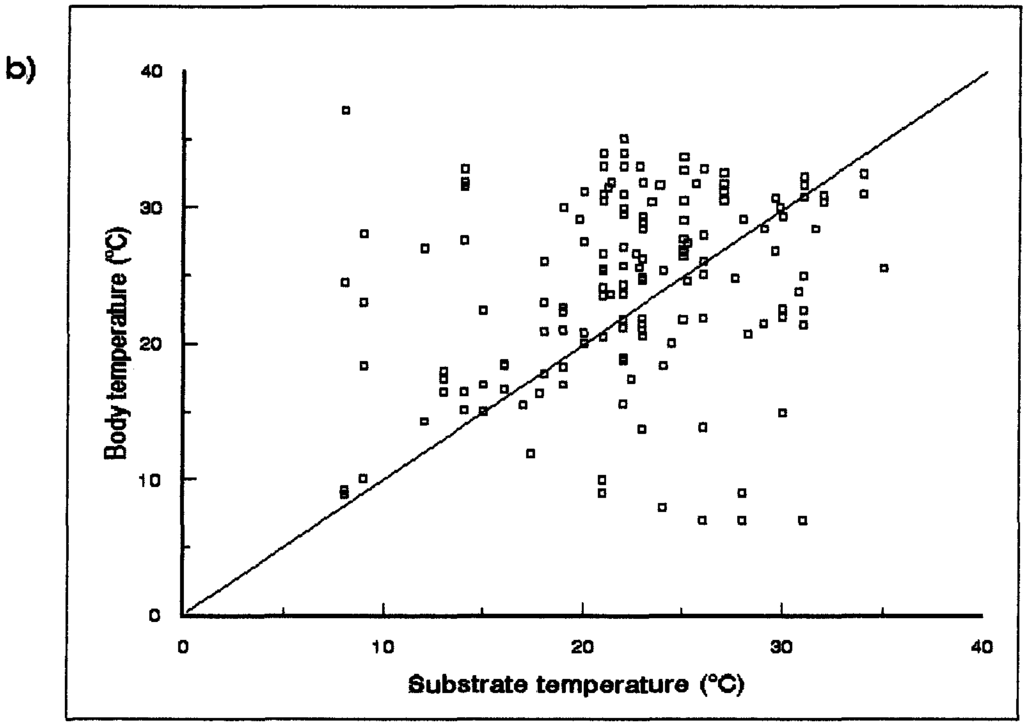


Figure 5.3 Scatter plot of grass snake body temperature (Tb) and substratum temperature (Ts), taken from point readings throughout 1988 and 1989. The fitted line shows Tb=Ts.
b) Males (n=(84)
a) Females (n=150)

Figure 5.4 consists of 30 graphs which show a selection of plots of body temperature taken predominantly from stationary snakes which were continuously logged. They have been selected to show various aspects of thermoregulation in the species and each is referred to in the discussion. They are not in chronological order, but the layout has been chosen to aid ease of explanation. A key is shown for each set of graphs and abbreviations used are as follows: Tb = body temperature; Ta = air temperature; Ts = substrate temperature.

Graphs a) and b) show logged Tb for a continuous 50 hour period during which the weather was warm and clear, and provide an overview of the nature of thermoregulation of an adult female snake. The snake was concealed under a piece of tin for much of the day and moved a distance of approximately 10m in the early evening to spend the scotophase underground. The snake maintained a high daytime Tb, a slow evening cooling rate, a relatively high nocturnal Tb and a rapid warming rate in the mornings.

Graph c) shows a typical warming phase, with Tb increasing to over 30°C and remaining high despite little or no change in Ta or Ts.

Graph d) shows data from a partly cloudy day; the snake raised Tb to 28°C and was moving between 14.30 and 15.00, during which time Tb dropped significantly. At 15.00, a prolonged rain shower began, and the snake took refuge, maintaining a constant but lower Tb, independent of Ta.

A rapid warming phase can again be seen in graphs e) and f) after nights where Tb was maintained at a constant level. Although it is not clear from the graph, the warming phases were initiated by direct sunlight reaching the refuges of the snakes, which in each case were on the south facing edge of a woodland.

Two types of cooling phase are shown in graph g). Between 11.30 and 14.30, the weather was sunny and warm, during which time the snake maintained a consistently high Tb. At 14.30, cloud cover increased to 100% and the snake was apparently unable to maintain such a high Tb, although the lower Tb was more or less constant. At 18.15, the snake took refuge and Tb dropped rapidly to a constant nocturnal level.

On cool, cloudy days, the snakes very often failed to emerge; this is shown in graph h). The morning of 11-5-89 was dull and dry and the constant nocturnal Tb was maintained at least until 11.30, independent of Ta and Ts.

Graphs i) to s) are paired, the left in each case showing body, air and substrate temperatures and the right showing body temperature and insolation for the same period. These data, when placed on the same graph produced plots that were difficult to read and the method used gave a preferable result.

Graphs i) and j) show a decline in Tb following a drop in Ts independent of Ta. Field observation showed that this occurred when the location of the snake was shaded from direct sunlight at 15.30 and 16.30 hrs respectively.

Graph k) demonstrates that early in the day, Tb was more closely related to both Ts and insolation than to Ta, from which it is apparently independent. The snake appears to track Ts fairly closely except during the middle of the day when Ts rises to very high levels. Tb is independednt of insolation in the latter part of the day. Thermoregulation is apparently imprecise and Tb fluctuates considerably, despite clear skies and therefore more or less constant insolation.

In graph l), the relationship is again complex, although the snake again maintains a very high Tb even late in the day when insolation is low.

Graphs m) and n) show the same snake on two days in different environments under different conditions. The former demonstrates a constant nocturnal Tb with a rapid rise in Tb as direct insolation is provided on a sunny morning. In the case of the latter example, the snake was located throughout the logging period in a rotting tree stump and was able to maintain a very high nocturnal temperature. At 8.00, continuous rain began and the snake cooled markedly, with a Tb lower than Ta and Ts at the cessation of logging.

Graph o) shows a different snake in the same tree stump during the day. A consistently high Tb was maintained until 18.30, when it dropped for reasons unknown, although possibly because the snake moved further underground, which was indicated by a loss in signal strength from the transmitter.

Graph p) is similar to graph h) and shows a constant nocturnal Tb, which barely altered in the dull conditions of the following morning. The snake showed a slight rise in Tb during a brief sunny period (as indicated by the rise in insolation), but failed to emerge from the night refuge during the logging period.

Graphs q), r) and s) show patterns for two snakes in the tree stump. Both snakes spent most of the time inside the stump, only occasionally emerging to bask. These periods are shown by a more fluctuating Tb. A very constant Tb, virtually independent of environmental variables was maintained while in the tree stump (graph q) and even during a sharp drop in Ta and Ts (graph r)), the drop in Tb was less acute. The rapid fluctuations in Tb at the end of the day on the 25-6-89 (graph r)) were caused by disturbance during observation of the basking snake and not by environmental factors.

Finally, graph s) shows a rapid decrease in Tb early in the morning followed by a rapid rise, despite a previously constant day and night Tb in the region of 27°C. The loss of data indicated was caused by the disappearance of the transmitter signal, suggesting that the snake had moved underground; the reasons for this movement were not known.

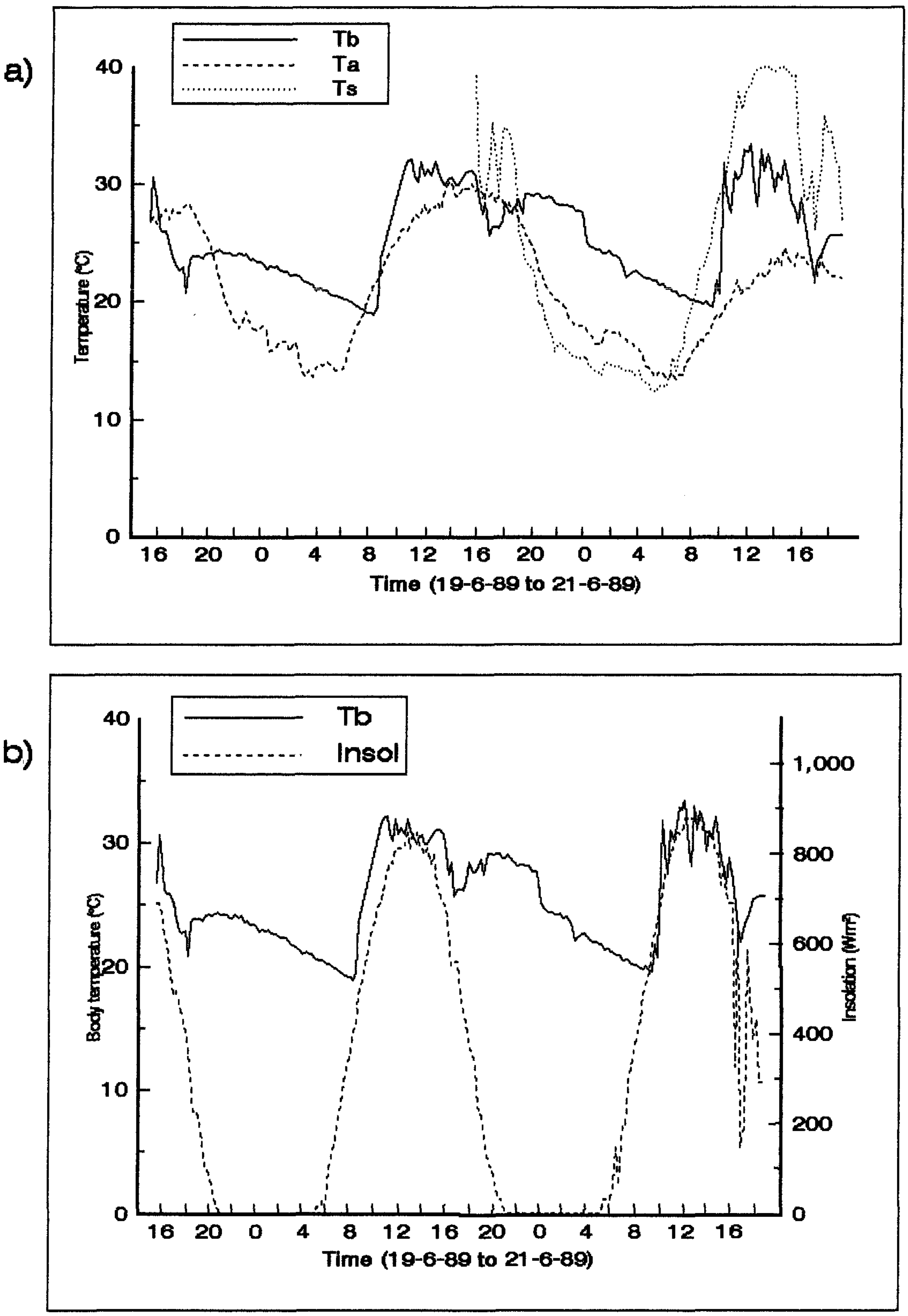


Figure 5.4 a) to b) Plots of logged readings of body temperature from a radio-tracked female snake, showing the relationship to: a) air and substrate temperature
b) insolation

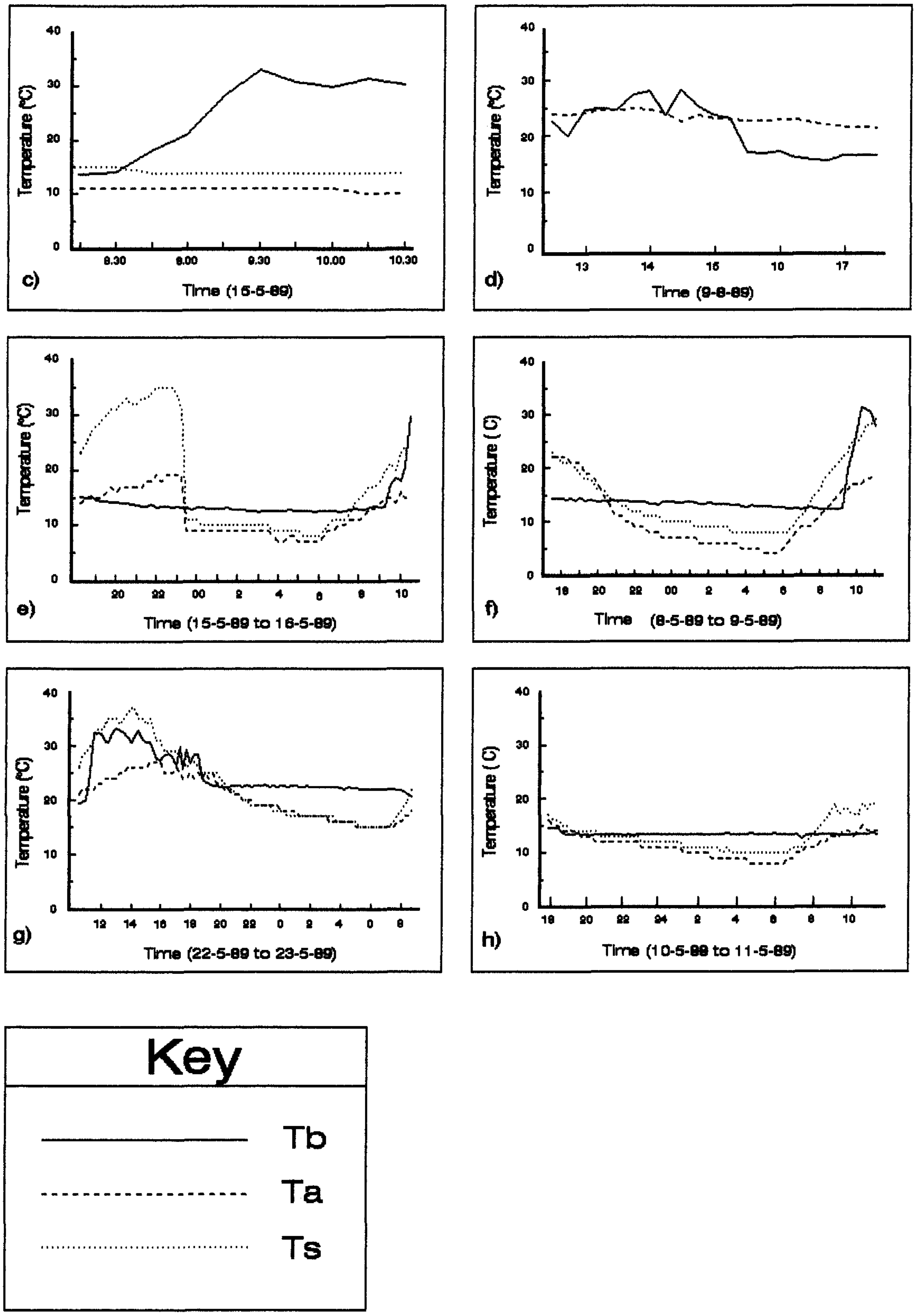


Figure 5.4 c) to h) Body, air and substrate temperatures of continuously logged stationary grass snakes.

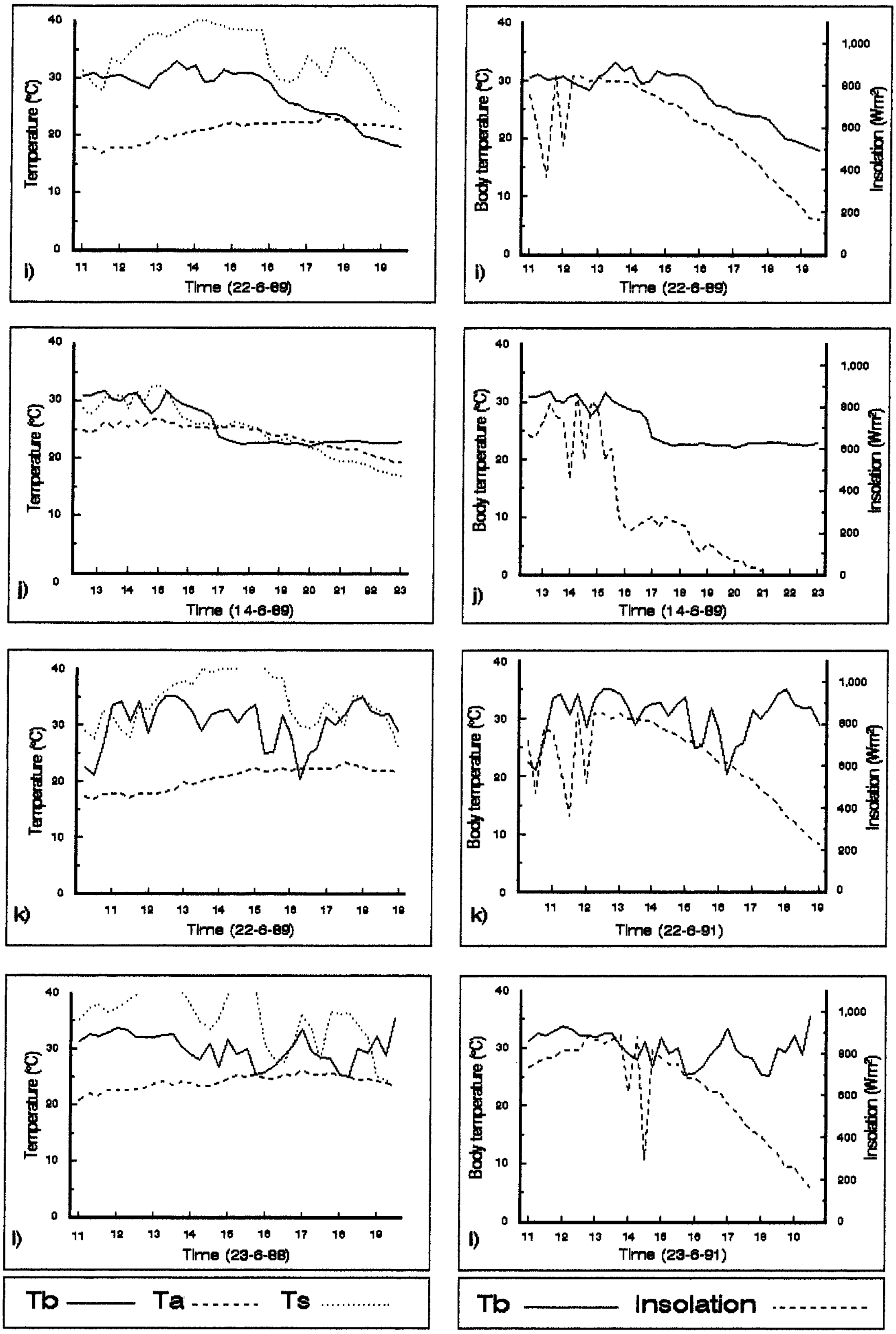


Figure 5.4 i) to l) Body, air and substrate temperatures (left column) and body temperature and insolation (right column) of continuously logged stationary grass snakes.

