UNIVERSITY OF SOUTHAMPTON

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Department of Biology

COMPARATIVE THERMAL ECOLOGY OF THE BRITISH SNAKES

Submitted by

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for the degree of

DOCTOR OF PHILOSOPHY

1990

To Mum, Dad and Lorraine

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UNIVERSITY OF SOUTHAMPTON

ABSTRACT

FACULTY OF SCIENCE
BIOLOGY
Doctor of Philosophy

COMPARATIVE THERMAL ECOLOGY OF THE BRITISH SNAKES

by Martin John Gaywood

A comparative study was made of the thermal ecology of the smooth snake *Coronella austriaca*, the grass snake *Natrix natrix* and the adder *Vipera berus*. Particular emphasis was placed on strategies employed in behavioural thermoregulation. Snakes were captured from several sites in Hampshire, England, and kept in landscaped outdoor vivaria. Operative temperatures available to the snakes in the outdoor vivaria were estimated using snake models. Body temperatures were measured and recorded using biotelemetric equipment, and their behaviour was observed. Snakes were also studied in a laboratory arena using time-lapse video equipment.

Adders attained the highest body temperatures with a mean selected body temperature (calculated from 'plateau phase' body temperatures attained after an initial heating phase and before a cooling phase) of 33.2°C ± 1.86 (n = 491) outdoors and 32.5°C ± 2.27 (n = 159) in the laboratory. The respective values for smooth snakes were 30.3°C ± 1.64 (n = 377) and 30.8°C ± 1.25 (n = 241) and for grass snakes 29.3°C ± 2.63 (n = 291) and 31.0°C ± 2.10 (n = 189). When conditions were thermally unlimiting, the snakes attained higher body temperatures than during periods of thermally limiting conditions.

Outdoor conditions were found to be thermally unlimiting for all 3 species for only a relatively small proportion of the time during their 'active' season. Adders displayed a greater ability to temporally utilise thermally unlimiting conditions. They basked in the open for relatively long periods. A sit-and-wait predatory strategy may be used in conjunction with basking. Adders emerged earlier and submerged later, emerged on a greater number of occasions and had a wide repertoire of thermoregulatory behaviour (e.g. dorso-ventral flattening, alteration of body aspect, body coiling, adjustment of body area exposure, basking site selection, thigmothermy). Smooth snakes were also heliothermic and were capable of very precise thermoregulation. Mosaic basking was observed far more than basking in the open and movement was observed less than in the adders or grass snakes. This related to the smooth snake's cryptic lifestyle. Mosaic basking was considered to be an extreme (and energy-efficient) form of shuttling heliothermy, utilising sunny and shaded areas simultaneously. Grass snakes engaged in movement more than the other species in the outdoor vivaria, especially during thermally unlimiting conditions. This was related to their widely foraging predatory strategy. Details of behavioural thermoregulatory strategies and other aspects of general thermal ecology are discussed.

ACKNOWLEDGEMENTS

I am grateful to the Science and Engineering Research Council for sponsoring this project. I would also like to thank everyone who has given help and advice throughout this work. In particular my thanks go to;

- The staff at the Forestry Commission in the New Forest for allowing me to undertake fieldwork and the collection of animals and providing me with valuable advice. In particular I would like to thank Mr. R.E. Hughes and Mr. M. Noble. Thanks also to the staff of the South Downs Forest District Office for giving me access to one of their forests.

- The Nature Conservancy Council who granted me permission to work on smooth snakes.

- The staff and students of Southampton University for support and encouragement over the last four years. Thanks to Rik Trenchard,William Handley-Garland, Barry Lockyer, Ray Cornick, Pete Hillier, Pete Brown, KelvinYapp, Dawn Trenchard and Dr. Rory Putman. Special thanks to Nick Smith. Special thanks also go to Dr. Ian Spellerberg who supervised the project.

Finally I would like to thank my parents for continual encouragement and support throughout the years, and who have never once suggested I might try finding employment in a more 'normal' line of work. Lorraine Barraclough prepared most of the final tables and helped with much of the artwork in the thesis, sacrificed many sunny weekends to go snake catching and showed amazing patience throughout the entire project.

CHAPTER ONE

INTRODUCTION

1.1. General Ecology and Distribution

There are six native species of reptiles in Britain, three of which are lizards and three snakes. The lizard species are the common lizard Lacerta vivipara Jacquin, the sand lizard Lacerta agilis L. and the slow-worm Anguis fragilis L. The three snake species include the grass snake Natrix natrix helvetica Lacépède and the smooth snake Coronella austriaca Laurenti, both members of the family Colubridae. The third snake species is the common viper or adder Viper berus berus L., a member of the family Viperidae.

The smooth snake is slender, comparatively small with a poorly defined neck and a fairly small head (Plate 1). The coloration of the body varies between grey, brown or even a reddish brown with a series of dark markings along the dorsal surface. These markings may take the form of small spots or blotches which sometimes connect to form bars. On the top of the head is a distinctive dark 'coronet'. A dark stripe run from the nostril along either side of the head. The name 'smooth snake' arises from the fact that the scales have no keels, unlike grass snakes or adders. Adults typically grow to a length of 600 mm and weigh between 40 to 50g. Males have longer tails relative to total body length than do females, and a greater number of subcaudal scales.

The activity season of smooth snakes begins with emergence in late March and April (Phelps 1978, Goddard 1981, Gent 1988). Goddard (1981) considered mating to occur between April and June and the females (which usually have a biennial breeding cycle) give birth to live young during September and October. Litter sizes may vary from between one to sixteen. Winter submergence commences around early October. They have been described as opportunistic predators, with a diet mainly consisting of lizards (Lacerta spp., Anguis fragilis), small mammals and mammal nestlings. Prey are subdued by constriction.

The distribution of the smooth snake ranges east into Poland and the USSR, southeast into Greece and Italy, southwest into northern Spain and north into southern Scandinavia (up to 60°, see Fig 1.1). In Britain it is now only to be found in the far southern counties of Surrey,

Plate 1. The smooth snake, *Coronella austriaca.*

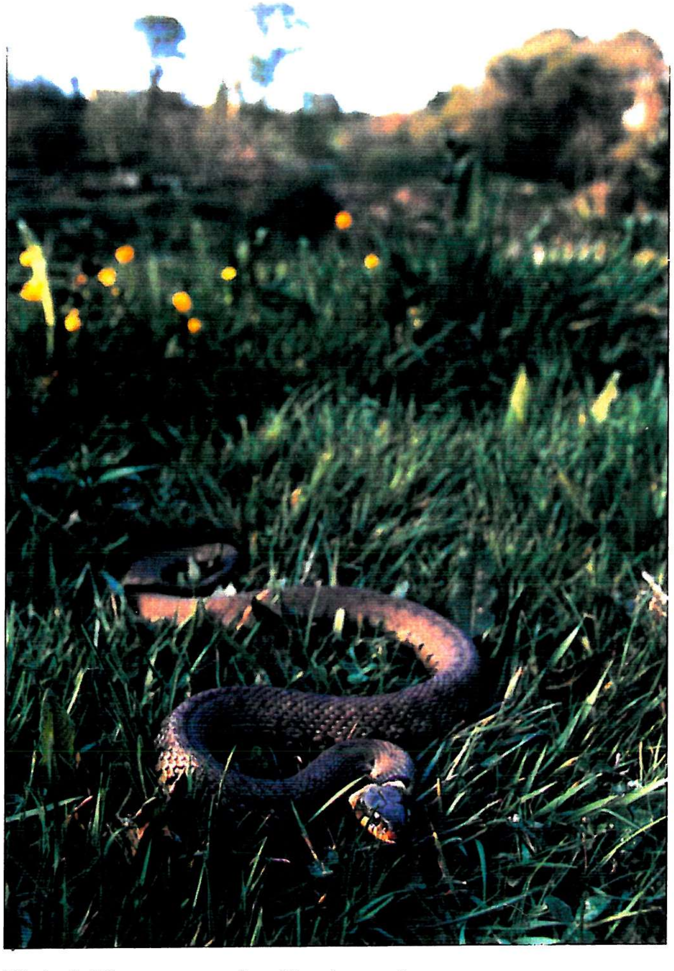
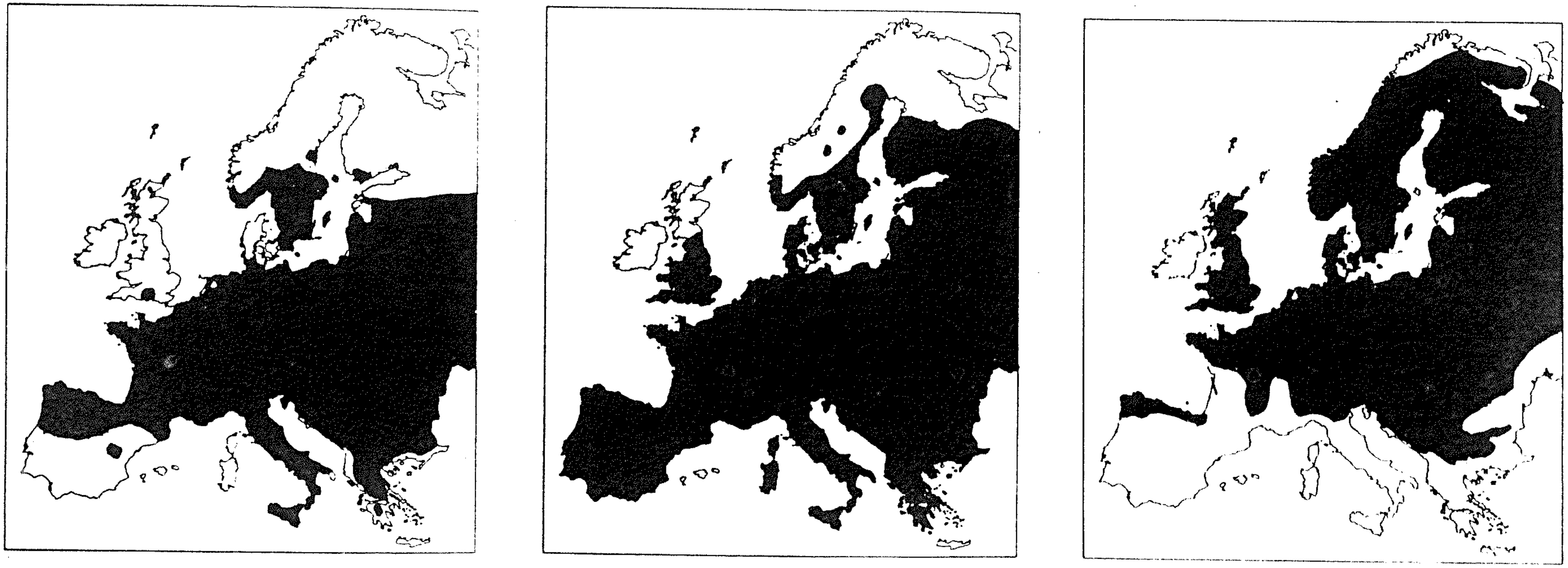