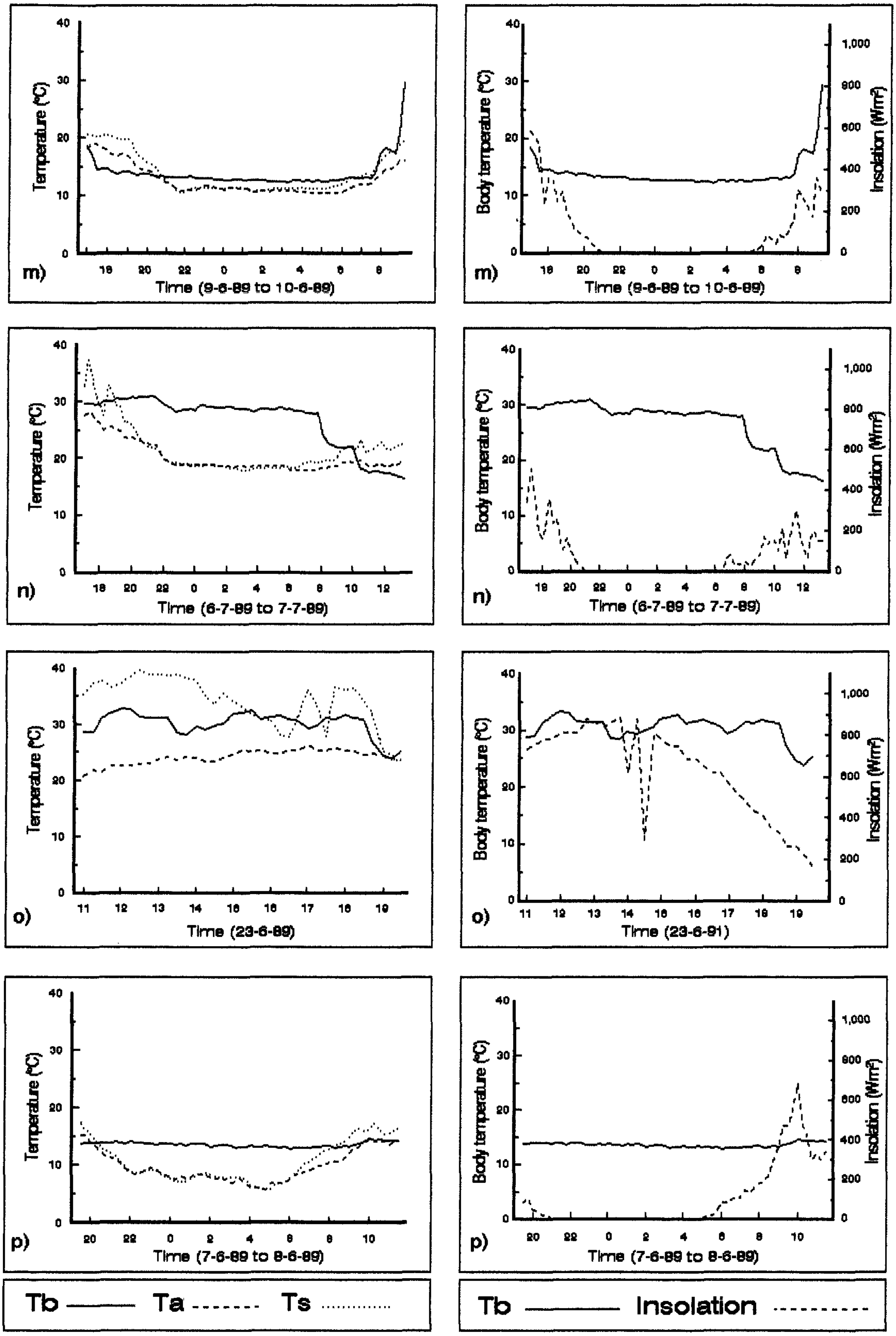


Figure 5.4 m) to p) Body, air and substrate temperatures (left column) and body temperature and insolation (right column) of continuously logged stationary grass snakes.

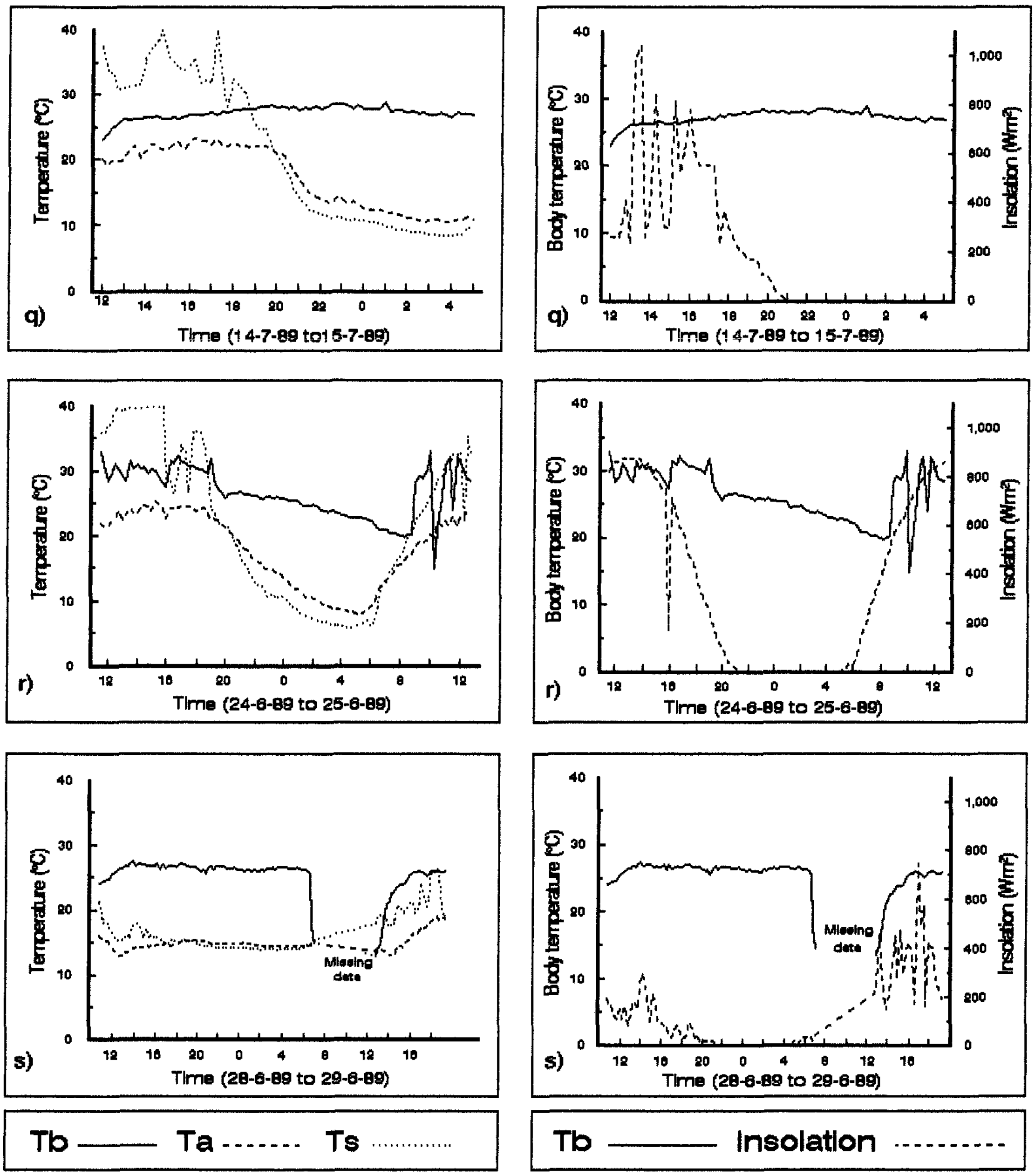


Figure 5.4 q) to s) Body, air and substrate temperatures (left column) and body temperature and insolation (right column) of continuously logged stationary grass snakes.

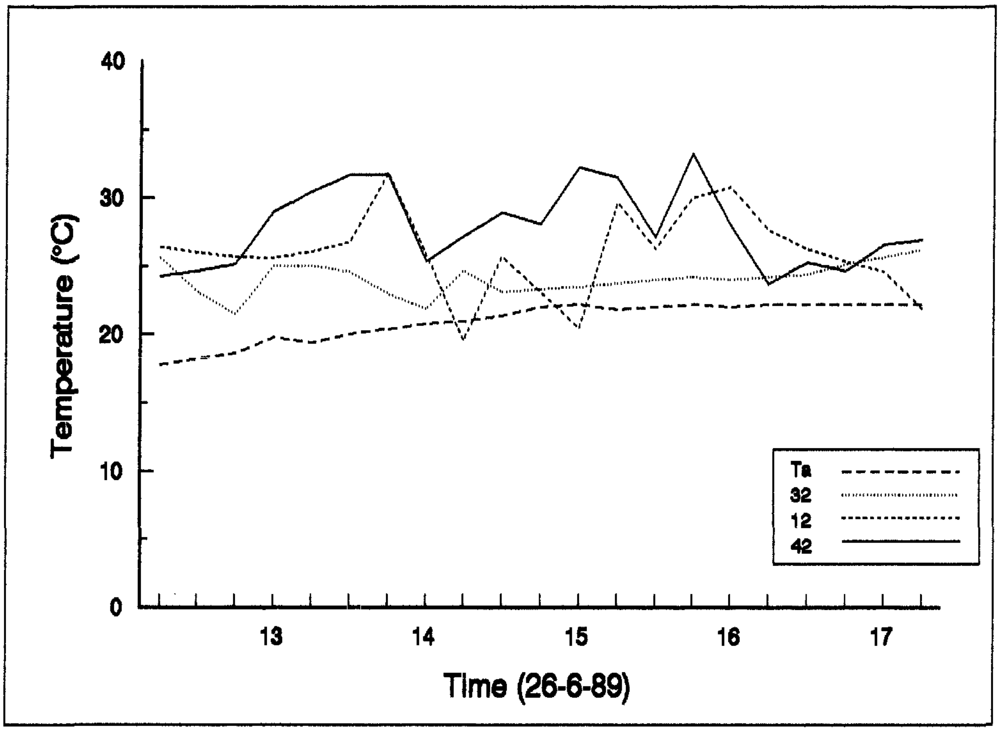


Figure 5.5 Plot of the body temperatures three simultaneously logged female grass snakes (Nos. 32, 12 & 42).

In Figure 5.5, plots are shown of three female snakes simultaneously logged. One snake (32), was concealed in a tree stump and maintained a more constant Tb than the other two, which were basking on the edge of a woodland and on the edge of a meadow respectively.

Figure 5.6 shows median, maximum and minimum temperatures achieved by male and female snakes under 21 categories ranging from 0-100% cloud cover. Best fit lines calculated for the median temperatures gave slopes of -0.1 (females) and -0.053 (males). There was no significant difference between male and female distributions for any cloud cover categories except at the 10% ($p<0.05$) and 25% ($p<0.05$) categories when U-tested. It is also clear that snakes can reach high body temperatures even under conditions of high cloud cover.

5.3.2 Thermal ecology of moving snakes

Figure 5.7 shows body temperature and activity detail of a male snake which was foraging on a warm, sunny day, partly in an open environment

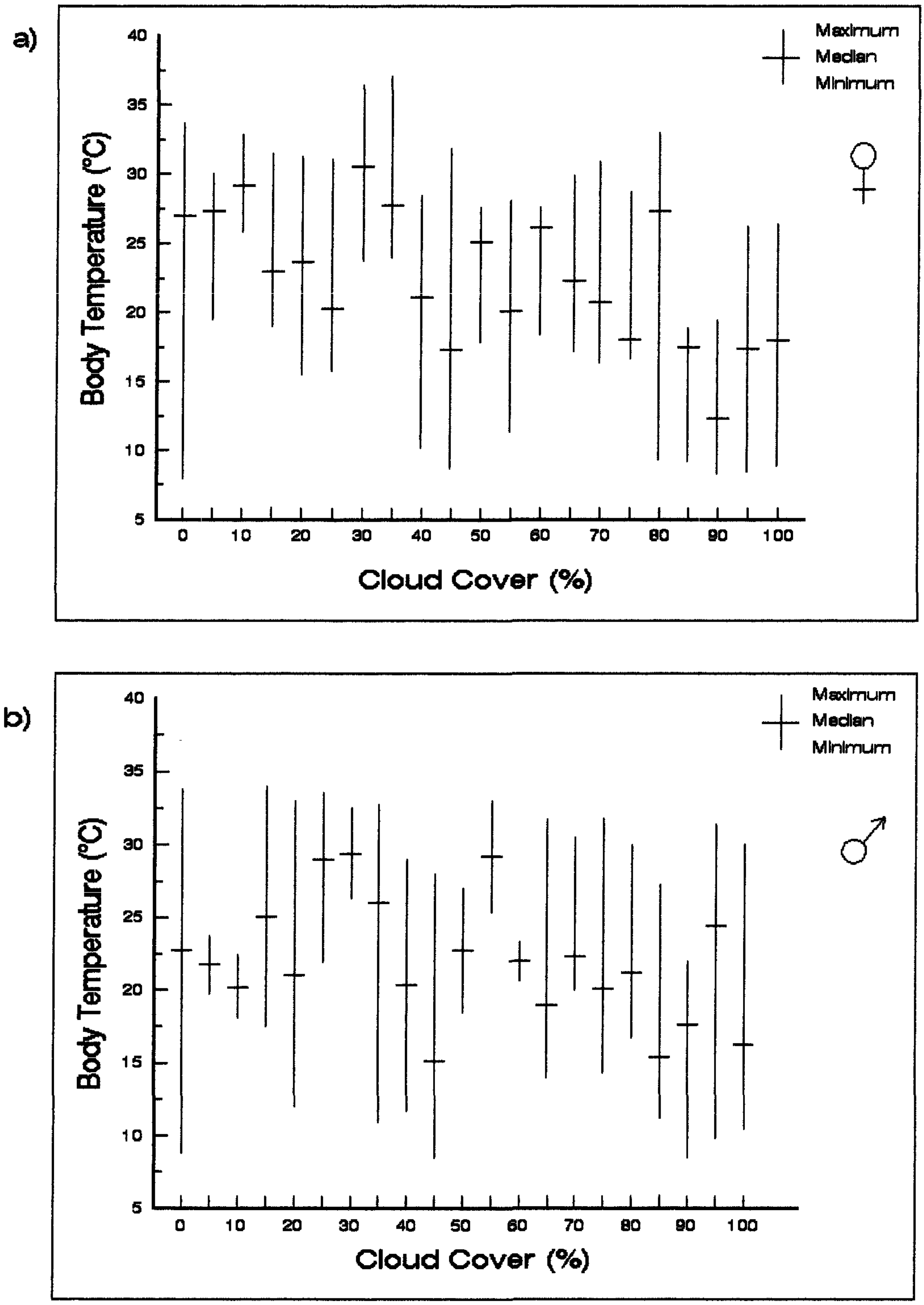


Figure 5.6 Plot of the maximum, minimum and median body temperature of grass snakes against percentage cloud cover. The graph represents data from all point readings throughout 1988 and 1989 (n_{min}=4, n_{max}=27).

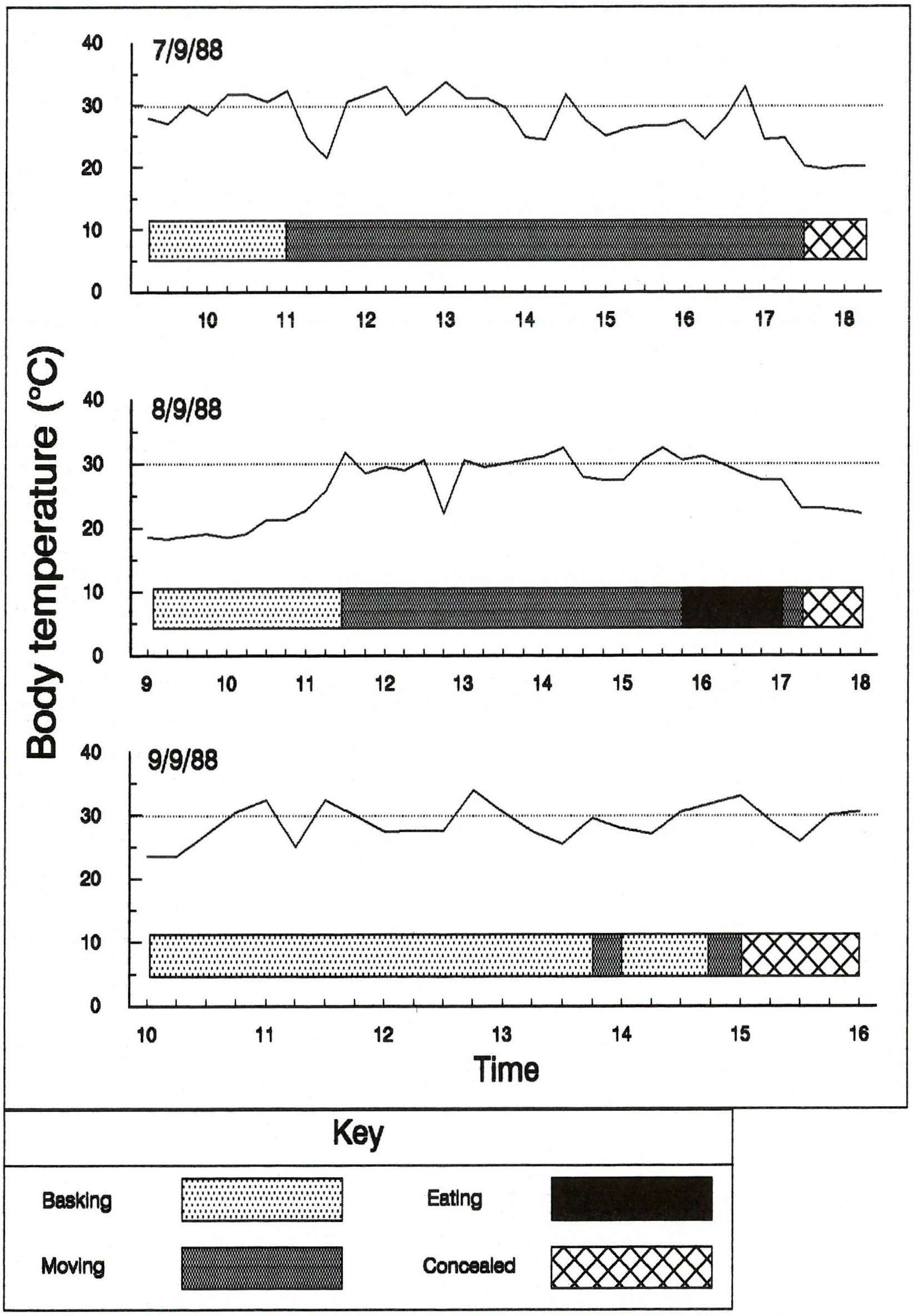


Figure 5.7 Plots of a foraging male snake on three consecutive days, showing body temperature before, during and after feeding. The horizontal bar shows activity at the time, with the solid black pattern repre-senting the time spent consuming an adult toad. Observations of the snake were made at fifteen minute intervals. The dotted horizontal lines at 30°C have no ecological significance, but are drawn so that relative temperature differences can more easily be seen.

fully exposed to the sun, which meant that the snake may have been thermoregulating to prevent overheating as well as to raise Tb; Tb fluctuated between 20-34°C. Field observations at the time showed that the snake did not move continuously, but frequently paused for periods of between one and five minutes before continuing to move.

Figure 5.8 shows similar data for a female snake foraging in and around a pond. Although the weather was again warm and sunny, the snake maintained a body temperature several degrees below the previous example, but was still active and alert. The biotic environment around the pond consisted of long grass and dense sedge and willow which largely obscured the sun. The snake made little attempt to bask and apparently thermoconformed throughout the foraging period. Much of the movement took place in the pond, although this had little effect on Tb.

The female snake moved only short distances after consuming prey and even during this time (14-6-88), maintained a high Tb, except for one occasion, when disturbed by passers-by (at 12.30 hrs).

5.3.3 Thermophilic response to feeding

Both of the foraging snakes maintained consistently high body temperatures for the periods immediately after consuming prey. Again though, the temperature patterns were different. The male snake (Figure 5.7) basked in a woodland edge, which was densely overgrown with bracken and brambles. The weather on the day (9-9-88) consisted of intermittent sun and cloud and this apparently affected the ability of the snake to maintain a uniform Tb.

In contrast, the female snake (Figure 5.8) basked on top of a wall covered with cotoneaster, (Cotoneaster horizontalis) on a warm and uniformly bright though hazy day. Such an environment is presumably more thermally constant than an overgrown woodland edge. Several other point readings were made of this snake during the day and showed temperatures of 27.8, 31.7, 31.3, 26.4, 29.2 and 29.2°C, which suggest that the snake maintained a high Tb throughout the day.

5.3.4 Thermophilic response to sloughing

Figure 5.9 shows data for a male snake one day before and two days after sloughing. Weather conditions were broadly the same for the two days, although the morning of the 14-8-88 was somewhat hazy. Body temperature on the day before sloughing was maintained at a consistently high level, whereas two days after sloughing, body temperature reached a maximum of 27°C and was more typically around 20°C.

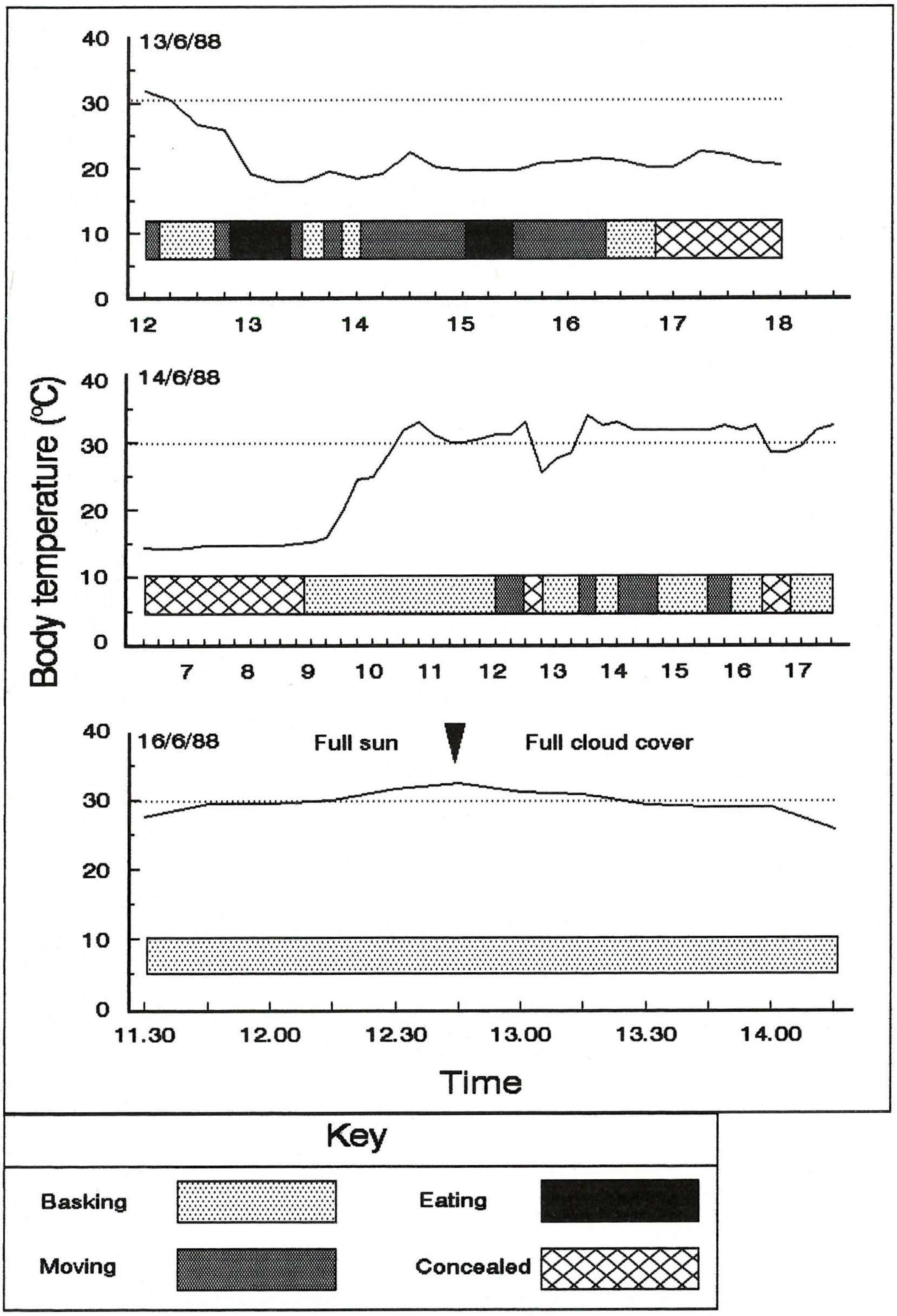


Figure 5.8 Plots of a foraging female snake on three consecutive days, showing body temperature before, during and after feeding. The horizontal bar shows activity at the time: the solid black pattern represents the time spent consuming tadpoles in a pond. Observations of the snake were made at fifteen minute intervals. The dotted horizontal lines at 30°C have no ecological significance, but are drawn so that relative temperature differences can more easily be seen.

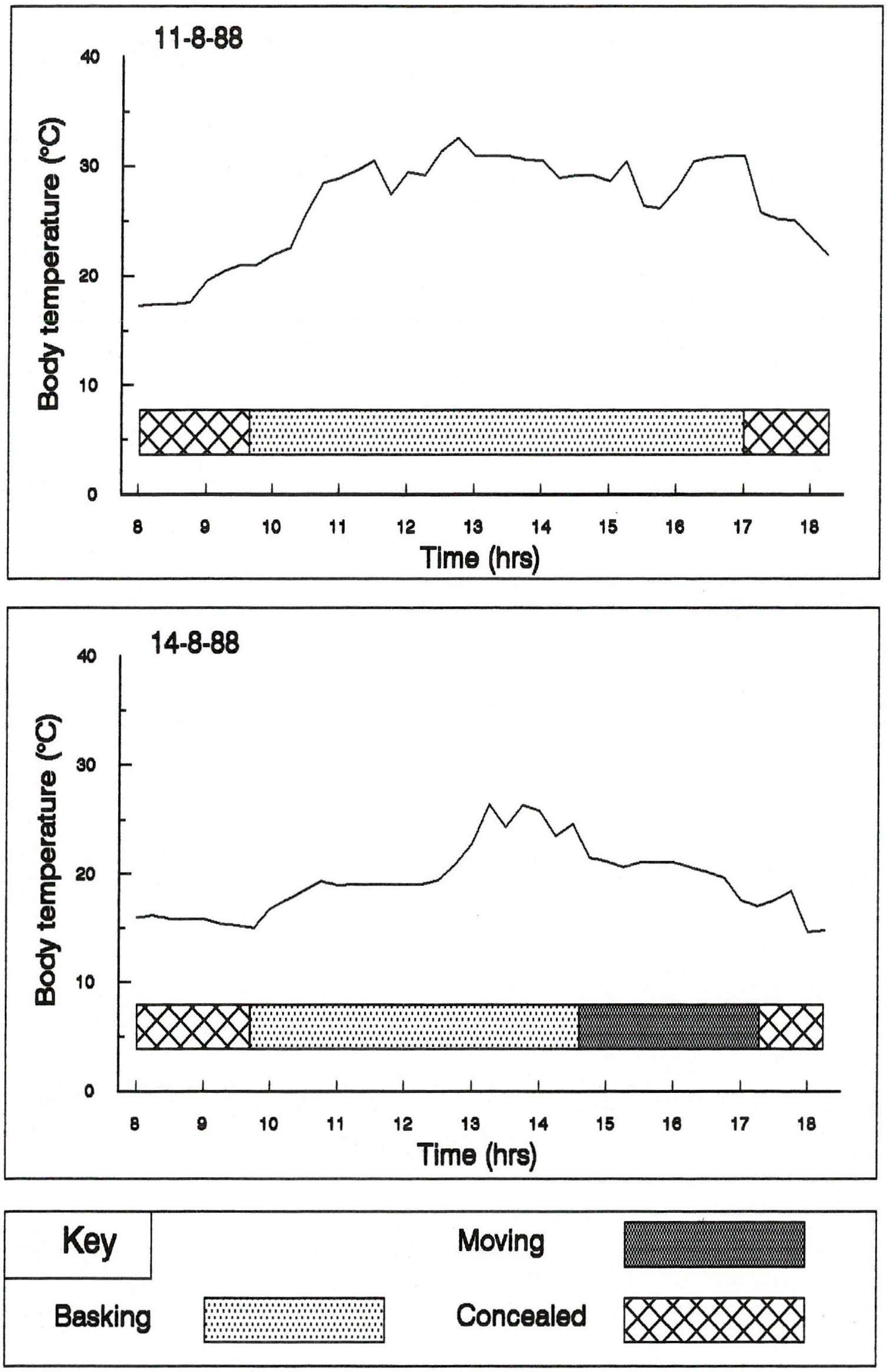


Figure 5.9 Plots of body temperature for a male snake one day before and two days after sloughing. The horizontal bars show activity during this time. Weather conditions were broadly the same on each day, with intermittent sun and cloud, and the maximum air temperatures recorded were 19.4°C (11-8-88) and 18.6°C (14-8-88). Observations of the snake were made at fifteen minute intervals.

5.4 Discussion

5.4.1 Overview and inter-sexual comparison

The range of body temperature (Tb) exhibited by the sexes was broadly similar and fell between 8-38°C. With the exception of sexual functions, many physiological functions, in particular metabolic rate, are likely to be broadly comparable between sexes, so this is not surprising. However, the data showed between sex differences in the distributions of Tb that were quite evident.

The higher median Tb of females and the difference in the distributions of male and female Tb suggested that either females are more successful at reaching and/or maintaining higher temperatures than males or that they require a body temperature than males. These results are similar to those presented by Goddard (1981) for the smooth snake, Coronella austriaca, who noted a negative skew in female Tb and a positive skew in male Tb.

The bi-modality in the distributions of both male and female Tb is more difficult to explain. The basking behaviour of the grass snake is such that individuals are vulnerable to predators while lying out (see Huey, 1982; Shine & Lambeck, 1985; pers. obs.) and there may be a trade off between this behaviour and attempting to reach Tb's approaching the upper limit in non-optimal conditions, thus resulting in a high number of readings at the lower modal level. The lower frequencies observed between the two modes may merely indicate that snakes basking in weather conditions where they are able to reach such a Tb are in a position to raise it further to levels approaching the preferred maximum.

The environmental conditions in which Tb recordings were made varied widely. It is also possible therefore that Tb's which were recorded in the higher modal category were of snakes which were basking in thermally unlimiting conditions and thereby able to reach a body temperature at or approaching the preferred maximum. Snakes which were basking in thermally limiting conditions in which high body temperatures were unobtainable would necessarily fall into the lower modal category.

The width of the modal 'bands' is considerably narrower in the female distribution than in that of the males. Again this suggests that females are more precise thermoregulators (ie. capable of maintaining a more constant Tb) than males. The larger size of the females means that the surface area to weight ratio is lower and therefore Tb is less likely to fluctuate as much as in the smaller males.

5.4.2 Relationship of body temperature to environmental variables

The correlation between Tb and both air temperature (Ta) and substrate temperature (Ts), were generally higher than expected considering the number of variables that can potentially affect Tb. Quite clearly individuals of both sexes can reach Tb's approaching the preferred maximum over a wide range of air and substrata temperatures, although presumably on cool days, insolation must have been high (ie. clear skies). Other studies have also found a high correlation between these variables (Goddard, 1981; Slip & Shine, 1988; Gent, 1988).

Tb often fell below both Ta and Ts, although the plots in Figures 5.2 & 5.3 do not show the time of day or the weather conditions at this time. The one exception was in the case of female Tb and Ts, where female Tb was frequently lower than Ts, by up to 25°C and where the Spearman co-efficient was lowest (r_s=0.267); the reasons for this are unclear, but the subject is discussed in greater depth below.

The 50 hour plots shown in Figure 5.4(a)(b) show a clear pattern of rapid warming in the morning, followed by one or more plateau periods of consistent high Tb followed by more gradual cooling overnight. This is consistent with the Tb patterns of other British snakes, although it differs from the warm climate diamond python Morelia spilota which had one shorter basking period of approximately one hour, after which it retreated under cover for the rest of the day, occassionally emerging at night to forage (Slip & Shine, 1988). This species has a lower heating rate than the much smaller grass snake and presumably a much higher thermal inertia, enabling much more time to be spent under cover hidden from predators, whilst maintaining a fairly high Tb. In warm climates, reptiles may also often be able to maintain a high Tb while thermoconforming, thus reducing the need to bask in the open. Grass snakes conversely appear to make use of a greater part of the day when thermal conditions are suitable, probably because they are unable to maintain a high Tb without at least some direct insolation. It was noticeable on very warm, sunny days that grass snakes rarely basked in the open and were apparently able to maintain a high Tb while under cover.

The Tb of the snake in the two plots tracks insolation closely during the day, whilst there is a lag between the morning rise in Ta and Ts and an increase in the Tb of the snake. This suggests that direct insolation may induce emergence, although the data shows that substrate warming may also be a contributory factor. Air temperature has no apparent effect on emergence.

Evening submergence in this case was almost certainly caused by the disappearance of direct sunlight reaching the piece of tin under which the snake was concealed during the day. On the 20-6-89, the snake was known to leave for the evening refuge underground at 17.05 hrs; the refuge was exposed to sunlight until 18.30 hrs, allowing the snake to raise Tb again.

The fluctuations during the plateau period could be due to a number of factors. The first is an inability to thermoregulate precisely; the second is that thermal conditions under the piece of tin may have varied, eg. with insolation; thirdly, and most likely in this case, is that the snake shuttled back and forth from under the tin as the temperature became too high under the tin. There is no firm evidence for this other than the snake was observed in the open for a brief period during the 21-6-89.

5.4.2.1 Emergence

Figures 5.4(e)(f)(m) and (r) show plots of morning emergence. In all four cases, emergence occured after Ts had risen above or equalled the Tb of the snake. In two cases, ((e) and (f)), Ta had also exceeded Tb. Insolation data is shown in two cases (m) and (r) in these examples, show that emergence occured when isolation was at about 100Wm^2 and 560Wm^2.

On cool, cloudy mornings, snakes often did not emerge at all (Figure 5.4(h)(p)). The graphs show that even despite a significant increase in Ts, the snakes stayed in their night refuge and behaved as thermo-conformers.

This, together with the data in the previous section, suggests that emergence is initiated predominantly by an increase in substrate temperature and that the snake will then emerge if there is sufficient insolation and therefore sufficient opportunity to raise Tb.

5.4.2.2 The warming phase

The morning warming phase shown in Figure 5.4(c) has been presented to show how the rise in Tb can be independent of the measured environmental temperatures. The snake raised Tb by approximately 20°C in 75 minutes, during which time both Ta and Ts dropped slightly. Insolation data is not available for this period, but it is reasonable to assume that the snake basked in more or less full sunshine for this period, and operative temperatures at the bask sites must therefore have been high.

Other more typical warming phases are shown in Figures 5.4(e)(f)(m), where Tb rose abruptly and rapidly to around 30°C soon after emergence.

5.4.2.3 The plateau phase

Typical plateau phases are shown in Figures 5.4(d)(g)(i)(j)(k) and (1). The most striking feature is that Tb, although often maintained at a high level, fluctuates substantially, often by 10°C or more. The data shown in graph 5.4(k) shows that Tb fluctuation is largely independent of insolation, although in this example, there is an apparent response in Tb to the variation in Ts. Conversely, there is no noticeable correlation of Tb with Ta.

In Figure 5.4(i), the bask site of the snake became shaded by trees at 15.40 hrs and the snake could have moved to maintain its' position in the sun. However, it did not move, but let Tb drop, despite the fact that a nearby site was in full sunlight for several more hours. Ta was high at this time and the snake managed to maintain a relatively high Tb for some time, despite being shaded from the sun.

Two other factors have a notable effect on the basking behaviour of snakes in the field. The first is rain, which is generally cooler than both the surrounding air and substrate, and which will have an evaporative cooling effect on the snakes which come into contact with it. Two examples are shown, in Figure 5.4(d) and (n). In graph (d), the rain began at 15.15 hrs and in graph (n), at 07.45 hrs. In both cases it resulted in a sharp decrease in Tb to the extent that it fell below both Ta and Ts. Field observations showed that snakes rarely basked in the rain, although this was observed with one untagged gravid female. Gaywood, (pers comm) observed that gravid snakes often took refuge during rain at a relatively later time than non-gravid individuals. This would seem to be an unsound strategy, as evaporative and conductive heat loss would certainly be rapid from a wet snake. However, gravid snakes have been shown by many authors to be relatively sedentary (eg. Madsen, 1984, N. natrix) and discomfort or difficulty in moving may account for this behaviour. Only once was it ascertained that a snake had moved during a period of rain; this occured with a tagged snake that moved 80m during a period of heavy, persistent rain during August, 1988.

The second factor is disturbance. During the course of this work, snakes were occasionally disturbed in the course of data collection, despite efforts to avoid this happening. In Figure 5.4(r) the snake was accidentally disturbed during observation at 10.00, 11.00 and 11.45. The disturbed snake took refuge each time and the normal thermoregulation pattern was disrupted, although each time the effects were only temporary. Disturbance during observation is discussed at greater length in Chapter 4.

5.4.2.4 The cooling phase

In all the example graphs shown except one (Figure 5.4 (o)), cooling rates were considerably lower than warming rates Figure 5.4 (a)(d)(g)(i)(j)-(n)(r). Field observation showed that slow cooling occured as a result of lower insolation and a general cooling of air and substrate, followed by a brief period of rapid cooling as the snake took refuge. This is in accordance with observations made on other species of both temperate and tropical snakes (eg. Saint-Girons & Bradshaw, 1981; Gent, 1988; Gaywood, 1990; Slip & Shine, 1988).