Plate 2. The grass snake, *Natrix natrix.*

Plate 3. The adder, *Vipera berus*.



Coronella austriaca

Natrix natrix

Vipera berus

Fig. 1.1: **Distribution maps of the three British snake species** (from Arnold and Burton, 1978).

Dorset and Hampshire in areas of lowland heath dominated by Erica and Calluna species (Spellerberg and Phelps 1977, Goddard 1981, NCC 1983). Gent (1988) noted that in the New Forest, smooth snakes occupied a range of habitat types but dry and humid heath, bracken and gorse/bramble bushes were primarily selected.

The grass snake is the largest of the three British species, with maximum recorded lengths for British specimens of 815 mm in the case of males, and 1830 mm for females (Frazer 1983, see Plate 2). The heaviest specimen measured in the present study was a female of 915 mm length which weighed 338.5 g. As well as growing smaller than females, male grass snakes have longer tails relative to total body length and a greater number of subcaudal scales. The dorsal surface is olive green or sometimes olive brown in colour although the shade can vary from light to dark. There may be rows of black spots along the back or sides. There is a distinctive yellow collar which can vary in intensity, bordered by black. The markings of grass snakes on the continent may be different and vary from region to region (Arnold and Burton 1978).

The activity period for grass snakes appears to be similar to that of smooth snakes. Mating takes place between the end of March and June and the females may lays eggs from mid-June through to July. Oviposition sites take the form of manure or compost heaps, or piles of saw dust. Clutches of about 10 eggs may be laid. The time of hatching depends on environmental temperatures but it is usually between late August to early September. The grass snake's main prey species include frogs, toads and newts.

Fig. 1.1 illustrates that the grass snake is distributed further north than the smooth snake (up to 67° in Scandinavia). The species is found throughout most of Europe and also occurs in northwest Africa and Asia east to Lake Baikal (Arnold and Burton 1978). The subspecies Natrix natrix helvetica ranges from the southern half of Britain to France, West Germany and Italy. In Britain, the grass snake is absent or virtually absent from Scotland although it has been recorded throughout much of England and Wales. It is commonly associated with damp habitats such as ponds, ditches, wet and boggy heath or grassy areas.

The adder is the only venomous species of snake in Britain. It is a generally thick-bodied snake, up to 600 mm in length although adults are usually in the range of 400 to 500 mm (see Plate 3). Females tend to be larger than males and can also differ in coloration. Males tend to a have white or pale grey background colour, whereas females may have a brown, brown-yellow or reddish coloration. A distinct, dark zig-zag marking runs along the back and there is usually a row of round or oval spots along the sides. The back of the head is marked by an inverted 'V' or 'X' shape. Melanic specimens are not infrequently found.

Emergence from the winter inactivity period occurs from March to early April, with the male adders appearing before the females. The adders submerge for the winter inactivity period throughout September and early October (Prestt 1971, Frazer 1983). Male combats may occur during the mating period which is at its peak during late April and early May. The females, which have a biennial breeding cycle, give birth to live young during late August and early September. Adders feed mainly on small mammals (including nestlings) but will also take reptiles and bird nestlings.

The adder is one of the most widely distributed reptiles in the world. It occurs over most of northern and central Europe, ranging south as far as northwest Spain, north Italy and much of the northern Balkans (see Fig. 1.1). Its northerly distribution extends beyond the Arctic Circle. The adder is widely distributed throughout the British Isles although not in Orkney, the Hebrides, Shetland or Ireland. Moorland, heathland, woodland rides and dunes are examples of the types of habitat in which it may be found.

Groombridge (1986) has categorised the status of the smooth snake within the EEC countries as being 'vulnerable'. This means that it is not yet in danger of extinction in the EEC but is likely to become so in the new future if the causal factors continue to operate. In the UK it is protected under Schedule 5 of the Wildlife and Countryside Act (1981). An amendment to Schedule 5 in 1988 also prohibited the deliberate killing of grass snakes. A Nature Conservancy Council (NCC) report by Cooke and Scorgie (1983) described the status of the grass snake as being widespread and fairly common in much of England although moderate declines were reported in southern and central England. Adders were described as widespread and common over much of Britain with decreases in the west Midlands, East Anglia and south England. Following the second quinquennial review of the Wildlife and Countryside Act in 1991, the adder is also now protected.

1.2. Previous Research

Within the past 20 years there has been an increasing amount of research on the smooth snake in Britain. The first ecological studies were conducted by Breeds (1973) and Spellerberg and Phelps (1977) on sites in Dorset and Hampshire. Information on body temperatures of smooth snakes were reported in Spellerberg and Phelps (1975) and Spellerberg (1976). The closely monitored behaviour of a young smooth snake was reported in Spellerberg (1977a) and Phelps (1978) published information on the seasonal movements of all three snake species at Dorset study sites. A three year research project on general aspects of smooth snake ecology and biology was carried out by Goddard (1981, 1984) which was followed by another three year study by Gent (1988). The latter project mainly concentrated on movement biology and habitat selection. On the continent of Europe the activity cycle of smooth snakes was investigated early on (Duguy 1961). General aspects of smooth snake biology in Nordic countries have been reported by Nilson (1975) and Andrén and Nilson (1979) and a study of the thermal ecology of free-ranging smooth snakes was undertaken by de Bont et al. (1986).

There appears to have been no published full-scale ecological investigation of grass snake ecology in Britain. The results of a three year study on movement biology and habitat selection of grass snakes undertaken at a Hampshire site are currently being studied (P.Brown, pers. comm.). Spellerberg (1976) recorded information on body temperatures of grass snakes monitored during laboratory conditions and Davies and Bennett (1981) and Hailey and Davies (1986) published information on aspects of thermal sensitivity of physiological processes. The latter study involved grass snakes from the U.K. and field data obtained from grass snakes at a Spanish field site. In Sweden, Madsen (1983, 1984, 1987) has studied growth rates, reproduction, movement biology and habitat use of grass snakes.

A study by Prestt (1971) on the general ecology of adders on several Dorset sites remains the only detailed ecological investigation of the species in Britain that has been published to date. Apart from this, there have been studies on body temperatures recorded for adders during laboratory experiments (Spellerberg 1976) and on competition for food and mates (Kelleway 1982). A three year study on the thermal biology of adders based at Nottingham University has been completed and the thesis has recently been completed (Vanning 1990). There have been many investigations on adder biology elsewhere in Europe, especially on various aspects of reproduction and population dynamics (e.g. Nilson 1980, Andrén 1981, Andrén and Nilson 1981, Andrén 1982, Stille and Niklasson 1987, Madsen 1988) and on the effect of melanism on fitness (Forsman and Ås 1987, Madsen and Stille 1988). Saint Girons (1978) has looked at the thermoregulation of adders in comparison with other European Vipera species.

Reptiles are ectothermic which means that body temperatures depend primarily on the absorption of heat energy from the environment. Mammals and birds are endothermic, their body temperatures primarily determined by oxidative metabolism. Some of the larger reptiles are known to use endothermic means of thermoregulation to a degree, for example the leatherback turtle, Dermocheys coriacea, which can maintain constant, high body temperature through their large body size, low metabolism and use of peripheral tissues as insulation. This has been described as 'gigantothermy' (Paladino et al., 1989). It was originally thought that the body temperatures of reptiles passively followed those of the environment but a series of studies in the 1930s and 1940s, culminating with a study on desert species by Cowles and Bogert (1944), demonstrated that they have rather specific preferences for body temperature and that behavioural strategies may be employed to achieve them. Such behaviour includes heliothermy (basking) and thigmothermy (absorbing heat by contact with warm surfaces).