It is not clear why snakes apparently conserve heat in this way, considering the energetic costs involved in maintaining a higher metabolism. This was particularly true of snakes that used the tree stump as a night refuge, where nocturnal body temperature was maintained at a relatively high level (Figure 5.4 (q)(r) (s)). Presumably the energetic costs are offset by the future reduction in effort needed to raise metabolism to the optimum level and by possible physiological requirements such as enzyme production, digestive efficiency and immunological response (see Dawson, 1975).

Hailey & Davies (1987) identified two distinct thermoregulation strategies; the first of these (r-thermoregulation) was a period of rapid heating to a maximum at which an activity such as foraging was pursued. The second strategy (K-thermoregulation) involved heating to a maximum and then continuing to thermoregulate. The authors suggested that the latter strategy was used inter alia, as an aid to long-term physiological processes such as digestion, maturation or reproduction. By these authors' definition, N. natrix is a K-thermoregulator, as was the congener N. maura in their study.

5.4.2.5 Submergence

The end of the plateau phase generally results in an observable decrease in Tb as the snake seeks refuge for the scotophase. Figures 5.4 (g)(i)(j) each show logged data for snakes covering this period. In each case, the insolation conditions at the location of the snake were noted and it was found that in all three cases, the end of the plateau period was caused by a decrease in insolation, (and therefore operative temperatures), in one case (g) because direct sunlight was terminated by the lowering of the evening sun (at 18.00 hrs) and in both other cases (i)(j) because cloud cover increased to 100% (at 15.45 and 16.30 hrs respectively).

As with emergence, submergence appears to be linked to the change in insolation and Ts, although it is well to be aware of the auto-correlation between the two variables.

5.4.2.6 Night temperature

Night-time Tb was noticeably more constant than the day-time Tb. This was to be expected, since during the night the snake had no opportunity to thermoregulate other than to move between substrates of different temperatures. Thus in a homogenous substrate, the snake behaved as a thermo-conformer, and only gradually lost heat.

Night time temperatures, in all cases, were several degrees higher than that of the lowest night-time Ts (Figure 5.4 (f)(g)(h)(j)(m)(p)). This pattern was consistent for all six examples shown and as hypothesized above, is due to thermo-conformity and an ability to retain body heat, probably by coiling in the refuge. The energetic costs of maintaining a higher nocturnal Tb may have been offset by an increase in ability to safely emerge the following day or by a reduction in the basking time that would be needed at that time to reach a Tb at which rapid flight from predators was possible. It was noticeable that very cool animals were easy to catch, and many snakes used in this study were caught early in the morning, whereas warm snakes were highly alert and difficult to catch. Alternatively, if the preferred nocturnal Tb of the snake was lower than that recorded, the snake would have needed to move nearer the surface to lose heat, thus exposing itself to nocturnal predators. The former explanation is more likely, as the snakes that spent time in the tree stump maintained a very high nocturnal Tb. Thus it would appear that snakes will maintain a high a nocturnal Tb as possible despite the energetic costs.

5.4.3 Optimal thermoregulation

A favoured location of two female snakes was in a rotting tree stump in an exposed area at the study site. During the course of the research, several snakes of both sexes were seen at the stump and in 1989, the stump was used on several ocassions by two female snakes both carrying thermo-sensitive transmitters. Plots of logged data are shown in Figure 5.4(n)(o)-(q)(r)(s). Graphs (o) and (r) show data from one of the snakes basking in vegetation on top of the stump on warm sunny days. The plots show consistent, high Tb's with fluctuations typical of basking grass snakes.

The other 3 plots (graphs (n)(q)(s)) all show data from the snakes thermoregulating thigmothermically inside the tree stump. In each case, the Tb was noticeably more stable but was generally less than 30°, which is lower than that for snakes basking in the open under similar weather conditions. Despite the lower Tb, the risk from predators was virtually non-existent in the tree stump and the lower Tb may have been a trade-off by the snakes for this advantage.

Both snakes stayed in the tree stump for several days before leaving, presumably to forage, and during the course of the study, several shed skins were found in the surrounding vegetation, where untagged snakes had stayed there while sloughing. The use of this and other favoured habitats is examined in Chapter 6.

5.4.4 Intraspecific variation in body temperature

The three femal snakes plotted simultaneously showed a variation in Tb as much as 10°C (Figure 5.5). None of the snakes were gravid and were apparently in a similar physiological condition. Snake 32 was in the tree stump and maintained a more constant, though generally lower Tb than both other snakes. Both other snakes followed a temperature pattern that matched the observations made above, but each was different from the other because of the different locations of each individual. Direct sun was shaded from snake 42 at 15.45 hrs and snake 32 at 16.00 hrs, but whereas snake 32 took refuge and made no effort to maintain a high Tb, snake 42 moved 35m into the sun. What the data shows is that location is an important factor in determining the opportunities for thermoregulation and that other aspects of the ecology of the animal such as foraging and concealment serve to obscure patterns of daily temperature in the species.

5.4.5 The effect of cloud cover on body temperature

The high-low-median plots shown in Figure 5.6. show that high Tb's can still be reached by snakes even during times when the sun is largely obscured and direct insolation not available. There was insufficient data to divide the sample up into smaller sizes (for instance warm and cool days) to further examine the effects of cloud cover. The best fit slopes fitted through the median points were both negative, which suggests that increasing cloud cover restricts thermoregulation opportunities. This reinforces the observations made above with the logged data. Snakes basked more frequently on mild days with intermittent cloud cover and were rarely seen on overcast or on very warm days (pers. obs.)

The lack of significant difference in the median Tb of male and female snakes at 19/21 divisions of cloud cover is rather surprising in the knowledge that male and female thermal ecology is different in other respects. However, some of the sample sizes were small (eg. for male Tb under 65% cloud was 3) and larger sample sizes would have enabled a more exacting result to be obtained.

5.4.6 The thermal ecology of moving snakes

The data shown in each of the two examples (Figures 5.7 & 5.8) serves to show that snakes can maintain a high degree of activity under a wide range of body temperatures. The female in Figure 5.8 made no apparent attempt to raise Tb throughout 13-6-88, while in contrast, the temperature plot of the male on 7-9-88 (Figure 5.7) was maintained at or near the level that would be expected from a basking stationary snake. The two foraging environments were markedly different and it would appear that the male maintained a high Tb because the conditions were suitable, whereas the female abandoned thermoregulation whilst foraging in a thermally hostile environment, trading off the thermal disadvantage against the advantage of catching food.

The female foraging in the pond sloughed shortly after these observations were made and it is not known if this affected her thermoregulatory performance. However, it has been reported (Smith, 1951) that snakes in an immediately pre-slough condition will often seek out water to soften the skin and thereby aid ecdysis.

5.4.7 Thermophilic response to feeding

Skoczylas (1970), in work carried out on Natrix natrix, found that digestive efficiency in the species is optimal at between 25-35°C and equally efficient at each end of that range. Optimality ensures that digestion begins rapidly and is completed as soon as possible. Several studies on other snake species have shown that body temperatures are elevated to similar levels and that this action increases digestive efficiency (Regal, 1966, Coluber constrictor; Greenwald & Kantner, 1979, Elaphe guttata; Hailey & Davies, 1987, Natrix maura). As the logged data shows, grass snakes spend much of their time between these two limits, presumably because selection has ensured that most or all other physiological functions operate optimally at such temperatures. Post-feeding Tb was almost always between 25-35°C during the day (Figures 5.7 & 5.8).

The food bolus in a recently fed snake is likely to have an adverse effect on the locomotory performance of the snake, making it more vulnerable to predators. It is therefore in the interests of the snake to digest the stomach contents as soon as possible. This action will also reduce the possibility of the food naturally decomposing and producing toxins in the stomach. Further examination of the behavioural response of grass snakes to feeding was shown in Chapter 4.

5.4.8 Thermophilic response to sloughing

The function of ecdysis is to maintain a sound integument as the body grows and as the skin becomes worn or damaged. The eyes become milky for several days before sloughing occurs and vision is presumably adversely affected during this time. An adult grass snake will typically slough 2-3 times each year (pers obs). Little published work has been produced on the thermal ecology of snakes undergoing ecdysis. Semlitsch (1979) showed that ecdysis is an energy intensive process and that rates of ecdysis were faster in Natrix fasciata and N. taxispilota kept in a warm environment than those kept in a cool environment. The normal behaviour of grass snakes is disrupted for several days during ecdysis (see Chapter 4).

On the day before sloughing, the snake maintained a high Tb, whereas two days after sloughing, basking began later in the day and the snake did not reach a high Tb before moving. Grass snakes typically undergo a period of non-movement before sloughing, perhaps because of impaired sight. Basking is therefore the predominant activity of snakes in this condition. More data will be needed before it is possible to examine whether body temperature during the sloughing phase is significantly different from that normally attained by the snakes. Gent (1988) found no difference in the body temperature of smooth snakes at these times.

5.4.9 General discussion

The data presented above suggests that the grass snake is predominantly a heliothermic ectotherm, but that substrate temperature probably influences emergence. Thigmothermy (conductive heat from adjacent surfaces may also be a significant factor under some conditions but it was difficult to assume this from the data above as there were many potential influences on body temperature that were ignored (eg. wind speed, aspect, humidity, etc.). The use of suitable cover under which high body temperatures can be reached is common in grass snakes. The tree stump mentioned above and pieces of corrugated tin were popular refuges for snakes at the study site. Corrugated tin was even placed in suitable areas so that snakes could be caught easily. It was also observed that on warm days, snakes could often maintain a high Tb by basking virtually concealed in light cover. Heliothermic and thigmothermic thermoregulation strategies were probably simultaneously utilised at these times, although to what extent is unknown.

The effect of snake posture and its' influence on body temperature has been examined in a number of studies (Prestt, 1971; Goddard, 1981; Gent, 1988; Gaywood, 1990). With this in mind, the posture of each tagged basking snake seen when located was noted on a scale of 1-6, with 1 being stretched out and 6 being tightly coiled. Postures other than six were rarely seen in the field, except for very early in the season at the overwintering sites, where snakes sometimes lay outstretched and on one ocassion when an untagged outstretched snake was caught late on a warm day with a very low body temperature. Posture therefore appears to be a little used behaviourial mechanism to control body temperature of snakes in the field. Gaywood (pers comm) noted that grass snakes tended to use a loose coiled posture only temporarily, for instance during warming phases.

Dorso-ventral flattening, as observed in the adder (Prestt, 1971; Gaywood, 1990) was not seen in grass snakes in this study.

5.4.10 Further research

Useful further research would be an examination of the body temperatures of male and female snakes of similar body sizes (ie. large males or small females) to explore the apparent difference in male and female body temperatures and temperature range distribution. Further work on the thermoregulatory behaviour and body temperature of moving and gravid snakes would also be of interest. Other work could include the body temperatures of overwintering snakes, with emphasis on the criteria for spring emergence and autumn submergence and the effects of prolonged mid-season cold spells on body temperature.

Chapter Six

Habitat use

Introduction

The definition of 'habitat' is somewhat vague and has been interpreted differently by various authors, although two definitions predominate. The first and most straightforward of these broadly encompasses well-defined vegetational communities, such as grassland, woodland and wetland and has been used by several authors (eg. Madsen, 1984; Stumpel, 1988). In this way, the habitats available to an animal can be compared directly to the habitats used by an animal and any relationship between the two thereby revealed. This approach has the advantage that relevant data is easy to collect and quantify, but is limited by its' simplicity and says little about the particular qualities of a habitat that are sought by an individual. However, results obtained by the collection of data of this nature can be useful when planning for the management or conservation of a species or population.

The second definition of 'habitat' encompasses a wide range of biotic and abiotic variables, such as time, microclimate and vegetation structure which can be quantified and analyzed in an attempt to establish which of the variables measured are important to the individual and to what extent. This is a measure of microhabitat as opposed to the macrohabitat approach of the former definition and has been used by many authors (eg. Reagan, 1974; Diaz & Valencia, 1985; Reinert, 1984; Dent, 1986).

Heatwole (1977) described habitat selection in reptiles as '...the interactive expression of responses which tend to maintain the association of an animal with a particular type of habitat'. He also pointed out that it is important to distinguish between home range, which is the delineation of an area regardless of habitat, and habitat selection, which is the use of habitats, regardless of area, although the two may coincide.

A further problem of definition arises when distinguishing between habitat use and habitat selection. It is quite possible that an animal may temporarily use habitats without necessarily selecting them, although in practice it may be difficult to decide if a habitat has been selected by mere observation of snakes. An example of this would be a route used (or perhaps selected) during a long-distance movement. Conversely, it could legitimately be argued that all habitats are chosen, because at each move, an individual can decide which route or habitat type to use. On balance though, such pedantry is liable to be counter-productive and for the purposes of this work, it was assumed that the number of observations made of an individual in each given habitat represented the degree to which such habitats were selected. Thus habitat use and habitat selection become more or less synonymous. This is elaborated further in the text where appropriate.

Although habitat selection has been investigated in many reptile studies, the Ophidia have not been well represented, probably due to their secretive nature, which has made them difficult to study. The use of miniature telemetry equipment has made the detection of snakes a simple task and virtually eliminated the problem of locating many snake species, which has resulted in a great deal of research into snake movement and ranging behaviour. However, the study of habitat use, except in a basic sense, has even now received little attention, despite the fact that such equipment has been widely available over the last two decades.

This is somewhat surprising as the use of telemetry eliminates one of the central problems connected with research into habitat selection, that of visibility of the study animals. Without the use of some means of remote location of animals, observations will be biased in two ways. Firstly, only animals in relatively open habitats will be seen at all in most cases, which will tend to bias results in favour of selection for that habitat. Gent (1988) recognized this as a problem in his work on the habitat use of the smooth snake Coronella austriaca.

Secondly, the disturbance caused by searching for snakes may well cause them to either alter their behaviour or to head for cover before being spotted. This would have been a particular problem in the case of grass snakes, which are often well camouflaged by their surroundings and readily take flight if disturbed.

The selection of a habitat by an individual presumably involves the potential fulfilment of a requirement for one or more resources and most studies of habitat selection in snakes have identified the most significant of these resources as protection from predators, prey availability and opportunity to thermoregulate. Madsen (1984) in a study of radiotracked grass snakes in which he noted the habitat in which snakes were observed during daily radio-locations, found that the habitat most frequently used was blackberry, Rubus fruticosus bushes in close proximity to stone walls and fences and suggested that these were selected because they offered good protection from prey and may have also been well used by amphibian prey species. The author, though, does not say how much habitat was available to the snakes as a percentage of the total. Nor does he state the activity of the snakes at the time of observation.

Weatherhead & Charland (1985) noted that the black rat snake Elaphe obsoleta showed a marked preference for woodland-field ecotone, suggesting that their fledgling bird and egg prey was most plentiful in this habitat and that the snakes maintained their preference for the habitat outside of the nesting season because thermoregulation opportunities were high.

Shine & Lambeck (1985) noted that the arafura filesnake, Acrochordus arafurae utilised a variety of damp or wet habitats in the wet season, but was restricted to bodies of water (billabongs) in the dry season, because they were the only places in which their prey (fish) could be found. The authors also found that diurnal movements of the snake were short and that the snakes remained under tree cover, probably to avoid predation by white-breasted sea eagles, which fed extensively on the snakes. Similarly Reinert & Kodrich (1982), Sistrurus catenatus catenatus and Shine (1987) Pseudechis porphyriacus noted that snakes tended to utilise damp areas to a greater extent in the dry season.

In this study, habitat selection has been interpreted in both of the ways mentioned above. Firstly, the selection by snakes of vegetational communities was examined by comparing the availability of a particular habitat to the habitats used by each individual. Results obtained in this way can be compared to Madsen's (1984) observations and will be of particular use to workers in the field who are interested in the management of this protected species. Secondly, a more strictly ecological approach was taken, which involved the measurement of a larger number of variables at snake locations and statistically analyzing these for preferences or requirements.

By using both of these methods together, it was intended to obtain an idea not only of the vegetational communities that were preferred by grass snakes, but some indication of why they were using these habitats. This is of particular importance to the understanding of a widely foraging species such as the grass snake which is known to use a variety of habitats. Such information is particularly relevant to the management of local grass snake populations for conservation purposes. Hilton-Brown & Oldham(1991), by surveying local herpetologists, identified that habitat loss was by far the main cause of the decrease in local grass snake populations. The provision or management of habitats known to be used by snakes and, ensuring that habitats avoided by grass snakes do not present barriers to dispersal may ensure the survival of local populations of the snake. The authors also stated that the main reason for local increases in grass snake populations was an increase in food availability and that the almost exclusive reasons for local increases in amphibian populations were the creation and colonisation of new habitats.

6.2 Methods

6.2.1 General

During the course of the research, each snake was located at least once a day and a number of variables related to habitat were noted. These are shown in Table 6.1.

Date
Time
Body temperature
Macrohabitat
Mesohabitat
Microhabitat
Slope
Aspect
Cloud cover (%)
Air temperature (1m)
Surface air temperature
Substrate temperature
Temperature (2.5cm)
Vegetation litter depth
Vegetation cover ($0.25m^2$ quadrat).
% Canopy
Canopy height (m)
Humidity (2.5cm)
Vapour pressure (2.5cm)
Vapour pressure deficit (2.5cm)

Table 6.1 Variables collected at snake locations.

The variables collected were intended to cover a range of microclimatic and physical characteristics connected with the site at which basking snakes were observed. Physical components of the microhabitat, such as canopy cover and vegetation variables were measured in order to estimate the importance of cover as a resource and microclimatic variables, such as temperature, humidity and vapour pressure were measured in order to estimate the importance of the thermal environment.

Because of the effort made not to disturb snakes, it was not always possible to collect all the variables shown although for some of the variables, the position of the snake was noted and the measurements made at a later time (within 24 hours). The variables used were chosen firstly because of their potential relevance to habitat selection by snakes and secondly because they were relatively straightforward to collect in the field with a minimum of portable equipment.

6.2.2 Vegetation communities

The habitat type (vegetation community) at each location was noted in three ways (as in Fig. 6.1). The first, (macrohabitat), was the general classification of habitat, eg. rough grassland, deciduous woodland, etc. The second, (mesohabitat) comprised the broad habitat classification within the 'macrohabitat', eg. bramble scrub in a macrohabitat of deciduous woodland. The third, (microhabitat), comprised the actual habitat with which the snake was in contact. Thus, a snake might be classified as observed in a bracken scrub clearing in a bramble scrub in a deciduous woodland. In this way a more complete evaluation of the habitat which the individual had selected was obtained.

The percentage cover of each mapped habitat at the study site was calculated using the 'Ranges IV' computer program (Biotrack, Wareham). The total area mapped was assumed to represent 100% of the habitat, as mapping was only carried out in and around areas which snakes were known to use. Areas covered by buildings were calculated by the program, but omitted from the analyses. The habitats which were used are shown in Table 6.2.