Since those first studies, there has been a large amount of research aimed at investigating thermal aspects of reptilian biology and its relationship with other ecological and general biological factors. However, the number of papers published is heavily weighted towards studies on lizards. There have been reviews and lists of references on the subject by Brattstrom (1965), Spellerberg (1977b), and Heatwole and Taylor (1987). Avery (1982) listed field studies on reptilian thermoregulation and body temperature and noted that the subject had been less thoroughly investigated in snakes. He attributed this to the fact that snakes are frequently less abundant, more secretive and cryptic, difficult to capture and often potentially dangerous. The suggestion was made that more research should be aimed at the thermoregulation of snakes, including basking ecology. Huey (1982) reviewed work that had been undertaken on various aspects of reptilian thermal biology, concentrating on physiology and ecology. Studies on lizards formed the greater part of Huey's paper. Reviews concentrating on the thermal biology of snakes have been presented in Peterson (1982) and Lillywhite (1987).

Many studies of snake thermal ecology have concentrated on an analysis of body temperatures in relation to environmental factors. From these it is possible to derive a picture of snake behaviour, activity and, specifically, thermoregulation. Often they are supplemented by direct observations of behaviour (e.g. Osgood 1970, Gibson and Falls 1979, Shine 1979, Peterson 1982, de Bont et al. 1986, Hailey and Davies 1988). However, there has been very little published on detailed observations of behavioural thermoregulatory strategies utilised by snakes, particularly from a comparative point of view.

1.3. Aims of the Present Study

The three British snake species have been recorded as having differing lifestyles and varying northerly distributions. General observations have suggested they appear to have different behavioural methods of thermoregulation (Spellerberg 1976). It was the intention of the present study to undertake a detailed quantitative and qualitative study of the thermal ecology of the three British snakes and to make interspecific comparisons. This involved an assessment of their utilisation of the thermal environment in terms of the body temperatures that were attained by the snakes and the behaviour that was displayed. Thermoregulatory behaviour is a particularly important activity for a reptile inhabiting cool, temperate environments such as to be found in Britain. Adders are known to display basking behaviour for long periods, sometimes using flattened, ribbon-like body postures to increase heat absorption (Appleby 1971, Saint Girons 1978) and this may be a factor in their more northerly distribution. Details of the behavioural thermoregulatory strategies employed by each species were examined and compared.

Experiments were undertaken in outdoor vivaria which were designed to simulate field conditions but permitted easier monitoring of snake behaviour, body temperatures and the thermal environment than would have been possible during a field study of free-ranging animals. Snakes were also studied in a laboratory arena during a series of experiments undertaken in conjunction with the outdoor vivaria experiments. The use of video equipment in the laboratory allowed snakes to be monitored 24 hours a day. Environmental conditions outdoors varied considerably and so the study of snakes in the laboratory meant that conditions could be kept relatively constant between individual experiments and direct comparisons between snakes could be made throughout the study period.

There were a number of specific questions that were set for the study;

1. What are the activity and selected body temperatures of the three snake species?
2. To what degree are the snakes temporally limited by the thermal environment?
3. How does the overall behaviour of the snakes vary in relation to thermal conditions?
4. What part does thermoregulatory behaviour play in their overall behaviour?
5. Exactly what thermoregulatory strategies do the snakes employ and how do they vary in relation to thermal conditions?
6. How do the above factors relate to the ecology of each species?

7. How do the species compare in all the above respects and can any differences contribute to the varying distribution of the three species?

Shortage of time prevented the inclusion of an examination of seasonal patterns and of intraspecific variation within snake species (see Section 6.2). It was an intention of the study to provide additional information to what is already available on the ecology and behaviour of the British snakes with the hope that it may be utilised in the conservation and management of snake populations.

1.4. Layout of the Thesis

Experiments were undertaken using snakes kept in outdoor vivaria and in a laboratory arena, as stated in Section 1.3 above. The results of both sets of experiments are presented in each data chapter. There were also other investigations performed during the course of the study on various aspects of snake thermal ecology but which have not been included in this thesis due to shortage of time. These are described in the final discussion chapter, Section 6.6.

The general methodology which applied to all three data chapters is presented in Chapter Two. This includes details on the capture and processing of snakes, biotelemetric equipment and the design and recording methods employed during the laboratory and outdoor vivaria experiments. In Chapter Three, the criteria used for the categorisation of thermal conditions during the experiments, which also applies to all three data chapters, is presented. These criteria are provided in Chapter Three rather than Chapter Two as they were calculated using the results of the body temperature investigations.

The first data chapter (Chapter Three) concentrates on the body temperatures attained by the snakes during different environmental conditions. The selected body temperatures and the range of body temperatures are investigated and an assessment made of the temporal utilisation of the thermal environment by each species. The second data chapter (Chapter Four) examines the general behaviour exhibited by each species, including overt thermoregulatory behaviour. General time budgets and details of the body temperatures measured while the snakes were engaged in each of the main behavioural categories are presented. The last data chapter (Chapter Five) concentrates on the precise strategies utilised by the snakes during behavioural thermoregulation. The final chapter (Chapter Six) is a discussion incorporating the findings of the previous data chapters.

CHAPTER TWO

GENERAL METHODS

2.1. Study Sites

All sites used for used the collection of snakes were situated in the southern half of Hampshire, England. The general location of the 7 main sites is shown in Fig. 2.1. They were all known to have good populations of snakes and were easily accessible from Southampton University.

Smooth snake specimens were collected from two locations in the New Forest, Hampshire. Both sites have been used in previous long term studies of smooth snakes, (Spellerberg and Phelps 1977, Goddard 1984 and Gent 1988). The capture of specimens at site one was restricted to a 100 m stretch of a southeasterly facing embankment. The area was dominated by mature ling (Calluna vulgaris) and bell heather (Erica cinerea) with large thickets of gorse (Ulex europaeus). Several spruce (Picea sitchensis) and willow (Salix spp.) trees grew on the embankment.

Site two was situated approximately 2 km southwest of site one. The collection of snakes was generally restricted to a 250 m stretch of a south facing embankment. In some areas the embankment was dominated by thick gorse but snake capture was restricted to areas of heather. Bracken (Pteridium aquilinum) and grasses (e.g. Agrostis setacea) were also common in this area.

Grass snake specimens were also captured at two main sites in the New Forest. Site three was a 1 km stretch of patchy oak (Quercus sp.) and birch (Betula sp.) woodland, with a maximum width of only 70 m. It was bordered by horse stables and intensively managed grassland to the southwest and an area of wet, rough grassland to the northeast. Large clumps of brambles (Rubus fruticosus) and rhododendron covered some of the area and there was a network of drainage ditches. The wood was relatively undisturbed although a well-used pathway was situated along the northeast edge.

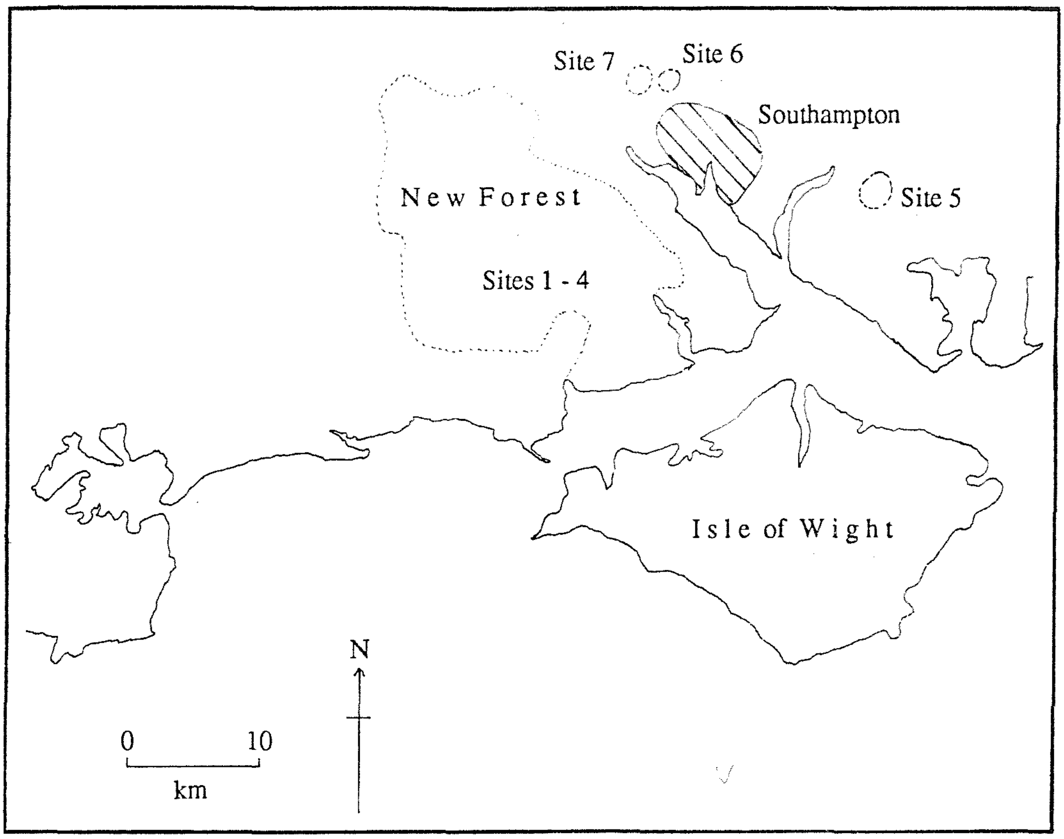


Fig. 2.1: General location of the seven sites used for the collection of snake specimens.

The fourth site was flanked by a small stream to the north, an area of birch woodland to the south and roads at the east and west ends. There was a system of drainage ditches throughout the area and a shallow pond (50 cm maximum) at the far western end. The site was mainly rough, grazed grassland with abundant Rubus fruticosus and Ulex europaeus bushes and clumps of Betula sp. The western end was surrounded by houses and there was a small degree of disturbance from people walking and horse-riding through the area.

Adder specimens were captured from areas outside the New Forest. Site five was a Forestry Commission plantation approximately 11 km southeast of Southampton. Although the dominant species in the woodland were exotic softwoods (e.g. Picea abies) the collection of snakes was restricted to the rides which were lined with oak, birch and poplar (mainly Populus nigra "Italica").

Site six was situated in the grounds of a manor 6.5 km north of Southampton. Although much of the gardens were ornamental some areas were secluded and undisturbed. To the north and west of the estate there was an area of broadleaf woodland and a 3.5 ha hay meadow. The best locality for the capture of snakes was around the woodland edge/lawn border where there were clumps of Rubus fruticosus and Pteridium aquilinum.

Site seven lay only 1.5 km west of site six at a motorway service station. It consisted of a 30 m, south-facing embankment situated next to a car park. The site was surrounded by thickets of gorse and there were several Betula sp. trees on the embankment. Due to its situation, disturbance was high and the area was usually strewn with litter.

Occasionally snakes were captured from different sites. Two adder specimens were captured from site two (a main smooth snake collection site) and several grass snake specimens were captured at site six (a main adder collection site). On a few occasions snakes were obtained from other sources. These tended to be private gardens. People occasionally contacted the University requesting help in removing snakes from their property.

2.2. Snake Capture and Processing

Specimens were located by walking through areas thought most likely to be used by basking snakes (i.e. south facing slopes with plenty of vegetation for escape from predators and open patches for basking). As soon as a snake was sighted, it was captured by hand. Leather gauntlets were worn whenever adders were being handled. The snakes were placed in cloth bags and kept in containers with plenty of moist paper to prevent dehydration.

Every time a snake was captured, body measurements and collection locality details were recorded. The following details were recorded:

(1) Species.
(2) Date.
(3) Time. Note that British Summer Time is referred to throughout this thesis.
(4) New or recaptured specimen.
(5) Scale clip number. Snakes were clipped following the method described by Spellerberg (1977c). The posterior edges of ventral scutes were clipped with scissors in a combination individual to each animal.
(6) Site location.
(7) Snout-vent length.
(8) Tail length.
(9) Weight.
(10) Number of subcaudal scales.
(11) Sloughing condition. Snakes were classed as being in a pre-slough, post-slough or inter-slough stage. Pre-slough animals were characterised by dull and/or loose skin and cloudy eyes. Post-slough specimens were those judged to have recently sloughed and which still had bright and sheeny skin. The inter-slough animals were in an intermediary stage after post-slough and before the pre-slough phase.
(12) Dietary condition. The presence or absence of a distinct food bolus was noted. This was assessed through gentle palpation. Regurgitation of food occasionally occurred and in these cases an attempt to identify the food item was made.
(13) Reproductive condition. The presence of a penial swelling was noted in males and sometimes a cloacal sample was collected to examine for the presence of spermatozoa. The breeding condition of females was assessed by palpation and classified as being gravid, non-gravid or uncertain. During 1989 three female smooth snakes were examined using ‘ultrasound scanning’ and it was possible to detect developing embryos where palpation had proven inadequate.

2.3. Biotelemetry Equipment

The experiments carried out in the field and in the laboratory required the recording of snake body temperatures. Thermo-sensitive radio transmitters were used because they have several advantages over other methods. The use of simple thermometers inevitably results in the animals being disturbed while their temperature is being taken and this method is also impractical over several days of continuous recording. An alternative was to use thermocouples. However, the snakes would have had to have been directly connected to recording equipment and so there would have been a risk of entanglement of the wires with objects in the experimental arenas. This was not a problem when using biotelemetric equipment.

There are three main ways in which thermo-sensitive radio-transmitters can be used to monitor snake body temperature. Transmitters can be surgically implanted (e.g. Shine 1979, Peterson 1982, 1987, Tiebout and Cary 1987). However, such devices have not yet been made small enough to implant into most smooth snake specimens. Implantable transmitters are usually employed in long term studies but as none of my outdoor experiments lasted longer than twelve days, externally mounted transmitters were used instead. Also, the smooth snake is a protected species and the risk of an animal dying during a surgical operation would be difficult to justify. Snakes can also be fed miniature transmitters. This method has been used by McGinnis and Moore (1969), Osgood (1970), Moore (1978), Saint Girons (1978), and de Bont et al. (1986). The disadvantage of this is that it is possible that the presence of a bolus in the stomach could initiate a thermophilic response (Greenwald and Kanter 1979 and Regal 1966). This could result in an elevation of body temperature above that maintained by snakes in a non-absorptive condition. Also de Bont et al. (1986) had to force-feed transmitters to snakes and prevented regurgitation by a fitting a piece of adhesive tape around each snake anterior to the stomach. It is likely that such actions would have affected the snake's behaviour. The method used in this study has also been used by Gent (1988) on smooth snakes in the laboratory and Vanning (pers. comm.) on adders in the field and in the laboratory. Fig. 2.2 shows the method of attachment of the transmitter to the snake.

The transmitters were 173 MHz, Biotrack SS-1 models and measured 15 mm x 8 mm x 5 mm with a thin projecting 45 mm lead mounting a thermistor. Each one required a Duracell hearing-aid battery (mercury cell RM13) which could power a transmitter for approximately five weeks. An entire transmitter package weighed approximately 2.4 g.

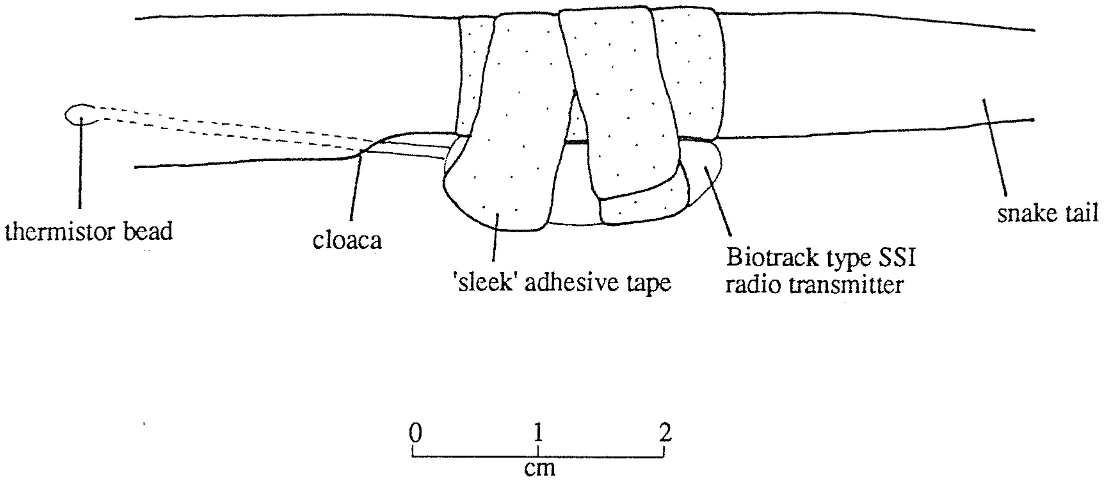


Fig. 2.2: Method of attachment of radio transmitter to a snake

The thermistor and lead were inserted into the large intestine through the cloaca and the transmitter package attached to the underside of the snake's tail with 'sleek' waterproof tape. Wilkinson (1987) carried out a laboratory experiment using these transmitters on adders to ascertain whether their presence affected the animals' daily pattern of behaviour. She observed no significant difference between tagged and untagged snakes for the average proportion of time performing each behaviour type or for activity sequencing. Gent (1988) undertook a similar laboratory investigation on smooth snakes. The transmitters he used were not thermo-sensitive and did not have a cloacal lead but they were similarly mounted on the snake and of about the same size. He concluded that the attachment of the transmitters had only a minor effect on activity patterns and time budgeting of captive smooth snakes and the effect was only limited to a few time periods during the day.

Pulses produced by the thermo-sensitive transmitter were picked up by an aerial linked to a 'Mariner 57' or 'AVM LA12' receiver. The transmitters were calibrated before and after every experiment using a mercury thermometer (accurate to 0.1°C) and a Grant water bath. The leads of the transmitters were placed in the water the temperature of the water was gradually increased. The transmitter pulse rate was measured at approximately 3°C intervals from about 7 - 37°C. Pulse rates were timed using a stop watch accurate to one hundredth of a second. As the water temperature increased, faster pulse rates were recorded. The difference in results for calibration curves established before and after every experiment indicated that the accuracy of individual transmitters varied from ± 0.1 - 1.0°C. The methods used for recording the radio pulses are described in the following sections.

2.4. Outdoor Vivaria

2.4.1. Design of the Outdoor Vivaria

Continuous observation of snake behaviour in the field is very difficult as they are cryptic animals and are easily startled by the presence of humans. The purpose of using outdoor vivaria therefore was to observe snake behaviour and record body temperature data under natural conditions without disturbing the animals. Snakes were provided with a variety of thermal microhabitats and the way they utilised them through behavioural means was monitored.