It was clear from the early stages of the research that deciduous woodland margins were heavily used by the snakes, so this category was further divided as shown in the table. Data throughout 1988 and 1989 was used together with some of the data collected in 1987.

It was possible to calculate the percentage of the total tracking time (in days) each individual snake spent in each of a number of macrohabitats and compare it directly with the area of habitat available to that snake over the entire study area. This was acheived by noting the habitats of the snakes either at their nocturnal refuge on days when no movement took place, or by using the location of the first observation made on each day the snakes were active. Because snakes generally did not make significantly long movements immediately before taking refuge and because they tended to bask at or very near to the refuge site on emergence, the locations used were representative of areas which the snakes used for significant periods. By further reducing the size of the habitat in which the snake was observed (ie. mesohabitat and microhabitat), it was possible to examine in greater detail the habitats which snakes selected and to offer hypotheses as to what qualities of the habitat snakes were selecting.

No statistical analyses are performed on this data because of inherent weaknesses in the methodology that make such analyses redundant. The first of these concerns the sample size used. The results represent at best, the observations made from seven snakes of the same sex and each of these used different macrohabitats to a greater or lesser degree. Thus there was great variation in the habitat use of individuals and the results could be influenced by the length of the tracking period for any particular individual.

The second methodological weakness occurs because it was not possible to map many habitats in great detail, either because they were too fragmented or because they changed as the season progressed (eg. bracken scrub). Woodland margins were greatly used by the snakes but are virtually impossible to map with any degree of accuracy, partly because of problems of definition (ie. where does an ecotone end and an adjoining habitat begin), and partly because they are dynamic throughout the season.

This notwithstanding, the method does allow a reasonably detailed analysis of habitat use of the grass snake population at Chilworth and allows hypotheses to be drawn up with regard to the components of a habitat that snakes might be selecting. These hypotheses were then tested using the methodology in the following section.

6.2.3 Microhabitat selection

Some of the variables shown in Table 6.1, such as air temperature and humidity fluctuate continuously and needed to be recorded at the location of the snake at the time of observation. Such data was obtained either from snakes that were disturbed during observation, or by using observations of untagged snakes that were observed by chance. Observations made allowed this data to be obtained on 331 occasions.

The data then underwent principle component analysis to determine the inter-relationship between the variables. Principle components are linear combinations among all the variables which explain progressively smaller portions of the total sample variance in a multi-dimensional hypervolume. These components are then correlated with the original variables to determine which combinations of variables have combined significance. The method ensures that variables are treated as statistically independent and broadly follows that used by Reagan (1974) in a study of habitat selection by the Box Turtle, *Terrapene carolina triunquis*.

In addition to the variables shown in Table 6.1, a more detailed analysis of vegetation structure was undertaken at 134 snake locations. To achieve this, a white painted plywood board measuring 10x80 cm was marked to give 6 divisions at 0-5, 5-10, 10-20, 20-40, 40-60 and 60-80 cm. Each division was marked with a grid which enabled the percentage of the board which was visible to be accurately estimated. The board was placed upright on the ground and each division surveyed from a distance of 1m, horizontal to the ground. For each sighting, five point readings were taken in a 0.5m quadrat centred on the location of the snake, one at the actual location and one at each corner of the quadrat. The maximum height of the vegetation at each point of the quadrats was also noted. Each quadrat was orientated towards the position of the sun along one edge. Sightings of both radio-tagged and 'visually observed' grass snakes were used in the sample.

The purpose of this analysis was to examine the trade off between the need for snakes to expose themselves to direct insolation with the need to remain close to cover in order to escape from predators. Snakes clearly need to expose themselves to direct sunlight when basking, but in doing so, also expose themselves to potential predators. It was noticeable on several occasions that snakes remained under cover even when a higher body temperature could have been reached by emergence and basking (see Chapter 5), which would suggest that a potential cost of basking exists.

Analysis of the difference in vegetation height at each of the five points in the quadrats was carried out to examine if the physical characteristics of the vegetation structure around basking snakes was consistent. The null hypothesis was that there was no difference in the vegetation heights at each of the five points and this was tested by using analysis of variance and least squares analysis. Secondly, the density of the vegetation at each of the height categories outlined above was tested with the null hypothesis that there was no significant difference in the vegetation density at each of the five points of the quadrats. This was tested by multiple analysis of variance and least squares analysis.

1.	Rough grassland	Mainly Dactylis glomerata, Holcus lanatus, Urtica dioica, Cirsium arvense & C. vulgare.
2.	Managed grassland	Mainly H. lanatus, Phleum pratense. Grass mat less dense than in unmanaged grassland.
3.	Bracken scrub	50% or more Pteridium aquilinum.
4.	Bramble scrub	50% or more Rubus fruticosus.
5.	Formal garden	Mostly exotic species, especially Rhododendron ponticum and Endymion non-scriptus.
6.	Deciduous woodland	Greater than 90% broadleaved trees with extensive ground flora and litter mat.
7.	Coniferous woodland	Greater than 90% coniferous trees, with no ground flora and dense mat of cones and needles.
8.	Mixed wood	Woodland that did not meet criteria 6 or 7.
9.	Pond	Body of standing water and the immediately adjacent vegetation.
10.	Stream	Including riparian vegetation.
11.	Artefact	Tin, roofing felt or other man-made debris.
12.	Damp grassland	Mainly Molinia caerulea and Juncus spp.
13.	Underground	
14.	Deciduous wood ecotone:	Woodland margins with... .1 Grassland .2 Track or path .3 Formal garden
15.	Nettle scrub	More than 50% U. dioica.
16.	Deciduous leaf litter	
17.	Open ground	Any habitat which provided no immediate cover. eg. lawn.

Table 6.2 Habitat types used for recording habitat selection.

6.3 Results

6.3.1 Vegetation communities

Habitat	Cover (%)	Macro		Meso		Micro	
		♂	♀	♂	♀	♂	♀
Rough meadow	8.8	16.9	22.6	15.6	27.2	31.7	34.2
Man. meadow	24.7	10.1	11.6	9.4	3.7	9.6	2.4
Dead bracken	*	3.1	0	21.9	24.8	19.2	24.0
Bramble scrub	*	0	4.8	10.7	4.3	5.8	3.2
Formal garden	8.7	0.9	2.3	1.8	0.7	0	0
Decid. wood	24.4	25.8	27.2	8.9	11.2	0	0
Conif. wood	12.7	0	0	0	0	0	0
Mixed wood	3.9	2.1	4.2	0	1.3	0	0
Pond	0.03	2.0	1.3	0	0.8	0	0
Stream	0.2	7.1	0.2	23.7	4.3	0	0
Tin sheet	<0.1	0	0	0	1.3	1.4	2.6
Damp meadow	<0.1	0	3.1	0	0	0	0
Underground	*	0	0	0	0.3	1.0	0.3
Wood ecotone	*	32.0	22.7	7.6	20.4	0	0
Nettle scrub	*	0	0.3	0	0	5.3	2.1
Leaf litter	*	0	0	0.4	0	22.1	26.4
Open ground	14.0	0	0	0	0	3.8	4.8

Table 6.3 Percentage area of a number of habitat types at Chilworth (total mapped area=100%) and the mean percentage of the total radiotracking period spent in each by male and female grass snakes. The table shows in more detail what 'sub-habitats' snakes selected as the scale of habitat size was progressively reduced. Habitats which were not mapped or directly measured are shown by asterisks.

The macrohabitats most used by both male and female snakes were deciduous woodland and rough meadow, which were used well in excess of their availability to the snakes. Nearly one third of the observations were made in deciduous wood ecotones. Coniferous woodland was not used at all by the snakes, despite covering 12.7% of the mapped area. Mixed woodland was used more or less in proportion to its' availability. Large areas of open ground were avoided by snakes. One other macrohabitat which was used in excess of its' availability was standing water, such as slow-moving streams and ponds.

When the use of smaller within habitat areas (mesohabitats) was examined, the pattern changed significantly. Males in particular were located in areas closely associated with streams and were observed in such areas on nearly one quarter of all locations, although the figure shown was partly influenced by snake 111, which spent much of 1988 in and around a stream. The percentage cover of streams was impossible to calculate with great accuracy because the deciduous wood contained many small ditches which fell into the category of 'streams', but the proportion of observations far outweighed the habitat available and was positively selected for by the snakes. Surprisingly, damp meadow was rarely used by snakes although it was often closely by-passed.

Other commonly used mesohabitats were rough grassy areas and bracken and bramble scrubs. No effort was made to calculate the areas covered by these habitats, but they were extensive over the area, particularly throughout the deciduous wood and along its' margins.

Further reduction in the size of habitat (microhabitat) and their use by snakes revealed a different pattern again. These were habitats with which the snakes were in direct contact. Rough grassy vegetation was in use in over one third of observations and leaf litter in over one quarter of observations. Nearly one quarter of observations were of snakes in bracken scrub. These three microhabitats accounted for 84% of observations. Caution must be exercised at this point, because clearly most microhabitats will have had one or more of these components. Snakes were occasionally seen on open ground (4.8%), which was relatively common in woodland and marginal habitats, and under pieces of tin (artifacts, 2.6%), which comprised a minute percentage (approximately 5m^2) of the overall study site.

6.3.2 Microhabitat selection

Principle component analysis of the variables shown in Table 6.1 showed that the first three principle components accounted for 57% of the total sample variance. Of these, the first component (42.1%), showed the highest correlation with air temperature at 1m, air temperature at 2.5cm and substrate temperature (r=0.67). Thus the first principle component was intricately linked with thermal variables. One variable which was notably absent from this first component was body temperature. The probable reason for this is that the three variables shown are all likely to autocorrelate to a fairly high degree, whereas body temperature does not correlate well with either substrate or air temperature (see Chapter 5). The second principle component (12.0%) did not correlate well with any of the other variables so it was not possible to say what other factors may have been influenced the selection of microsites by the snakes.

The results indicated that the thermal component was the primary consideration of snakes when selecting a microhabitat. None of the variables measured were statistically connected with cover (predator avoidance), which appeared during field observations to be an important consideration of basking snakes.

Two-way analysis of variance showed that the vegetation heights at the five quadrat points were significantly different (d.f.=4; F=2.8; $p<0.05$). Least squares analysis showed that the vegetation heights at the quadrat points towards the 'front' of the quadrat (ie. between the sun and the snake) was significantly shorter than that 'behind' the snake.

A further two-way analysis of variance showed that the vegetation density was significantly different at the six vegetation height categories (d.f.=133, F=2.412; $p<0.05$) and least squares analysis indicated that vegetation density was higher at the two quadrat points 'behind' the snake than at the two quadrat points 'in front' of the snake, except at the height categories of 0-5 and 5-10 cm ($p<0.05$). These results suggest that whilst snakes, not surprisingly, tended to choose basking sites that were exposed to the sun, they also chose sites that were immediately adjacent to more dense cover into which they could retreat if disturbed.

Discussion

Although snakes were found in sixteen habitat 'types' during the course of this study, very few were used with regularity or to any great extent. Between one quarter and one third of observations were made in deciduous wood ecotones and over one quarter made in deciduous woodland. The majority of the remaining observations were made in grassland with less than 15% made in all other habitats combined.

Open habitats such as south-facing woodland edges and grassland offer snakes the opportunity to raise body temperature, whilst at the same time providing cover from predators and from overheating. The use of deciduous woodland by snakes may also be connected with the search for prey and it may be that prey species such as amphibians are more abundant in these habitats, especially outside of the breeding season and several authors have noted disproportionate use of ecotone habitats by snakes (eg. Hebrard and Mushinsky, 1978; Reinert and Kodrich, 1982; Madsen, 1984).

Strijbosch (1980), in a study of habitat selection by amphibians showed that of six anuran species sampled, all were most abundant in closed woodland, although some species selected damp areas within the habitat or stayed near to the wet breeding areas. In the present study, damp areas were also favoured, particularly by males, although the figure of 23.7% shown (see Table 6.3) is biased by two snakes which stayed in damp areas for long periods.

Strijbosch also stated that Bufo bufo, a known prey species of the grass snake, also made use of more open land and this may explain in part the disproportionate use of grassland by grass snakes in this study. Heusser (1961) found that Bufo bufo used closed woodland almost exclusively during the summer and positively avoided the more open grassland between the woodland areas. Van Gelder et al (1986) stated that radiotracked migrating Bufo bufo sought out woodland for cover on nights when the weather was unsuitable for movement.

In Chapter Four, it was shown that grass snakes move only short distances after consuming prey, until the bolus has been digested. All but two of the grass snakes observed during this study that contained noticeable food boli were observed in deciduous woodland or associated ecotones and snakes were observed actually consuming toads on two occasions in deciduous woodland.

Nocturnal searches were carried out for amphibians on several occasions during 1988, by transecting a selection of habitats by torchlight and overturning logs, etc., but only two toads were found (one in woodland) and no other amphibians, except in the pond. The possibility of trapping amphibians by the use of drift fences was investigated, but this was not done, firstly because much of the woodland became densely covered in bracken or brambles for almost the entire season and secondly, because of the resources that would have been needed to cover the study site.

However, during February, March and April each year, toads could be found in the pond, often in great abundance, and many thousands of neonates left the pond when metamorphosis was complete. It would therefore appear that toads were abundant at Chilworth, although their distribution over the area was not known.

The selection of habitats which provide thermoregulatory opportunities for snakes would appear to preclude the use of deciduous woodland in favour of woodland edges and grassland. However, when the use of smaller habitat areas (mesohabitats) was examined, it became clear that snakes selected more open areas within the macrohabitats. This is in accordance with observations made by Semlitsch et al (1981), who noted that 'microhabitats' which offered cover were more important to the snake Tantilla coronata than the predominant vegetation type.

In the current study, between one fifth and one quarter of observations were made in clearings where dead bracken was the predominant vegetation. Although snakes were often relatively easy to see in such habitats, they were often difficult to catch, as good cover was immediately available. Selection of microhabitats that provided easy access to cover indicates the importance of such sites to snakes and very few observations were made in which snakes were not within easy reach of cover.

The fact that no snakes were observed or radiotracked in coniferous woodland suggests that these habitats are avoided by the snakes; the sun only rarely penetrates the canopy in the mature forests at Chilworth and prey species are likely also to be less common here, if only for that reason. Untagged grass snakes were see on two occasions in clearings in the coniferous forest, and must have traversed the forest in order to reach the clearings.

The selection of damp areas such as streams, ponds and damp areas may be related to the search for food. The amphibian prey of the grass snake are themselves likely to select damp areas which prevent desiccation and thermoregulation opportunities in these areas are frequently reduced, as the vegetation is often taller and denser than the surrounding vegetation. Moving grass snakes were frequently seen in such areas and snakes may favour these areas during foraging periods.

It is hardly surprising that snakes select microhabitats which offer a degree of both cover and exposure, but the relative importance of each of these is difficult to estimate and in any case is likely to be a dynamic process, dependant on a number of other variables, such as body temperature, time of day and the condition of individuals. Examination of microhabitats as a set of discreet resources showed only that the thermal qualities of the site were of importance. Non-thermal resources, such as moisture content of the air (humidity and vapour pressure), cover (% canopy, canopy height and litter depth) and other non-biotic variables did not contribute towards the first principal component and it was therefore not possible to quantify the degree to which those resources were selected, but it would be misleading to assume that air and substrate temperatures were anything other than contributory factors, however important they may be. Other variables, such as canopy cover and humidity measured may not only be of importance to the snakes, but may well have an indirect thermal component themselves.

Analysis of vegetation height and density showed that whilst snakes needed to expose themselves to direct insolation, cover was an important factor, and this suggests that to some extent, the snakes were compromising to some extent security from predators in order to raise body temperature. Further evidence for this was provided by observations made early in the season which was the only time in which snakes were seen to bask with their bodies fully outstretched. Spermatogenesis in males may have been a prime consideration at this time of year as the snakes emerged from overwintering and crypsis or basking very near cover, although safer, may have been less thermally efficient.

One further observation from the data above concerns the use of artificial cover by snakes. At the study site, eleven pieces of corrugated sheet, each approximately 0.25m^2 had been placed in two areas known to be used by snakes. Many species of animal used these shelters, including adders V. berus, slow worms Anguis fragilis and grass snakes. In both 1988 and 1989, a female adder spent the entire summer period under one piece of tin and this and several of the other sheets were used for short periods by grass snakes. The use of these microhabitats was much in excess of their availability over the site and may have been selected because they offered a thermally suitable habitat without the need to expose the body to direct sunlight. Gent (1988) also observed disproportionate use of similar artificial habitats by the smooth snake C. austriaca.

One observation not included in the data set and only indirectly related to habitat selection is the use of roads. Only one snake, an introduced male (see Appendix 1), was known to cross a road, although one tagged female disappeared whilst adjacent to the M27 motorway and the possibility cannot be discounted that it was killed on the road. If roads present barriers to the dispersal of snakes, the fragmentation of habitats by development may have adverse consequences on local grass snake populations.

Further work on the costs and benefits of body exposure and concealment would be better performed in a laboratory situation where variables can be changed one at a time, but in the field, where a large number of dynamic variables are all possible considerations quantification is difficult. Further interesting work could be carried out using a technique similar to that used by Mattison (1970), who used infra-red photography to map the thermal conditions in a woodland environment. This method could reveal to a greater extent the degree to which such conditions are selected by snakes.

Chapter Seven

Intra- and Interspecific Interactions

7.1 Introduction

The social behaviour of many species of snake is unusual because although most studies of snake species in the field have shown them to be solitary for much of the season, an approximately equal number have documented aggregative behaviour at some time during each season for most of the same species. The definition of aggregation has been defined by Gregory et al, (1987) as '...any concentration of snakes in a relatively small area such that the density of snakes in the area contrasts sharply with that in the surrounding area. There is no necessary implication of physical contact among the snakes in the aggregation, but this may occur.'

The reasons for aggregative behaviour fall into several main categories, all of which tend to be of a short term nature. Firstly, many species of snakes have been shown to overwinter communally (eg. Madsen, 1984; Phelps, 1978; pers obs: Natrix natrix; Gregory & Stewart, 1975: Thamnophis sirtalis; Brown and Parker, 1976; Firth et al (1969): Coluber constrictor). Suitable overwintering sites may be limited, which would result in aggregation, but the two overwintering sites known at Chilworth, although similar in some respects (south-facing, sheltered from severe frost and dense ground vegetation), differed visibly in others and many other sites apparently suitable for overwintering snakes were unused.

Secondly, gravid females may aggregate until parturition (eg. Reinert & Kodrich, 1982: Sistrurus catenatus; Gregory, 1975: Agkistrodon contortrix, Opheodrys vernalis, Storeria occipitomaculata, Thamnophis sirtalis; Gannon & Secoy, 1985: Crotalus viridis; Völkl & Biella, 1988: Vipera berus). Finally, snakes may aggregate at areas where food is abundant (eg. Arnold & Wassersug (1978: Thamnophis spp.)