The outdoor vivaria were situated at Chilworth Manor, a site owned by Southampton University. They are illustrated in Plates 4 and 5 and Fig. 2.3. Three vivaria were constructed adjacent to each other to allow the observation of three snakes simultaneously. All three vivaria were landscaped as identically as possible.

Each vivarium measured 3 m by 2.5 m with 80 cm high galvanised sheet steel walls. The base of the walls were buried about 10 cm deep. The east sides of the vivaria were bound by a 2 m high brick wall topped by a curtain from behind which the snakes could be observed. Care had to be taken so that no nuts or bolts protruded from the walls as these allowed a route for the snakes to escape from the vivaria. Any unavoidable projections were covered in waterproof tape to prevent the snakes from gaining a grip. In addition to this, the area in the immediate vicinity of the walls were regularly checked for mouse holes as snakes occasionally used these as a means of escape.

As Fig. 2.3 and Plate 5 illustrate, a variety of refuges and substrates were incorporated into the design of the vivaria; a pond, woodpile, Calluna vulgaris and/or Erica tetralix bushes, a stone pile, a mound of decomposing vegetation and a large mound of earth. Below the latter was an underground refuge connected to the surface by a plastic pipe (Fig. 2.4). Most of the area in each vivarium was grassed over and so this had to be regularly cut to prevent the arena from becoming overgrown. Potential basking sites (e.g. stonepile, woodpile and the mound) were kept free from shade while in other areas the grass was allowed to grow thickly to provide snakes with areas of cover. Some of the vegetation which was cut was placed on the piles of decomposing plant material in the northwest corners. The ponds were regularly topped up with fresh water and all the vivaria were covered with a light garden netting to reduce the threat of bird or cat predation.

2.4.2. Recording of Body Temperatures

Transmitters were placed on the snakes as described in Section 2.3 above and signals were received on a 'Mariner 57'. When the snakes were actually being observed the receiver was connected to a portable 'Yagi' aerial and transmitter pulse rates were measured at regular intervals for all three snakes (one in each vivarium) from behind the wall. However, during periods when the vivaria were unattended the receiver and automatic recording equipment were kept in a secure metal box built on to the side of the arenas (see Plate 4). An

Plate 4. The outdoor vivaria.

Plate 5. Landscaped interior of one of the three outdoor vivaria.

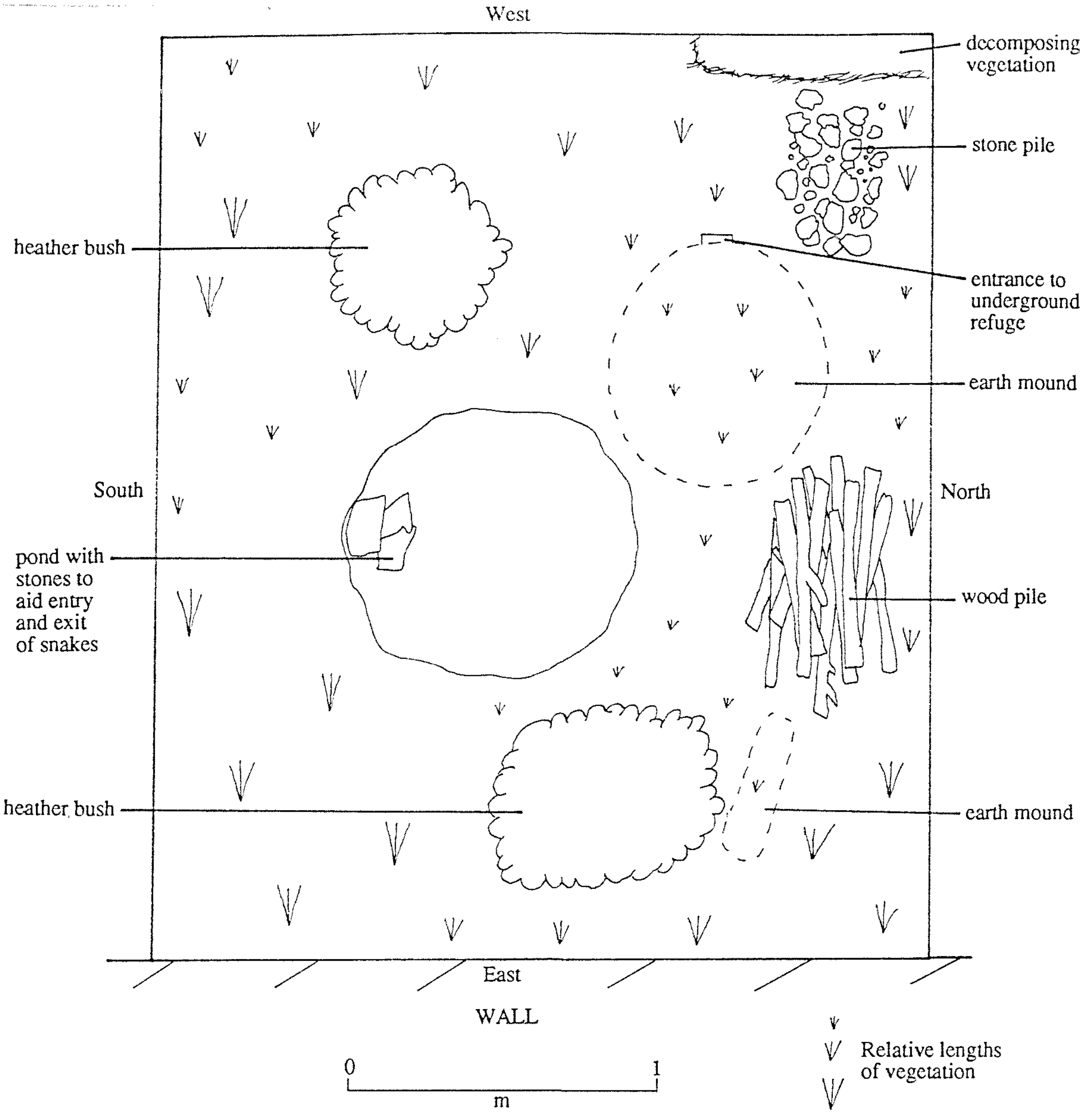


Fig. 2.3: Plan view of an outdoor vivarium

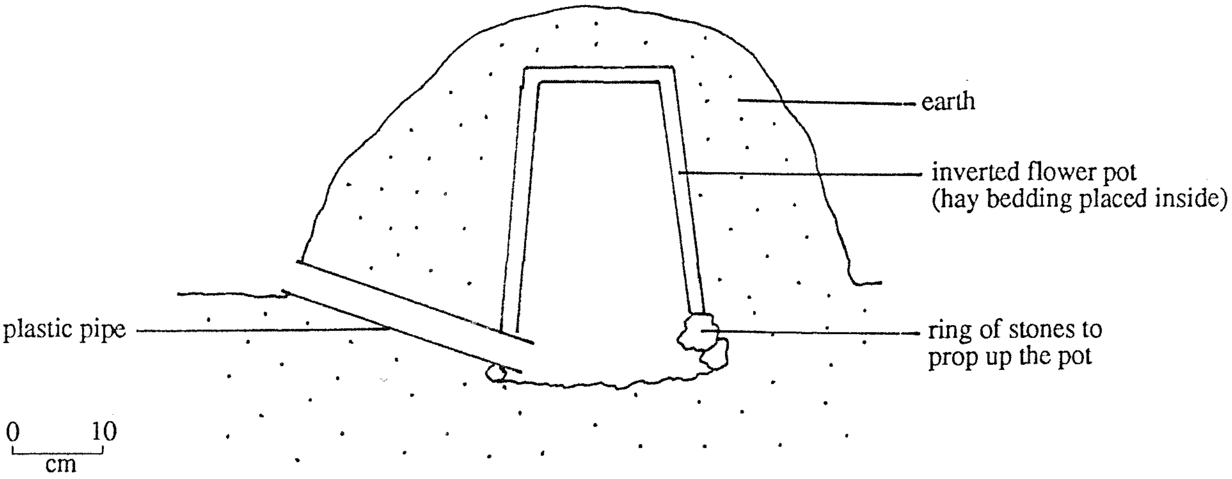


Fig. 2.4: Cross section of the earth mound showing the underground refuge

omni-directional aerial was kept permanently in position above the middle arena and was connected to the receiver by a 5 m lead.

The automatic recording equipment could only record the body temperature measurements from one snake. The receiver was set to pick up signals from the transmitter of the chosen snake and left permanently on. A car battery was used to power the receiver when it was left on for long periods. The receiver was connected to a cassette tape recorder (an Elf tone compucorder or a Cathay CC311) containing a 90 minute cassette tape. The cassette recorder in turn was linked to an interval timer which was programmed to switch on the recorder for 16 seconds every 15 minutes. One side of a 90 minute tape would fill up after about 42 hours at which point it had to be changed over.

After a recording session had been completed the cassette tape was reviewed and the pulse rates determined for the 15 minute intervals. The cassette recorder playing and recording speeds were measured to check if it was necessary to make adjustments to the pulse rate figures. The recorders were powered by rechargeable batteries and care was taken that they were never allowed to run down.

2.4.3. Recording of Meteorological Conditions

Operative Temperatures

Daily records of general meteorological data were obtained from Southampton Weather Centre which has a station 7 km south of Chilworth. Details of daily minimum and maximum air temperatures, grass and soil temperatures, rain measurements, sun hours and monthly averages were provided.

At Chilworth, air temperature was recorded in a Stevenson's screen. A 'Squirrel' meter/logger (Grant instruments, Cambridge) was usually employed to collect the data at precise 15 minute intervals. On other occasions a similar 'home-made' device was used and this recorded data at regular but approximate intervals of 15, 30 or 60 minutes.

Measurements of only air and substrate temperatures are insufficient to characterise thermal environments. A number of other factors are important in determining body temperatures. The routes of heat exchange (through convection, radiation, evaporation and conduction) involve the animals physiological and morphological characteristics (e.g. shape, colour and metabolic rate) as well as environmental variables (e.g. air and ground temperatures, wind velocity, radiation etc.). Bakken and Gates (1975) integrated all of these factors into a single variable called the 'operative environmental' or 'equivalent blackbody' temperature (T_e). It is now generally referred to as the 'operative temperature' (Bakken et al., 1985).

Bakken and Gates described the operative temperature as 'the temperature of an inanimate object of zero heat capacity with the same size, shape and radiative properties as the animal and exposed to the same microclimate', in other words, the true environmental temperature 'seen' by that animal. They produced the simple equation:

$$T_b = T_e + T_\Delta$$

where T_b = Body temperature

T_e = Operative temperature

T_Δ = Physiological offset temperature

T_Δ is the amount an animal may offset T_b from T_e by utilising metabolism, evaporation and insulation. For an ectotherm in which the metabolic heat production is about equal to the heat loss through the evaporation of water, $T_b = T_e$. This means the body temperature of an ectotherm can be predicted by determining its operative temperature for a given microclimate. This can be done through the complicated measurements of the appropriate micro-meteorological variables and animal characteristics or by simply using a physical model (or 'animal thermometer') that duplicates the heat exchange properties of the real animal. Bakken and Gates (1975) and Bakken et al. (1985) describe how to make such a physical model.

Initially models were made for all three snake species. Smooth snake models were made from 55 cm lengths of 10 mm copper tubing, each weighing about 95 g. Fifty five cm was the mean length of mature smooth snake specimens taken from several sources (Goddard 1984, Gent 1988 and measurements taken during this study). Copper tubing was used as this has a rapid response to temperature change. The spectral reflectances of several grey paints were compared with that of the dorsal surface of a smooth snake skin using a Spectron SE590 spectroradiometer. Comparisons were also made between 'Spectra grey primer' was eventually used for the models. A temperature probe was placed in each model and then the tubes were sealed with rubber bungs at either end.

Fifteen millimetre copper tubing was used to make adder and grass snake models. The mean length of a mature grass snake was calculated as 70 cm (using data from Brown, pers.comm. and this study) and for a mature adder, 55 cm (using data from Appleby, 1971 and this study). Copper tubes of these lengths weighed about 195 g and 160 g respectively. Grass snake models were painted matt green (BS 4800-12.B.25) and adder models painted with 'Spectra grey primer' and Fiat brown (GL35223) for the markings.
The models were placed in various locations around the vivaria, the aim being to estimate what operative temperatures were available to the snakes and how they utilised them to regulate their body temperature. It was assumed that the three vivaria had the same microclimates (i.e. the model temperature on the woodpile in vivarium 2 was the same as that of the woodpile in vivarium 1 and 3). A temperature probe was also placed in the underground refuge beneath the mound. Environmental temperatures were recorded from 6 sites in the outdoor vivaria at any one time;

1. Air temperature in underground refuge.

2. Model temperature at base of heather bush (east segment). This provided an estimate of operative temperatures in a partially covered (and partially shaded during sunny periods) microhabitat.

3. Model temperature on woodpile (north segment). This provided an estimate of operative temperatures in a totally exposed microhabitat. During sunny periods the model was directly exposed to the sun from early/mid morning until mid/late afternoon.

4. Model temperature on stonepile (northwest segment). This provided an estimate of operative temperatures in a totally exposed microhabitat on a stony substrate. During sunny periods the model was directly exposed to the sun from early morning until early afternoon.(This was only used in the very first experiment, April 1988).
4. Model temperature on woodpile (north segment). The model was placed beside model 3 to allow direct comparisons between different model designs as described in section 2.4.3 'Comparative Tests between Models' below. (This was only used in experiments 2 and 3).
4. Model temperature on decomposing vegetation pile (northwest segment). This provided an estimate of operative temperatures in a totally exposed microhabitat. It was so positioned that

during sunny periods it was directly exposed to the first sunshine falling on the vivaria in the morning, until midday.(This was used from the fourth to the last experiment).

5. Model temperature on short grass and in total shade (southwest segment). The model was in the shade of the vivaria walls throughout the whole day (1988 experiments only).
5. Model temperature on short grass (southeast segment). This provided an estimate of operative temperatures in a totally exposed microhabitat. During sunny periods the model was directly exposed to the sun from mid-afternoon until the last sunshine falling on the vivaria in the evening (1989 experiments only).

6. Model temperature in total shade of dense grass (south segment).

The latter two temperatures were recorded from vivarium 3 (the northern arena) and linked to a Squirrel logger model SQ8-2U2V. The other four temperatures were recorded from vivarium 2 and linked to a Squirrel logger model SQ8-4U. The models were positioned around the vivaria so that an estimate of the range of operative temperatures available to the snakes could be made. Models 4,3 and 5 (1989 only) were situated so that on a sunny day, at least one of them was in the direct sun and could therefore measure the maximum model temperature. Model 4 received the first early morning sun but was in the shade of the vivaria walls by around midday. However, by then model 3 was in the direct sun and when it too became shaded, model 5 received the evening sun. Model 6 recorded an estimate of operative temperatures under cover and in the shade above ground and probe 1 recorded the air temperature in the refuge below ground. Snakes were often observed mosaic basking and so model 2 estimated operative temperatures available at the base of a clump of heather.

Both Squirrel loggers were placed in waterproof boxes and buried for security. They were programmed to take readings every 30 minutes. It would have been preferred that instantaneous temperature measurements were taken but the Squirrel loggers that were available averaged 100 readings over the previous 30 minutes and recorded that value. Another problem was that their temperature range went from -10°C to only 40°C. On a number of occasions the temperatures of models in direct sunlight went over 40°C. However precise values over 40°C were not essential as body temperatures just over 40°C are lethal and therefore avoided by the snakes.

Comparative Tests between Models

During any one experiment, usually two or all three species of snakes were being investigated in the vivaria. There were only six temperature inputs between the two Squirrel loggers so a choice had to be made between recording operative environmental temperatures in several different microhabitats and recording them using the three types of animal model thermometers in comparable microhabitats (i.e. grass snake models, adder models and smooth snake models). A comparative test was made between the three types of models in identical environmental conditions to investigate whether their temperatures differed to any great extent. In the test, two grass snake models, one adder model and one smooth snake model were placed side by side on a patch of open grass and their temperatures recorded at 30 minute intervals over a period of 114 hours.

The results indicated that the model temperatures were remarkably similar. For the purpose of the analysis, if one or more of the models recorded an over-range value (i.e. ≥40°C) then it was removed, together with the other model temperatures recorded at the same time. The temperatures were compared via a one-way ANOVA and no significant differences detected ($F = 0.166$ with 3 and 812 d.f., $p > 0.05$). Variances were found to be homogeneous (Bartlett's test, $F = 1.002$, $p > 0.05$). At any particular time the difference in temperature was recorded between the four models and the mean temperature differences calculated (see Table 2.1). The mean temperature difference ranged from 0.23°C ± 0.359 ($n = 204$) between the first grass snake model and the adder model to 0.54°C ± 1.123 ($n = 204$) between the second grass snake model and the smooth snake model. The mean temperature differences were in fact less between the first grass model and the smooth snake model than between the two grass snake models. The smooth snake model might have been expected to have heated up and cooled down faster than the larger grass snake or adder models but this was not the case.

In conclusion, although the models of the three species were of differing sizes and colour, a comparative test under the same environmental conditions revealed that they recorded very similar temperatures. It was therefore decided to use grass snake models for all the vivaria experiments which meant that estimates of operative temperatures could be made from a wider range of thermal microhabitats. The only occasions when a grass snake model was not used was in experiment 2 (when an adder model was placed on the woodpile next to the grass snake model) and experiment 3 (during which a smooth snake model was placed on the woodpile next to the grass snake model until 3.6.88 when it was changed for an adder model).

Model comparisons

	$T_{m\,Nn1} - T_{m\,Nn2}$	$T_{m\,Nn1} - T_{m\,Ca}$	$T_{m\,Nn1} - T_{m\,Vb}$	$T_{m\,Nn2} - T_{m\,Ca}$	$T_{m\,Nn2} - T_{m\,Vb}$	$T_{m\,Ca} - T_{m\,Vb}$
Mean temperature difference ° C	0.46	0.34	0.23	0.54	0.47	0.52
Standard deviation °C	0.647	0.514	0.359	1.123	0.396	0.822
Maximum temperature difference °C	4.4	3.4	2.4	7.0	2.8	5.0
Minimum temperature difference °C	0	0	0	0	0	0

Table 2.1: **Temperature differences of snake models using measurements from 204 half-hour time intervals.**

Key

$T_{m\,Nn1}$: temperature of model *Natrix natrix*, number 1
$T_{m\,Nn2}$: temperature of model *Natrix natrix*, number 2
$T_{m\,Vb}$: temperature of model *Vipera berus*
$T_{m\,Ca}$: temperature of model *Coronella austriaca*

This was during the early vivaria experiments when comparisons between different model types were still being made.