The benefits to be derived from aggregative behaviour are not always clear and it has often been suggested that aggregation occurs as snakes seek out a limited habitat that favours a particular activity such as basking, egg-laying or overwintering (Gregory et al, 1987).

During the course of this study, apparent aggregations of snakes were noted in the field and in the laboratory and although it was often easy to hypothesize about the reasons for such behaviour, it was nevertheless difficult to reconcile all aggregative behaviour with the normally solitary existence that grass snakes were observed to exhibit in the field.

Examples of such behaviour included female aggregations at an egg-laying site which consisted of a large domestic compost heap covered with black plastic. For two years this site was regularly inspected and in the first year (1988), females were regularly seen during the period before egg-laying, but not afterwards. Madsen (1984) noted that females would travel large distances to favoured egg-laying sites, where many females could be simultaneously found. Habitat selection would therefore appear to be the mechanism behind such behaviour. However, on one day in 1989, four males also were found at the site at the time females were present. Whilst the thermal environment of the site must beem have favourable, neither females or males were found after the eggs had been laid. The hypothesised mechanism behind the male aggregative behaviour would thus seem to be something other than habitat selection.

On several occasions, two or more grass snakes were observed basking in close proximity to each other (under tin sheeting, in pond-side vegetation and in a tree stump) but it was unclear whether there was physical contact between them, as there undoubtedly was at the egg-laying site. Aggregation at these former areas appeared to be the result of habitat selection rather than of positive intraspecific interactions.

These examples excepted, radio-tagged grass snakes were always solitary away from the overwintering sites except for three occasions when they were observed basking in very close physical contact with adders.

In captivity, all grass snakes used in this study were provided with one basking lamp and at least two upturned flower pots in which to take refuge. In many cases, snakes that were kept together in tanks used the same flower pot, and it has been observed that when the flower pot was 'full up', the last snake to enter would move into the pot as far as it could even if that meant leaving part of its' body exposed, thereby showing apparent disregard to the (non-existent) danger of predation. This behaviour seemed to suggest that the presence of other snakes had a higher priority than a safe refuge.

What is not clear from all of these observations is whether such aggregations are the results of chance or of a more positive action. Furthermore, if grass snakes either actively aggregate for 'social' purposes or actively avoid conspecifics, what mechanism is involved and to what extent are the snakes governed by their 'aggregative drive'?

Spacing behaviour in snakes in the natural environment is unlikely to be visually based except at a local level (Drummond ,1979) and chemoreceptive responses are likely to be of greater importance. Mushinsky (1988) stated that much of a snake's behaviour is initiated by information gained from the Jacobson's organ or vomeronasal organ. Much subsequent research, mainly in the area of response to the chemical stimuli provided by prey scents has been carried out and it has been shown that the vomeronasal organ is functional during foraging (Kubie & Halpern, 1979) and other behaviour (Chiszar et al, 1976).

The results and observations documented elsewhere in this work, particularly with respect to ranging behaviour (Chapter 3), are generally inconclusive as regards the nature of intraspecific interactions except during well defined events. Indeed, there are anomalies in the observations of social response that warrant further investigation and it would be insufficient to make detailed statements about the ranging behaviour of the species without at least a basic understanding of the specific response of one snake to the presence of another.

For this reason, a laboratory study was made of the response of a number of grass snakes to the chemical stimuli provided by the presence or absence of conspecific and sympatric snakes. The study was carried out in May and June, 1989, a period when events that might stimulate aggregation are not timed to occur. Although the experimental plan was designed independently, the methodology in part followed the work of Porter & Czaplicki (1974), who used a similar experimental arrangement in a study of Natrix rhombifera and Thamnophis sirtalis. The method those authors used for quantifying their results was not followed in this study however, as it was considered inappropriate and this is discussed below.

7.2 Methods

7.2.1 Experimental procedure

A series of identical experiments were carried out over a period of five weeks, involving four male and four female grass snakes and two adders. Two identical 110 cm aquarium tanks were placed into an arena and the sides covered with cardboard to obscure the adjacent surroundings. The tanks were modified so that they could be easily divided into 2 equal halves. The floor of each half tank was covered with paper towel and a water bowl and upturned flower pot were placed in identical positions into each half (Figure 1). The tanks were covered with lids comprising a frame with fine mesh metal gauze that let heat, air and light into the tank, but prevented the snakes from escaping. After each experiment, the tanks were cleaned in a detergent liquid and rinsed and dried before further use.

Ambient light was provided by fluorescent 'Trulight' strips on a day-night regime that approximated natural conditions at the time of the experiment and 60W basking lamps were set up to allow normal basking from 9am to 6pm. Many grass snakes and adders had previously been kept in similar conditions for varying periods following capture during the course of the research and the method had proved successful.

Snakes (stimulators) were introduced into one half of each of the divided tanks according to the plan below and left for forty-eight hours, after which they were removed and the tank divider withdrawn. At this point, a grass snake (responder) was introduced to the tank for twenty-four hours and videotaped using a Panasonic WV-1550/B video camera connected to a Panasonic NV-8050 time lapse video recorder. Infra-red light was used for 24 hours per day to allow filming during darkness.

During this 24 hour period, the position of the snake in the tank (ie. in the previously occupied or the previously unoccupied area) was noted at 5 minute intervals (total observations = 288/24 hours). Where the snake was stretched between the two halves of the tank, its' position was assumed to be that of the head of the animal.

Four male (M1, M2, M3, M4) and four female (F1, F2, F3, F4) grass snakes and two adders (V1, V2) were placed in the tanks as follows:

1. Male grass snake into one half of the divided tank for 48 hours, then removed and a different male grass snake placed into the undivided tank (Experiment 1).

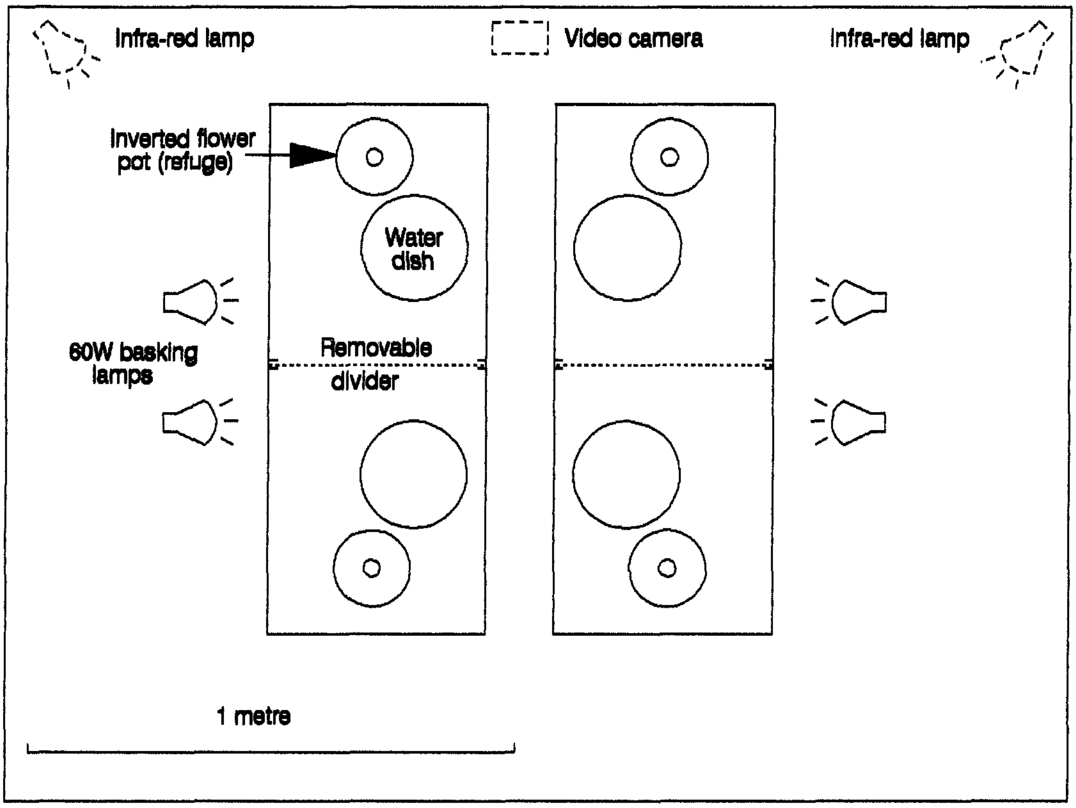


Figure 7.1. Plan view of the video arena, showing the position and arrangement of the tanks and other equipment. The infra-red lamps and camera were placed approximately 2m above the floor of the arena.

2. Adder into one half of the divided tank for 48 hours, then removed and a male grass snake placed into the undivided tank (Experiment 2).

3. Divided tank left empty for 48 hours, then a male grass snake placed into the undivided tank (Experiment 3).

4. Male grass snake into one half of the divided tank for 48 hours, then briefly removed and the same snake replaced into the undivided tank (Experiment 4).

5. Female grass snake into one half of the divided tank for 48 hours, then removed and a male grass snake replaced into the undivided tank (Experiment 5).

Each experiment was duplicated simultaneously in the adjacent tank and the snakes were alternated between experiments. The procedure was subsequently repeated using female snakes (Experiments 6-10). A detailed plan of the snakes used is shown in Table 1.

Experiment Number	Divided tank (48 hours)		Undivided tank (24 hours)	
	Tank 1	Tank 2	Tank 1	Tank 2
1	M1	M2	M3	M4
1	M3	M4	M1	M2
2	V1	V2	M1	M2
2	V2	V1	M3	M4
3	Empty	Empty	M1	M2
3	Empty	Empty	M3	M4
4	M1	M2	M1	M2
4	M3	M4	M3	M4
5	F1	F2	M1	M2
5	F3	F4	M3	M4
6	F1	F2	F3	F4
6	F3	F4	F1	F2
7	V1	V2	F1	F2
7	V2	V1	F3	F4
8	Empty	Empty	F1	F2
8	Empty	Empty	F3	F4
9	F1	F2	F1	F2
9	F3	F4	F3	F4
10	M1	M2	F1	F2
10	M3	M4	F3	F4

Table 1. Placement of snakes in tanks during an experiment to investigate chemo-receptive response in grass snakes. Columns 2 and 3 show which snakes were initially placed in one half of a each divided tank. Columns 4 and 5 show which snakes were subsequently placed in the same tanks when the dividers were removed.

Male Natrix natrix: M1-4.
Female Natrix natrix: F1-4.
Female Vipera berus: V1-2.

Most of the snakes passed faeces during the initial 48 hours in the tank and no effort was made to remove it before replacing the snake. Furthermore, when handled, most grass snakes gave vent to a quantity of foul-smelling fluid, much of which sprayed the interior of the half-tank into which they were placed and again this was left.

Both before and during the experimental procedure, participant snakes were housed in individual tanks in the same room with heat, shelter, food and water available.

7.2.2 Statistical analysis

The number of observations made in the 'previously occupied' half of the tanks was converted to a proportion of the total time (t/288) and transformed using an arcsine transformation. This transformation is particularly appropriate to proportions (Sokhal & Rohlf, 1981). Two way analysis of variance was then used to determine 'between sex' and 'between stimulant' response. Sex data was combined and pairwise least squares analysis carried out on the five stimulant data sets.

This differs from the approach taken by Porter & Czaplicki (1974), who computed a preference score for each snake by deducting the number of observations made in one side of an experimental tank from the number made in the other. The use of this statistical method meant that scores that showed a strong preference for either side of the tank could be significantly different from scores that showed a weaker, but possibly still significant preference for the same side of the tank. Furthermore, the method used in those authors' study precluded the use of more powerful parametric statistics and was therefore rejected in favour of the use of ANOVA.

7.3 Results

Figures 7.2 (a) and (b) show the positional behaviour of snakes for the twenty-four response period during which they had free range of the tanks in which they were placed.

A two way ANOVA found no significant between-sex difference in the amount of time spent in each half of the tank during the response period(d.f.=10; F=0.067; p>0.05) but a significant difference between samples in the five treatments (d.f.=10; F=7.151; p<0.01). Data for the two sexes were combined and pairwise least squares analysis on the five different stimulant procedures indicated that response to the 'adder' and 'same snake' stimulant treatments was significantly different to the response to the 'same sex', 'opposite sex' and empty (control) treatments (p<0.05).

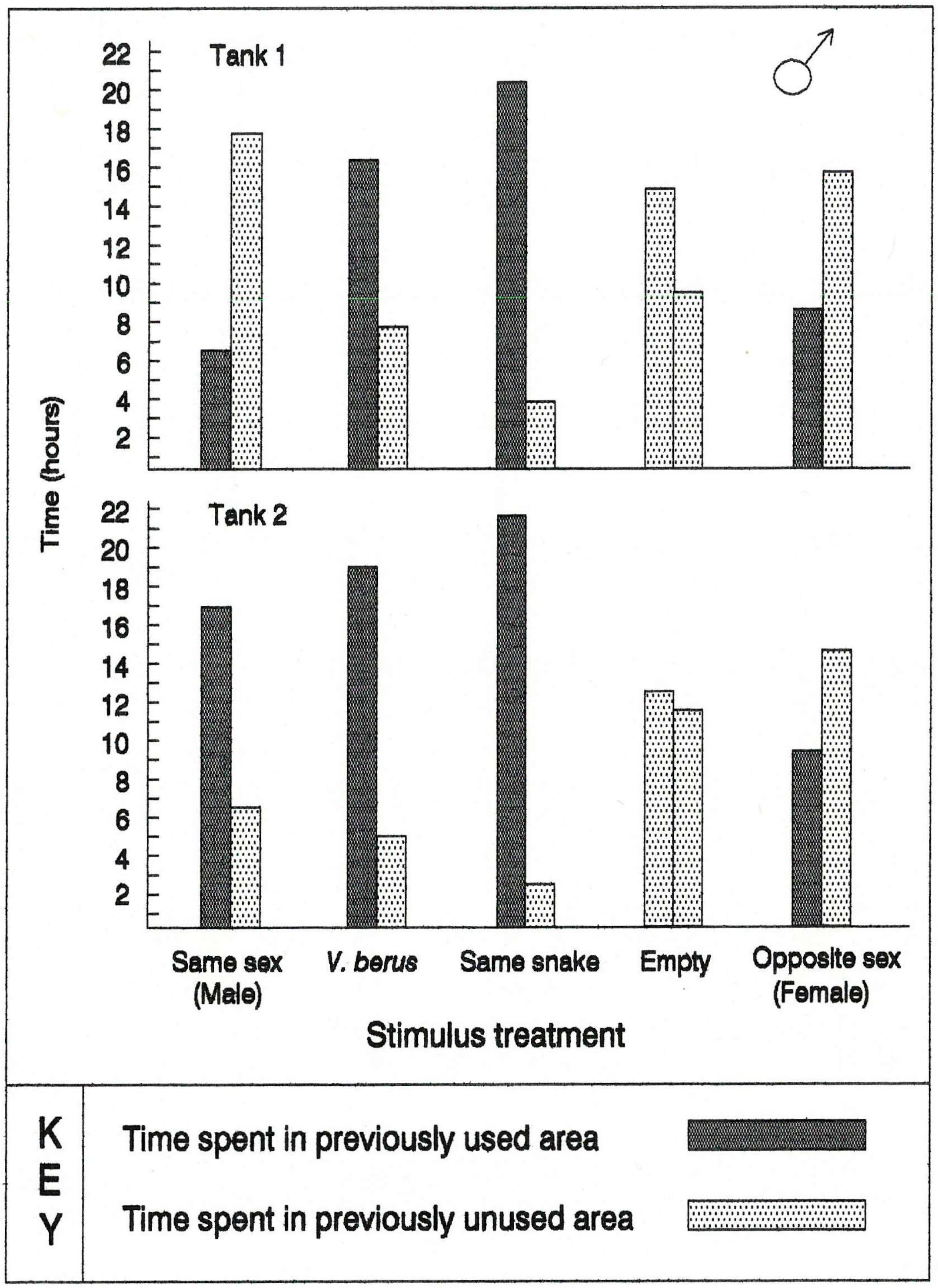


Figure 7.2 (a) Time spent by male grass snakes in previously occupied and previously unoccupied halves of an aquaria tank during a 24 hour period. Observations were made from time lapse video every 5 minutes but have been converted to time here to aid clarity.

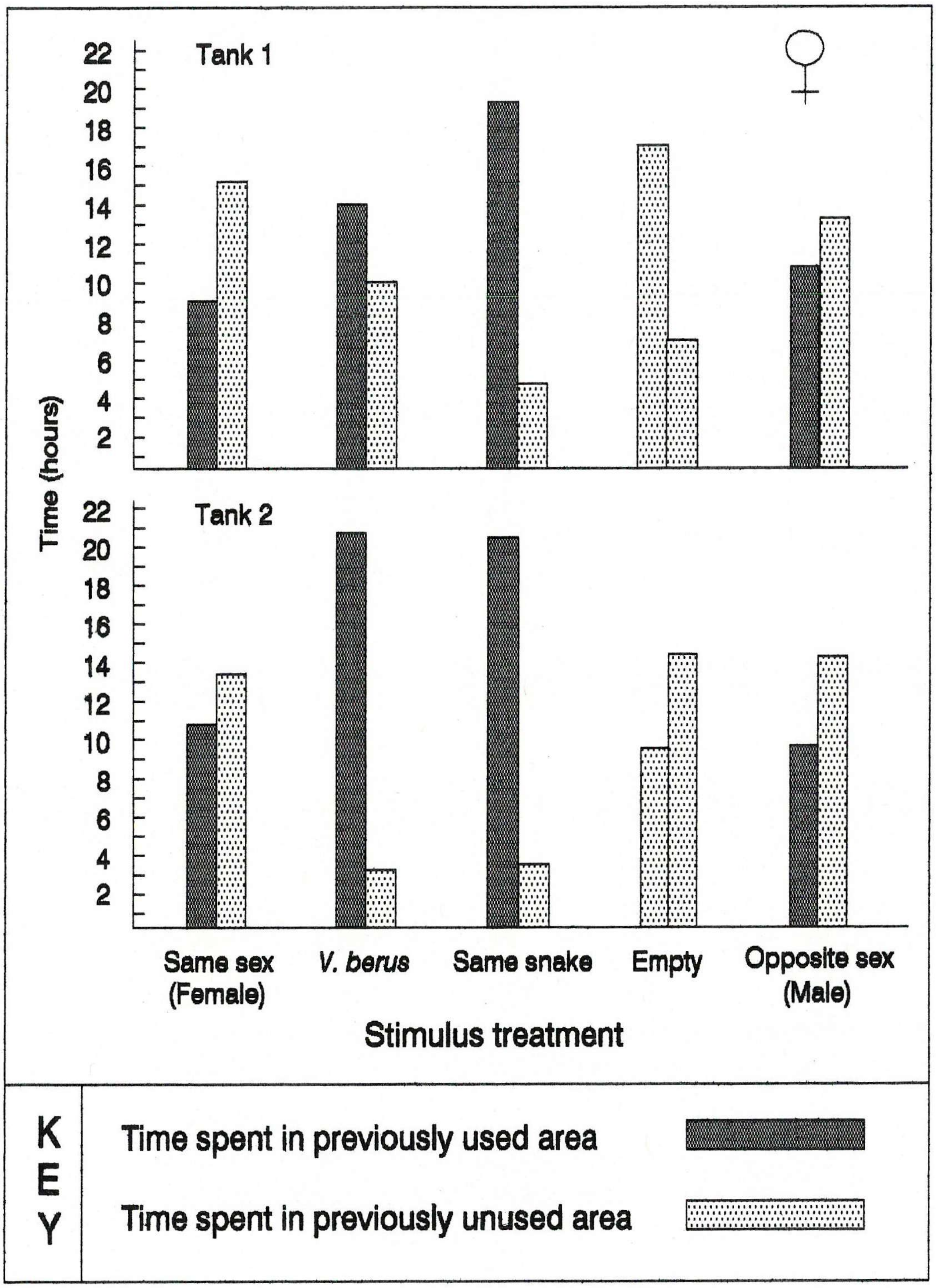


Figure 7.2 (b) Time spent by female grass snakes in previously occupied and previously unoccupied halves of an aquaria tank during a 24 hour period. Observations were made from time lapse video every 5 minutes but have been converted to time here to aid clarity.

7.4 Discussion

The results shown above suggest that N. natrix exhibits a behaviourial response to the presence of the sympatric species Vipera berus, but the evidence is somewhat equivocal. The most striking result is the behavioural response of grass snakes of both sexes to a 'refuge' area in which they had previously spent time themselves ('same snake' in Figures 7.2 (a) and (b)). Whilst this may be a response to scents deposited in these refuges, it is also possible that the individuals merely had time during the stimulus period (48 hours) to establish a favoured refuge to which they returned during the response period.

In the field, grass snakes occasionally returned to precise, previously used locations and on the few occasions in the field that it was possible to observe moving grass snakes without disturbance, tongue flicking was very much in evidence, which suggests that scent recognition is an important mechanism during movement. It was not possible to tell whether movements were directed by scent trailing or by visual cues and memory. Landreth (1973) provided evidence for the use of solar cues in orientation in Crotalus atrox, but overall there is little understanding of the orientation mechanisms of snakes.

The apparent response to areas previously occupied by adders was unexpected, despite the fact that adders and grass snakes were observed basking in close physical contact on three occasions in the field. There seems to be little or no competition between these two species; the snakes take different prey species, overwinter in separate refuges (pers obs) and do not appear to compete for basking sites or space; no interspecific aggression was ever observed. It is possible that during the stimulus period, the adders somehow 'conditioned' their refuges in some unidentified way and that the responding grass snakes merely took advantage of this, although the question is then raised of why this should not have happened with other stimulant grass snakes.

Observations made during this study showed that grass snakes are vulnerable to predators. At least three snakes were killed and at least partly eaten by predators and several snakes were lost owing to transmitter failure that could potentially have been caused by damage to the transmitter package during an attack by a predator. The secretive nature of the snake is almost certainly a defensive response and other defences shown by the species (feigning death and the venting of a foul-smelling discharge) are merely responses to attack and may therefore be ineffective. Adders, conversely, have a more potent defence mechanism and were frequently seen in this study in more exposed locations. Adders were also less likely to move away when disturbed and unlike the grass snake, could usually be caught with ease.

It is conceivable therefore, that a grass snake will be less vulnerable to predation if in close proximity to an adder. The costs of this behaviour are minimal to the adder and there may be thermal benefits to both species as heat loss will be reduced. The response shown by the grass snakes to the half of the experimental tanks occupied by adders suggests that grass snakes may recognise the scent of adders and favour such areas. Such a response could indicate that co-evolution has occured.

There was a slight, but non-significant tendency for both male and female snakes to favour the previously unoccupied half of the tank, although the time spent in each half of the tank was not significantly different from the control (empty) tank. Clearly, a more detailed examination is warranted.

The use of scent trailing and scent recognition by snakes is of particular evolutionary importance to neonate grass snakes (and some other species of snake), which often begin life some distance from suitable overwintering sites. At Chilworth, neonates were found at two locations, both of which were a considerable distance from known overwintering sites. The problem for these naive snakes is that for the period of approximately 2 months between birth and the onset of winter, fat reserves must be built up to enable winter survival and a suitable winter refuge must be located.

Reinert and Zappalorti (1988) described an instance of possible conspecific trailing of an adult Crotalus horridus by a neonate to an established overwintering site and observed tongue flicking in the neonate, suggesting that scent trailing was used as an orientation mechanism.

Observations of adult grass snakes confirm that specific overwintering sites are used (Madsen, 1984; pers obs), but if the aggregation of snakes at this time is a function of reproductive behaviour rather than habitat selection, non-breeding neonates may find suitable overwintering sites close to the place at which they hatched, or may overwinter singly. It is possible that winter mortality could be a key factor in the population ecology of the species. No neonates were seen near known overwintering sites during the course of this study, but such small snakes are extremely difficult to locate.

If neonate snakes did overwinter at the known winter refuge sites, their lack of knowledge of the area would mean that scent trailing would have been the only realistic way that they could have located these sites. Neonates were not found at a known oviposition site outside of the immediate post-hatching period, suggesting that neonates disperse soon after hatching. Rapid dispersal and 'random' overwintering would therefore negate the need for conspecific scent recognition.

As with all other species of snake, little is known of the movements of young animals and the development of a technique for following and locating small snakes would be of immense benefit in the study of the ecology of the species.

The results of this experiment suggest that scent recognition may be a factor in the social organisation of the grass snake. However, the results are not equivocal and are only significant at relatively low confidence levels. Nevertheless, further investigation is warranted and a more detailed study, particularly one involving naive animals is indicated.

Chapter Eight

Discussion

8.1 Introduction

The preceding chapters of this thesis represent the only major research to be carried out into the ecology of the grass snake Natrix natrix helvetica, which is the last of the three British snake species to be studied in detail. It follows the work of Madsen (1983, 1984, 1987) into the Scandinavian sub-species N. n. natrix, which represented the first major research into the ecology of the grass snake. In addition to these two ecological works, Thorpe (1979, 1984) has examined the phylogeny and population systematics of the species throughout Europe. No other significant contributions have been made to the study of the species, although the potential for further work is great.

8.2 Interpretation of results

The grass snake is a widely ranging species and an opportunistic feeder. This is consistent with the thermal ecology of the snake, which has a wide range of body temperatures during activity and thermoregulates with less 'precision' than the less active adder, even when basking (see Chapter 5 & Gaywood, 1990).

Predation of the population at Chilworth was high, which is also consistent with a widely foraging animal with few defence mechanisms. This fact, together with the high potential birth rate and lack of parental investment are typical of r-selected species. Further evidence that the grass snake falls into this category come from Madsen (pers comm), who stated that the population of grass snakes at his site in Southern Sweden fluctuated considerably in the 1980's.

This study has necessarily presented certain aspects of grass snake ecology into neatly divided chapters which have each attempted to make some sense of the way in which the animal behaves. However, at any given moment, snakes will give consideration to several of these components and develop a strategy which may appear on the surface to be either straightforward or impossible to explain. One example of this concerns long-term mechanisms for avoiding predation, which are not possible to detect in the field and may not even exist. However, if it is accepted that grass snakes eat only rarely, which would appear to be the case from observations made, why do individuals not remain in one smaller location (or have one range nucleus) for longer periods? There are apparent reasons for effecting such a strategy (safety from predators, Prestt, 1971; thermal benefits, Chelazzi & Calzolai, 1986), but there may be disadvantages by allowing predators to discover that an individual will regularly use the same location. This has been mentioned only briefly in this work (Chapter 3), but may form an important component of movement behaviour. The number of grass snakes killed by predators was relatively high and suggests that predation is underestimated as an influence on the behaviour of the snake.

Within a population, the ranging behaviour and dispersion patterns of individuals are determined largely by the distribution of resources (Mace, et al, 1984). This corresponds with the theory that animals will behave in ways which maximise their Darwinian fitness (Krebs, 1978). In this study, it was clear that snakes simultaneously considered more than one resource and nowhere was this more evident than in the choice between basking/thermoregulation and seeking cover, where the two may be connected in a way that is virtually impossible to differentiate in the field.

It would appear from a map of the distribution of the grass snake in Europe (Figure 1.1, p.2) that the species is at the edge of its' range in Britain. Shine (1987) stated that oviparity in squamates would tend to occur in species whose geographic distribution lay in warmer regions where soil temperatures favoured egg development, whereas viviparity would be favoured in colder areas. The grass snake occurs in considerably warmer climates than that of Britain and it is therefore possible that egg mortality increases with latitude. Egg mortality may thus be a key factor in the population ecology of the species in Britain, although the grass snake has to some extent circumvented the potential problem of egg mortality by laying eggs in active compost heaps which produce heat, a single one of which may be used by many gravid females (Madsen, 1984; pers obs).

The results shown in Chapter 3 reveal a wide variation in home range in the grass snake population at Chilworth and this is typical of many snake species (Macartney et al, 1988). The reasons for this are not clear, but it is possible that resources, particularly food, are often widespread and patchy, which would necessarily mean that snakes would need to move over increasing distances and areas until prey items were located (Brown, 1971). Movement by foraging grass snakes in this study (see Chapter 4) was extensive and animals were active for several hours a day at these times, although the relocation distances (ie between successive night refuges) were not necessarily large. Some extensive movements made during this study may have fallen into this category, but not all, as on many occasions, snakes were observed to make large and rapid movements, often to previously visited sites. Such movements may have been a mechanism to avoid predators as discussed above.

Migration or other large seasonal movements will also affect home range size, particularly if the Minimum Convex Polygon method is used to calculate the range area. In this study, this problem was circumvented by using a method that excluded movements to or through areas which were only minimally used, and the results showed that snakes actually use only very small areas, although foraging was excluded from those analyses. However, comparison of these results with those of other studies will be difficult unless similar methods of range calculation are used.

Gregory et al, 1987 stated that major patterns of movement by snakes seem to be related to the variation in abundance and dispersion of critical resources. Movements thus vary as much within species as between them. In order to further understand the use of space by the grass snake, it will be necessary to study the snake at more than one site and to examine the resources available at each site in order to ascertain any relationship that exists.

8.3 Discussion of methods

The project relied heavily on the use of miniature radio-transmitters and most of the data presented in this thesis was collected in the latter two years of the study during which time the transmitters were surgically implanted into the snakes. This technique, although used extensively in studies abroad, had never been used on snakes in Britain as it was prohibited by law. The Animals (Scientific Procedures) Act, 1986 permitted the technique to be used, and after consultation with veterinary surgeons at the Royal College of Surgeons (Cooper, pers comm) and London Zoo (anon, pers comm) and a visit to Sweden to investigate the work of Madsen, who had implanted tags into grass snakes (Madsen, 1983, 1984, 1987), details of the proposed surgery such as anaesthetic, recovery time and surgical procedure were determined.

The anaesthetic used on the snakes was successful and non-toxic, although intravenous injection was difficult owing to the small size of the sub-caudal vein and resistance from the snakes. One snake died without making a full recovery from the anaesthetic, but the snake was possibly already in a weakened condition owing to mite infestation. Other snakes made a rapid and complete recovery from surgery (see Chapter 2 and Appendix II).

Implantation of tags into gravid females presents special problems. The two alternatives are either to implant into the uterus or to implant, as with other snakes, into the peritoneum. The former method will mean that the tag will be ejected with the eggs and the snake subsequently lost. The latter method was attempted during this study and resulted in the death of the snake as the eggs could not be ejected and this resulted in a fatal pressure necrosis.

Although strictly within the law, there is a strong moral case for not causing distress to an experimental animal and for this reason, if for no other, the implantation of tags into gravid females is not recommended unless tags become available that are considerably smaller than those used in this study or unless a different surgical technique is used that circumvents the problems mentioned. A further argument against implantation of gravid grass snakes is the potential loss of the offspring of a protected species in the event of the snake dying.

In the other cases, surgical implantation of tags provided an excellent method of locating individual snakes and was preferable to the use of external tags, which could fall off, become tangled in vegetation, had a limited battery life, which were lost during exuviation and which could not be used for remote measuring of body temperature.

The method also has considerable advantages over the force-feeding of transmitter packages to snakes. Chapter 4 of this thesis examined the movement of recently fed snakes and showed it to be severely curtailed whilst digestion was in progress. It is likely that force fed radio-tags would elicit the same response in snakes, so movement studies carried out at this time would be of little value. The fact that implanted snakes were very mobile, even less than a week after surgery, would suggest that the surgically implanted tags had no such effect on the movement of the snakes.

The limited range of the transmitters meant that searching for snakes could be a time-consuming process. The need for extreme miniaturization meant that the antenna on the tags was small and therefore relatively inefficient and this led to many hours in the field looking for 'lost' snakes. Furthermore, predation of grass snakes was known to occur at Chilworth and if tagged snakes were killed and the tag destroyed or damaged, many hours could be spent fruitlessly searching for the animal. Clearly there had to be limits, both in time and in the area covered as to the effort expended looking for lost snakes. If the tags had possessed a larger range, a greater area could have been covered which may have located a snake (or a tag) which had travelled a very long distance.

The reliability of the tags compounded this problem. Missing snakes may have been killed and the tag destroyed or removed from the site. Alternatively, sudden tag failure merely meant that the position of the snake was irrevocably lost. Of the snakes lost in the field, no positive instance of tag failure was identified, nor was there any failure of transmitters in the laboratory. However, the external tags used in 1987 were known to become less reliable with age (Cresswell, pers comm; pers obs) and the same was presumably true with the implanted equipment. If tag failure did occur, it would mean that snakes would carry tags in perpetuity, which may cause physiological problems at a later date, particularly in female snakes.

The surgical techniques used in this study were novel, having only been permitted in Britain since the Animals (Scientific Procedures) Act, 1986. The anaesthetic used (see Chapter 2) showed a recovery rate that was far quicker than other drugs reported in the literature for similar purposes (cf. Madsen, 1984) and more humane than surgery without anaesthetic (Shine, 1979). Further work in this area is justified on the basis of the success of the present study, as it is only by continued work that the theory and practice of surgical implantation of tags will be improved.

One inherent weakness in a study of this nature concerns the small sample size of animals from which the data are gathered. Most of the data from this study were obtained from implanted snakes in 1988 and 1989, with a limited quantity coming from the externally tagged snakes used in 1988. The expense of the tags and the fact that several of the tags, particularly in the early stages of the work, were insufficiently powerful to be useful, meant that only a relatively small number of snakes could be used at any one time. Further losses due to predation and possibly tag failure compounded this problem. A possible useful strategy for future research would be to use a small number of animals, but to radiotrack them on a long-term basis, perhaps over several years.

Tags are now available which have a probable field life of one year, which would mean that snakes would only need to undergo surgery once each year. If this were done, late summer would be a good time to replace the tags as healing at this time would be rapid and complete by the time snakes overwinter, and removal of the snakes from the field at this time would have a minimal disturbance on annual patterns of behaviour and ecology. Care though, and further work is necessary before females can be implanted with tags if it is anticipated that they will develop eggs with the tag in situ.

8.4 Conservation

As the pressures of development and associated loss of habitat on the grass snake increase as they undoubtedly will in the foreseeable future, conservation of the species in protected areas such as nature reserves and timber producing woodlands may become the only viable means of preventing or slowing a decline in the British population. At present, in southern Britain the grass snake is widely distributed and locally common, and although local populations exist at least as far north as Wearside, these tend to be small, scattered and geographically isolated (Spellerberg, 1975). As the south is developed, it is conceivable that southern populations of the snake will also become isolated and a population decline would then be likely.

In Britain, the designation of protected areas is complex and haphazard. Sites of Special Scientific Interest, although strictly meant to be selected for their 'typicality' of a particular habitat type or species composition, are in practice used largely to protect rare or endangered species or communities, including the smooth snake, C. austriaca and the sand lizard Lacerta agilis, and therefore tend on the whole to be small in area. Other protected areas tend to be larger and include National Nature Reserves and many areas bought and managed by private interest groups such as the National Trust and County Trusts. All have one common element, which is that none is in existence purely to manage grass snakes and it is therefore important that habitat management which is not detrimental to grass snakes is given consideration when managing reserves for other purposes. Many reserves are intensively used by visitors and this in itself may detrimentally affect local snake populations. In order to achieve successful management, both of reserves and of non-protected areas, basic ecological knowledge of a species is vital if colonies are to establish and thrive.

The first consideration is the size of the proposed area. This study has shown that although grass snakes only intensively use small areas, they are a widely foraging animal and small areas are unlikely to sustain viable populations of snakes even if resources such as food are abundant.

Development of land adjacent to existing snake populations may increase the pressure on snakes from domestic cats, collecting and traffic and affect such areas as overwintering sites or egglaying sites. Grass snakes apparently stay in the vicinity of overwintering sites for several weeks after emergence, so identification of general overwintering sites should be possible by conducting fairly rudimentary surveys.

It may also be possible to identify egg-laying sites because these may be in established compost heaps, although no such sites existed at Chilworth and the snakes certainly laid eggs in other habitats at the site although these were not located. Gravid females appeared to aggregate at egg-laying sites before parturition and the presence of several gravid females at one location would provide an indication of the site. If, as suggested (Hilton-Brown & Oldham, 1991; pers obs), egg mortality is significant in Britain, the identification and management of known incubation sites could be of great importance to the management of local grass snake populations.

The results of the research show that grass snakes frequently use edge habitats, particularly of south facing woodland edges with dense ground cover. These linear habitats allow grass snakes to move and at the same time to remain in a habitat that allows thermoregulation, provides cover and which may contain a higher density of prey species than many other habitats. It was also noticeable that at some sites in the New Forest, snakes made use of small 'island' habitats of dense shrubs and bramble which are abundant at the edges of the 'lawns' and in some other areas (pers obs). Thus, localised fragmentation of habitats would seem to provide grass snakes with a greater suitable area and is compatible with the management of areas for other conservation purposes.

Dent (1986) and Dent & Spellerberg (1988) suggested that forest rides may offer the greatest opportunity for the management of habitats for the sand lizard L. agilis, and these may also provide suitable habitats for other reptiles, including the grass snake. One side of east-west orientated rides are effectively south facing forest edges and are important for the amenity value of many forests, in particular the many thousands of acres of Forestry Commission woodland throughout Britain. With minimal management, these habitats can be maintained and thereby provide suitable habitats for many years.