Comparative Tests between Models and Body Temperatures

Figure 2.5 illustrates the validity of using animal thermometers to predict snake body temperatures. It shows the results of a comparison of model temperatures and snake body temperatures made in identical environmental conditions. The experiment entailed attaching temperature-sensitive transmitters to four snakes;

Smooth snake: Male, weight 45.5 g, total length 452 mm
Grass snake: Post-gravid female, weight 111.5g, total length 695 mm
Adder (specimen 1): Gravid female, weight 148.5 g, total length 562 mm
Adder (specimen 2): Gravid female, weight 149.0 g, total length 575 mm

The four snakes were placed in empty, glass tanks positioned in the open on a mild cloudy morning. A grass snake model was placed in an identical tank positioned in the same place. After one hour, body temperatures and model temperatures were recorded at 15 minute intervals. Ideally the snakes should have been anaesthetised and laid out like the model but satisfactory methods of anaesthesia were not available. Instead the snakes tended to move around, searching for a means of escape.

The snakes were exposed to the same thermal conditions as the model and the result was that body temperatures and the model temperature matched fairly well (correlation coefficients of 0.935 for the smooth snake, 0.980 for the grass snake, 0.981 for adder specimen 1, 0.967 for adder specimen 2, $n = 13$ in all cases). During the first half hour shown on the graphs, the sky was overcast. The sun came out between 0945 hours and 1000 hours. It is possible that there might have been an even closer correlation if the snakes had remained still and positioned in the same relation towards the sun as the model. Air temperature was shown to be a poor predictor of body temperature.

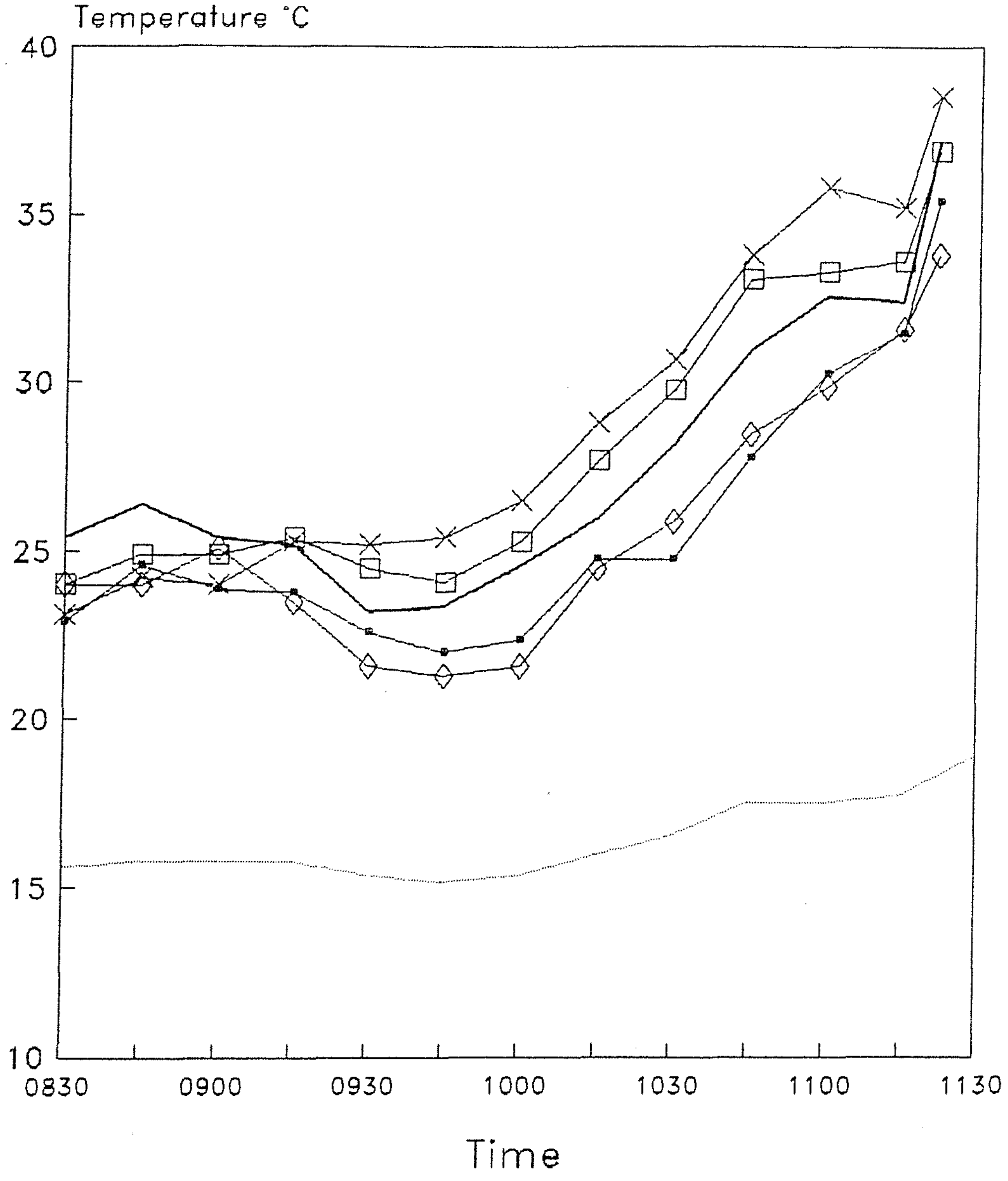


Fig. 2.5: **Comparison of body temperatures of *Coronella austriaca*, *Natrix natrix*, and *Vipera berus* specimens with snake model temperatures.** The experiment was carried out on 23.8.88.

——— Snake model
—×— *Coronella austriaca*
—◇— *Natrix natrix*
—▪— *Vipera berus* (specimen 1)
—□— *Vipera berus* (specimen 2)
········ Shade air

2.4.4. Recording of Behaviour

After a snake had been captured and brought from the field, it was usually taken back to the laboratory for a few days. Radio transmitters were attached to the animals immediately prior to release in the vivarium. The snakes were always placed in the entrance to the underground refuge and they invariably descended down the plastic tube. Only one snake was ever kept in a vivarium at one time so as to rule out the possible effects of conspecific interactions. Snakes that were caught in the New Forest were subject to conditions specified by the Forestry Commission, one of which limited the amount of time that a transmitter could remain on a snake's body to 7 days at a time. Consequently, acclimitisation periods had to be limited to one day before behavioural or temperature readings were taken. Although snakes caught outside the New Forest were not subject to such conditions, acclimitisation periods were kept at one day for all snakes to allow consistency between experiments.

Snakes were studied in outdoor vivaria during 1988 and 1989 over periods lasting from 4 to 10 days (excluding the acclimatisation period). After an experiment had been completed the transmitters were carefully removed from the snakes. The animals were weighed once again and were then returned to their home site and released at their exact place of capture.

Snake observations at the vivaria usually started between 0645 hours and 0900 hours. Body temperatures measurements were taken at 15 minute intervals for all three snakes, and at about 5 minute intervals during the heating phase. Once these measurements had been taken, the behaviour of the snakes were immediately noted. A platform allowed me to look over the wall at the snakes in the vivaria below and a simple curtain prevented me from being seen by them (see Fig. 2.6). The prevailing southwesterly wind reduced the risk of snakes detecting me by smell. Observation of the snakes was aided by a pair of 8 x 30 binoculars capable of focusing to close range. These were essential as the snakes were remarkably well hidden on some occasions.

The following details of snake behaviour were recorded;

1 General Behaviour

B Basking - >95% in open, not moving.

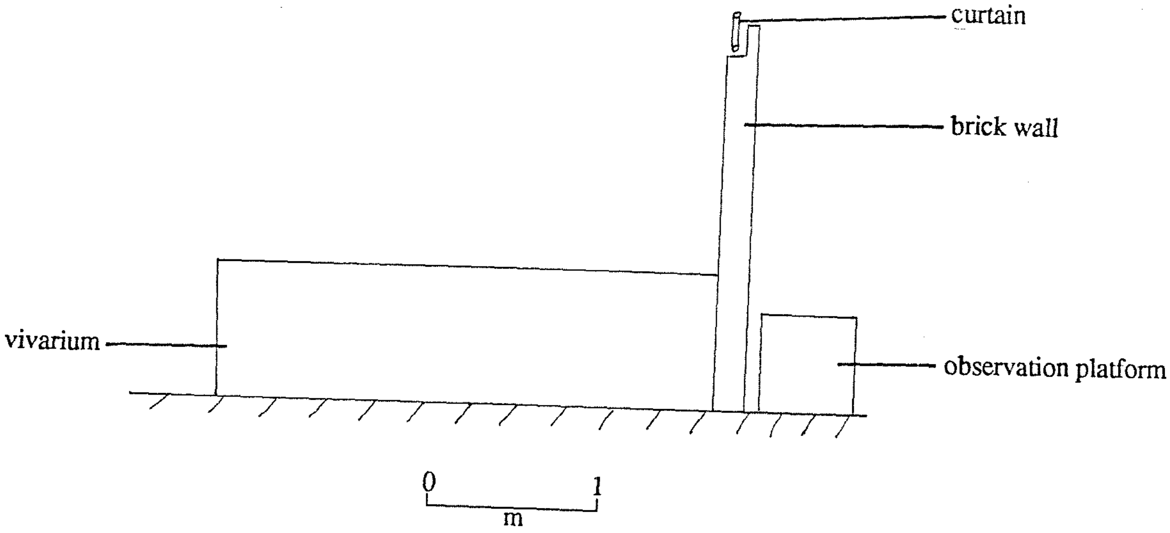


Fig 2.6: Side view of the outdoor vivaria, Chilworth

MB Mosaic basking - not moving but 5-95% of the body shaded by vegetation etc.