One further linear habitat that could be of crucial importance not only as it may provide a suitable habitat for the grass snake, but because it offers the opportunity for dispersal to other areas, is the hedgerow. Agricultural development since the second world war has meant that hedgerow destruction has been widespread in Britain, which has resulted in the loss of a vast area of 'natural' habitat. The trend now appears to be reverting to one of hedgerow planting, not only for amenity and conservation value, but also because many agricultural pest predators overwinter in hedgerows. The creation of new hedgerows would effectively increase the area of edge habitats which may well be of benefit to the grass snake and would also allow the migration or dispersal of snakes and may be consistent with the use of space by snakes, whereby they make periodic large movements but intensively use only small areas. The use of wildlife 'corridors' is of increasing scientific interest (Spellerberg & Gaywood, pers comm) and the creation of such habitats would seem to have a general conservation value and would therefore not merely be a strategy specific to grass snakes.

Management of prey species may be a central consideration in the management of the grass snake. The amphibian prey of the grass snake would be seriously affected by pond removal or degradation and it follows that pond creation, together with the possible introduction of spawn to newly created ponds would result in an increase in amphibian populations. Cooke & Scorgie (1983) stated that pond creation was by far the primary reason for the increase in local frog and toad populations and their data suggests that relocation and the introduction of these species can be a potentially successful strategy. Furthermore, Hilton-Brown & Oldham (1991) stated that increased food availability was by far the primary reason for increases in local reptile populations. Although grass snakes were not, in this study, observed to be intensive users of pond habitats, their prey depend on such habitats and attempted grass snake management would be worthless without an examination of their prey requirements. Many local Trusts and conservation organisations have adopted a policy of relocating 'spare' amphibian spawn to new or disused ponds, which may ensure the widespread availability of prey species into areas which could potentially be used by dispersing grass snakes.

Large, open habitats were rarely used by radiotracked grass snakes and it may be that these present a barrier to the dispersal of populations. This may well include roads, which may appear to snakes as large, open habitats. A snake was known to have crossed a road on only one occasion during this study and that was an introduced snake (see below), although grass snakes have been observed crossing roads on other occasions (pers obs), although in every case the road was a narrow lane. Wider roads may not be crossed by grass snakes and if they are, there is an obvious danger from traffic. Gent (1988) reported a smooth snake killed on a busy road and noted that snakes at that site regularly used a tunnel under the road.

Other similar barriers to dispersal may include managed fields where the grass is mown, or walls and fences which are impenetrable to snakes. The apparent reluctance or inability of snakes to cross such barriers serves to emphasise the importance of providing corridors through which snakes and other animals can move to disperse.

Two final measures which can be taken to improve the status of the grass snake are legislation and education. The Wildlife and Countryside Act, 1981 now provides substantial protection for the snake, making it illegal to kill grass snakes or take them from the wild, either as pets or to sell. The enforceability of such legislation is difficult to gauge, but may deter organised collecting for sale, although it is doubtful if it will prevent the indiscriminate collecting of individual snakes by members of the public.

The latter problem can be approached through education. During the course of the research, the children's group of the local Naturalist's Trust were invited to the study site to wander round selected areas looking for reptiles. On each occasion a captive snake was also brought, in case none could be found in the field. The children were clearly fascinated by being able to see wild snakes and to handle grass snakes. They also enjoyed seeing photographs of eggs and young snakes and asked many questions. It is fair to say that this was one of their most popular and well attended outings of the year. It was also noticeable that they were considerably less nervous about handling snakes than their parents, many of whom also attended. Persecution of grass snakes is still reported (Hilton-Brown & Oldham, 1991) and this may well be due to fear or mistaking the identity of grass snakes. By teaching children about the snakes and encouraging respect for them, the problem of persecution will be reduced in the future.

One final method of improving the status of grass snakes is by the introduction of individuals to new habitats, although such a strategy must be considered with great care (Anon, 1973) and requires an initial knowledge of their ecology (Spellerberg, 1975). In particular, the questions of available resources and the liklehood of snakes remaining in the area need to be addressed.

The data obtained from the introduction of two male snakes to Chilworth in 1989 suggests that if the habitat is suitable for snakes and resources are available, which they clearly were in this case, that snakes will stay in the area. Neither of the snakes introduced into Chilworth made an apparent effort to leave the area altogether, although one formed a fairly large home range (see Appendix I) and spent most of the time it was released at some distance from the release site. It was however, returning in the general direction of the release site when it was recaptured at the end of the tracking period. Both introduced snakes fed during the tracking period and appeared to behave no differently from indigenous individuals and the Multi-nuclear range sizes of the snakes were much smaller than the Convex Polygon areas, which showed that certain areas were used more intensively than others.

Spellerberg (1975) suggested that barriers around areas into which reptiles are introduced would encourage home range formation in the area, although this was with specific reference to the introduction of sand lizards, L. agilis. In the case of grass snakes, this would need to be a substantial construction as snakes seem able to breach all but the most secure barriers. Such a strategy would be impossible in all but purposefully designed reserves and would only be worthwhile if planned to secure the future of a very rare species. Spellerberg also states that introductions should be made early in the season in order to allow animals time to adjust to their new surroundings and to establish or find overwintering sites. The provision of egg-laying sites would also be of particular importance as grass snakes are known to travel long distances to find suitable incubation sites (Madsen, 1984).

8.5 Further research

Further research on the grass snake could usefully be directed towards two main objectives. The first of these is a broad continuation of the work carried out during this study and would involve further long-term radio-tracking of individual snakes. At present, the grass snake is not a rare species, and as such, the additional risk to individuals as a result of surgery and the implantation of radiotags is not such a contentious issue as it would be for an endangered species such as the smooth snake in Britain. Radio-tracking using the methods developed in this study appears to offer an excellent opportunity to follow individual snakes for periods of several years, which would provide an improved indication of range formation and demonstrate whether snakes use the same range from year to year.

Further work should take place at a selection of study sites in order to investigate the size and nature of home ranges in different habitats and under different climatic conditions. Of particular interest would be studies at sites at which prey species are known to be abundant and at which they are known not to be abundant and comparative studies in areas with markedly different climates, so that the effects of these variables on the vagility and range use of snakes could be identified.

The social interactions of grass snakes have been investigated in this study and although no profound conclusions could be drawn from the results, there was an indication that intraspecific and interspecific social interactions may exist. The laboratory investigation of such interactions at different times of the snakes' annual life-cycle would demonstrate the presence or absence of social behaviour and the strength of positive interactions. At present there is no published information of this nature with respect to the grass snake, although such information exists for several other species (see Chapter 6).

Habitat selection studies at various sites may provide an indication of the resources which snakes are seeking when selecting various macro-habitats, but studies on the selection of microhabitats may be better performed under controlled laboratory conditions where subtle differences may be better observed. Information concerning habitat selection and use is of particular importance when designing reserves or planning for the conservation of grass snakes.

Introductions of grass snakes to new areas would be of particular interest, for as well as providing information that would be crucial when relocating and introducing snakes to new areas, the results may also help to explain the behaviour of indigenous snakes. Experimental manipulation of populations in this way may provide more detailed explanations of behaviour than those in this study, which has been more observational than experimental. Information which could be obtained from such a study should include the relative success of introduced animals, which could be measured by observing relative growth rates and weight gain of introduced and indigenous snakes. In this study, both introduced snakes gained weight, but such a small sample size precluded a meaningful comparison.

The second important objective for future studies should be long-term studies of population dynamics at various sites. No such information has to date been published, but basic studies would be relatively simple to carry out with virtually no equipment. Radio-tracking, although useful, would be of little value in such a study. Information needed should include the growth rate, location, condition and social behaviour of individuals and annual estimates of the population size and sex ratio of the areas studied.

Neonate snakes are virtually impossible to find, but can be located on occasion, particularly near incubation sites or if sites can be found where artificial hides, such as corrugated sheet, can be placed. This would help in the capture of snakes. It may be possible to carry out such studies on reserves or on private estates.

The current study has provided some detailed information on the ecology of the grass snake, but much still remains to be done if a more thorough understanding of the species is to be achieved. Such an understanding will be important if the potential decline in the abundance of the grass snake in Britain is to be halted.

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Glossary

Acclimation: Adaptation by an animal in the laboratory to changes in one or more variables, such as temperature or day/night length.

Acclimitization: Adaptation by an animal in its' natural environment to changes in one or more variables, such as temperature or day/night length.

Aerobic metabolism: Metabolism which occurs in the presence of oxygen.

Aerobic metabolic scope: The difference between resting metabolic rate and maximum oxygen consumption.

Anaerobic metabolism: Oxidative metabolism which occurs in the absence of oxygen. Often referred to as glycolytic metabolism.

Ectotherm: An organism which relies on external heat sources to raise body temperature.

Endotherm: An organism which produces heat metabolically to maintain an optimum body temperature.

Eurythermal: An organism which can operate under a wide range of body temperatures.

Fix: A single geographical location of a series taken from an individual tagged animal.

Harmonic Mean Analysis: A method of home range calculation which calculates an activity centre and draws surrounding contours of activity (isolines).

Heliothermy: Use of direct solar radiation as a means of raising body temperature.

Homoiotherm: An organism that maintains a constant body temperature.

Lying out: Basking by snakes, particularly at or near the overwintering site (Prestt, 1971).

Minimum convex polygon: A home range calculation method whereby a convex polygon is drawn round a series of plotted locations and the area of the polygon calculated.

Multi-nuclear cluster analysis: A method of home range calculation whereby a series of plotted locations are analysed in turn and placed mathematically into a number of clusters. Cluster areas are then calculated. The method has the effect of excluding large unused areas.

Photophase: Period of time in which light is avalable (usually daytime).

Poikilotherm: An organism that has a variable body temperature.

Scotophase: Period of time in which no light is avalable (usually night time).

Tag: A radiotracking transmitter and battery package as fitted to or implanted into a grass snake. Also tagged, tagging.

Thermo-conformer: An organism whose body temperature fluctuates passively with ambient temperature.

Thermoregulation: Behavioural regulation of the body temperature of an ectotherm.

Thigmothermy: Thermoregulation using heat conducted from objects in contact with an ectothermic organism.

Utilisation distribution: A plot of the decrease in home range area as outlying fixes are excluded.

Vagility: The tendency of an organism or population to change its' location or distribution with time.

Appendices

Appendix I

Movement behaviour of introduced snakes

It had been planned to introduce to Chilworth two male and two female snakes captured at Whiteparish in Hampshire and to compare the behaviour of introduced snakes with that of indigenous animals. However, owing to a lack of suitable transmitters, it was possible only to implant three snake (nos. 11, 41 & 42). No. 42, a gravid female, died in the field after 7 days and the transmitter in no. 41 lost power after 26 days and it was decided to retrieve the snake. Only no. 11, tagged for 94 days, provided a significant quantity of data.

Because of the overall lack of success with respect to introduced snakes, only limited data can be presented here. Home range areas of the two male snakes (11 & 41) are shown in Table A1.1 and maps of 100% Minimum Convex Polygon and Multi-nuclear Clustered Polygons in Figure A1.1.

Snake	n	MCP	100% MNCP	95% MNCP	90% MNCP	70% MNCP
11	94	20.08	6.11	0.07	0.1	0.00
41	26	3.09	1.71	0.83	0.497	0.01

Table 3.1 Length of tracking period in days (n), minimum convex polygon (MCP)and four multi-nuclear polygon (MNCP) areas (ha) for implanted snakes.

Habitat use of introduced snakes

No formal analyses were performed on the data collected from the introduced snakes, but snake no. 41 was released in deciduous woodland and did not leave the wood for the entire tracking period. Snake 11 was released at the same site and after making only short movements for several days, moved to a site 0.6km distant where it remained for the remainder of the tracking period. The snake was the only grass snake observed during the entire three year study that was known to cross a road, which it did twice. When picked up at the end of the tracking period, the snake was moving back in the direction of the place at which it was released.

Both snakes showed ranging behaviour similar to that of the indigenous snakes, as shown by the reduction in MNCP areas as outlying fixes were excluded. No homing behaviour was evident and both snakes gained weight during the tracking period, although neither was observed with a large food bolus.

Observations of the ranging behaviour of introduced snakes would have a great value in explaining the behaviour of indigenous snakes. A further extension of this would be to move indigenous snakes to a new site outside their normal ranging area and to observe the subsequent ranging behaviour.

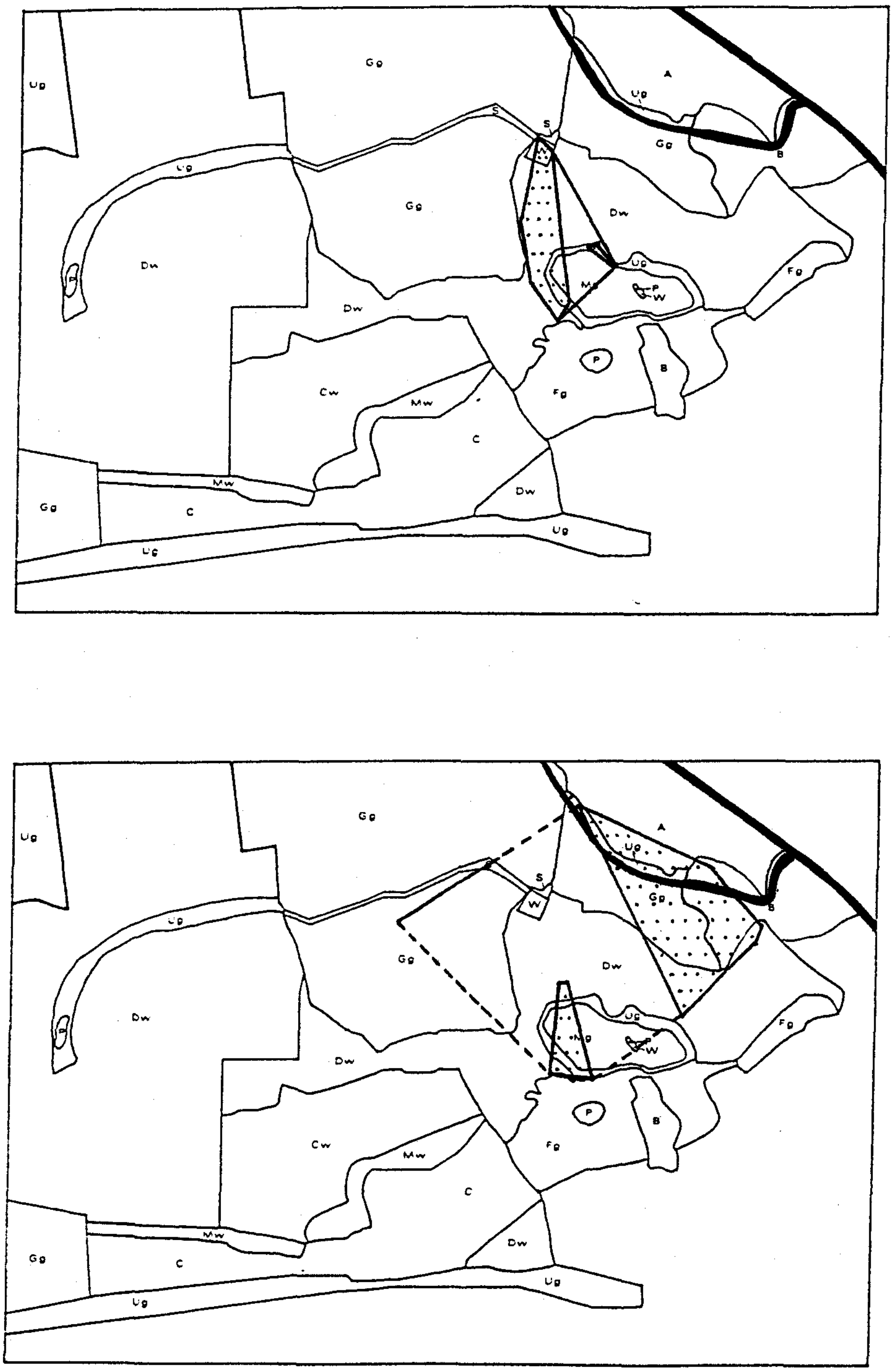

Fig. A1.1 MCP and MNCP ranges for introduced snakes. MNCP ranges are the shaded areas. The key to the habitat types shown on the map is as follows: Dw:Deciduous wood; Cw:Coniferous wood; Mw:Mixed wood; Gg:Grazed grassland; Ug:Ungrazed grassland; Mg:Managed grassland; W:Wet grassland; Fg:Formal garden; P:Pond; A:Arable land (cereals); C:Cultivated (tree nursery); S:Stream; B:Built environment; Roads are shown coloured bold black.

Appendix 2

Snake	Date	Sex	Weight (g)	Saffan I/V (ml)	Comments
122	30-3-88	♀	160	0.2	Induction: 7 mins; good surgical anaesthesia; recovery in 35 mins.
181	15-4-88	♂	81	0.1	Induction: 8 mins; surgical anaesthesia: 10 mins; recovery: 35 mins.
192	22-4-88	♀	132	0.15 0.1 0.15	No response to first dose after 35 mins; twice repeated; poor anaesthesia; local anaesthesia used at point of incision.
141	22-4-88	♂	80	0.1	Good induction; duration: 10 mins; total recovery: 35 mins
172	29-4-88	♀	159	0.2 0.2	Poor induction even after repeat dose; local anaesthesia used at point of incision.
111	29-4-89	♂	68	0.08	Good induction, anaesthesia and recovery.
122	5-7-88	♀	180	0.2	Good induction, anaesthesia and recovery.
151	25-7-88	♂	90	0.1	Good onset and anaesthesia; slow recovery; died after 48 hours; P.M. showed poor physical condition.
111	1-8-88	♂	86	0.08	Good onset and anaesthesia; rapid recovery.
181	8-8-88	♂	107	0.09 0.09	Poor induction; repeated after 20 mins; slow recovery and profuse bleeding at site followed by death.
1161	8-8-88	♂	91	0.11 0.11	Poor initial induction; good anaesthesia and recovery.

Table 1 (a) Observations made during surgery of implanted snakes.

Snake	Date	Sex	Weight (g)	Saffan I/V (ml)	Comments
192	15-8-88	♀	169	0.17	Poor induction; repeated after 12 mins; light anaesthesia; local needed at incision site.
12	21-9-88	♀	130	0.14	Good onset, anaesthesia and recovery.
11	29-3-89	♂	134	0.1 0.15	Onset slow; anaesthetic and recovery good.
21	29-3-89	♂	71	0.1	Good onset, anaesthesia and recovery.
22	29-3-89	♀	132	*	Poor induction; repeated twice to give fair anaesthesia.
32	6-4-89	♀	106	0.12 0.12	Poor induction; repeated after 20 mins. Good anaesthetic plane and recovery.
31	6-4-89	♂	67	0.08	Good onset, anaesthesia and recovery.
192	25-4-89	♀	161	0.14	Good onset, anaesthesia and recovery.
41	24-5-89	♂	82	0.1	Rapid onset (5 mins); Good anaesthetic plane and recovery.
51	1-6-89	♂	52	0.06	Good onset, anaesthesia and recovery.
42	2-6-89	♀	140	0.15	Good onset, anaesthesia and recovery. Gravid snake: tag implanted intra-peritoneally; died in the field.

Table 1 (b) Observations made during surgery of implanted snakes.