M Movement/Foraging.

H Hidden - out of sight from observer or <5% of the body visible while below cover and inactive.

S Swimming.
D Drinking.

2 Coiling Postures.
(For B and MB categories only)

The degree of coiling of body on a scale of 1-6. See Fig 2.7.

3 % Body Area Exposed.
(For MB category only)

The % snake body area out of the shade of cover (e.g. vegetation). When the sky was overcast the % snake body area out of cover (rather than shade of cover) was estimated.

(i) 5-35% body area exposed
(ii) 36-65% body area exposed
(iii) 66-95% body area exposed

Note;
When snake had <5% body area exposed it was classed as H.
When snake had >95% body area exposed it was classed as B.

4 Basking Conditions
(For B and MB categories only)

(i) Conditions sunny and snake basking in sunny area.

(ii) Conditions sunny and snake 'basking' in shaded area.
(iii) Conditions overcast or sun clouded over temporarily.

5 Substrate Type

(For B and MB categories only)

Substrate type on which the snakes were basking.

(i) Logs
(ii) Stones
(iii) Bare soil
(iv) Live vegetation
(v) Litter/decomposing vegetation
(vi) Any of the above plus in contact with the metal wall

6 Cover Type

(For MB category only)

(i) Unknown
(ii) Live vegetation (excluding heathers)
(iii) Heathers
(iv) Logs
(v) Litter/decomposing vegetation

7 Body Aspect

(For B and MB categories only)

The position of the snake's body in relation to the sun. This was only recorded when the snake was basking on a flat surface (0-20°) and not between 1030 hours and 1430 hours. Between these times the sun was relatively high in the sky and it was difficult to categorise the body aspect (see Fig. 2.8).

8 Slope Direction

(B and MB categories only)

The direction of the slope on which a snake was basking. A slope was defined

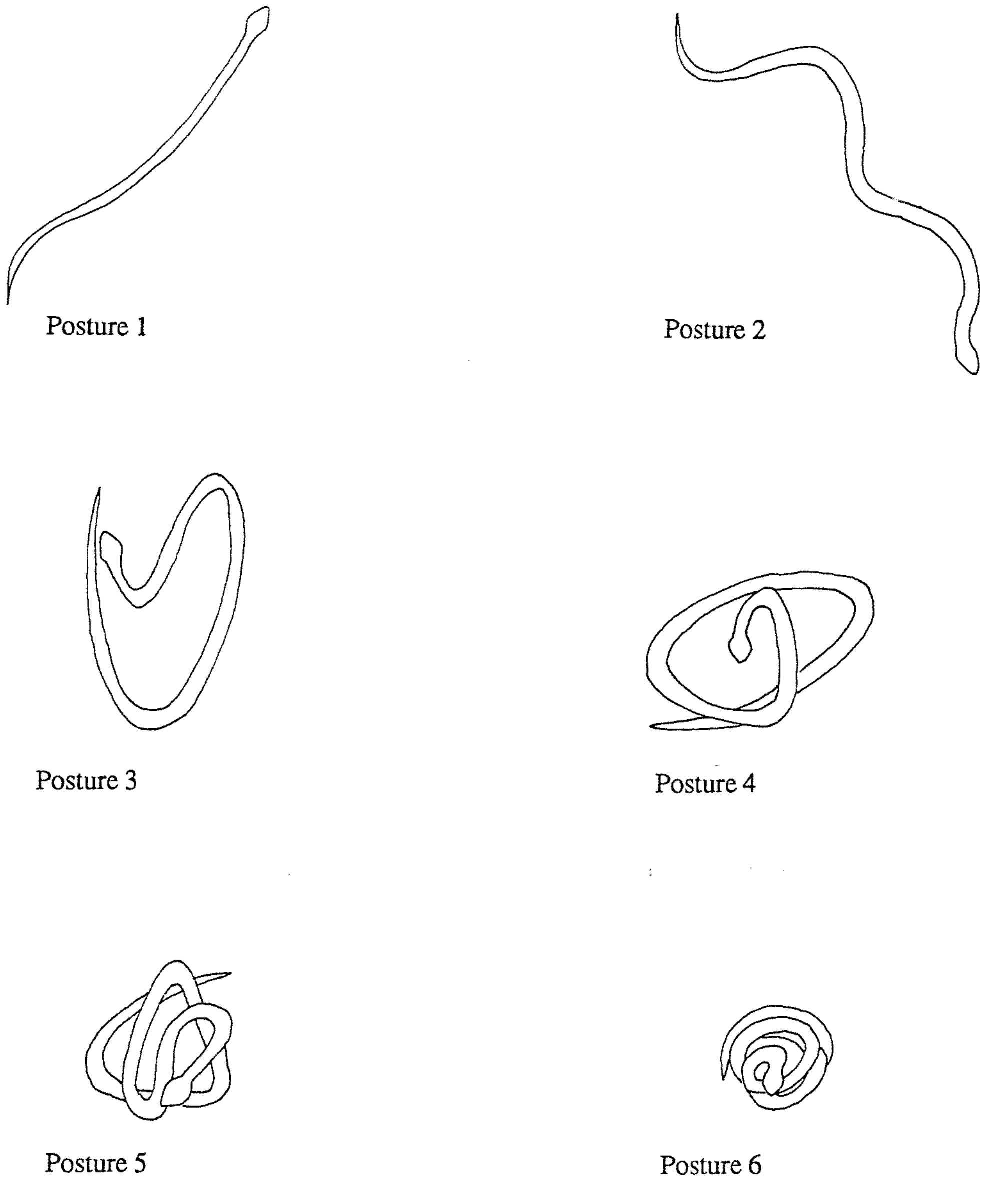


Fig. 2.7: Categorisation of snake coiling postures during basking behaviour

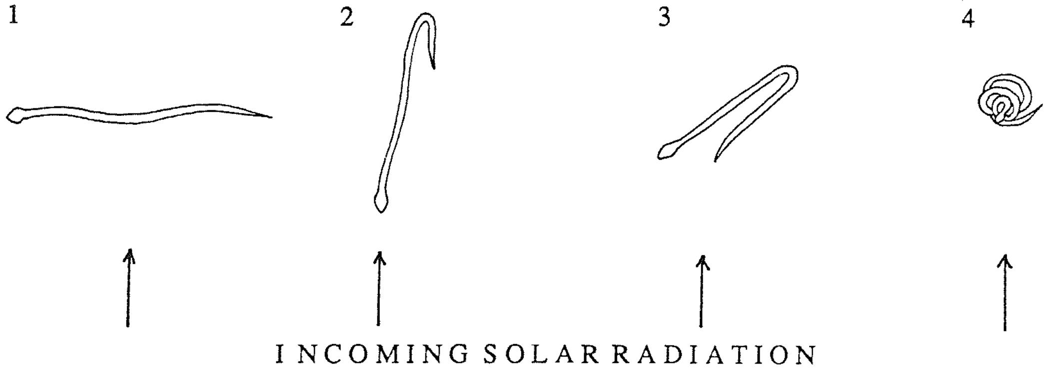


Fig. 2.8: Categorisation of snake body aspects in relation to incoming solar radiation during basking behaviour

as being greater than 20° and the direction categories were north, northeast, east, southeast, south, southwest, west or northwest facing.

9 Slope Angle
(B and MB categories only)

As above but the angle of the slope on which snake was basking. The three categories were;

(i) 21-30°
(ii) 31-40°
(iii) 41-50°

10 Grid Reference

Each vivarium was divided into nine squares; north, northeast, east, southeast, south, southwest, west, northwest and central. The position of the snake was recorded at each observation.

2.5. Laboratory Investigation

2.5.1. Design of Video Arena

In this series of experiments the daily behavioural patterns of individual snakes in an indoor arena were recorded on video equipment over a period of several days. Conditions were kept as similar as possible for each experiment to allow comparison of the results. Experiments were undertaken during 1987 and 1988.

Snakes were captured in the field, taken to the University and placed in a glass tank provided with refuges, bedding and fresh water. The tank was in the same room as the video arena to allow the snake to acclimatise. The windows of the room were blocked off and light was provided by a "Trulight" strip lamp. A fan heater connected to a thermostat ensured that the air temperature never fell below 16.5°C. A direct heat source was provided by a 60 watt bulb in an angle-poise lamp positioned directly above the tank and was set to turn on and off at the same time as the heatlamp in the arena. The light and heatlamp cycles were as follows;

Light on : 0545 hours
Heatlamp on : 0725 hours
Heatlamp off : 1925 hours
Light off : 2025 hours

As the study of the three snake species occurred throughout their whole "active" season, a decision had to be made upon a light-dark cycle which represented a compromise between the short daylengths of early spring/late autumn and the longer daylengths of midsummer. Snakes in Britain are active from about the end of March to early October and for this period the average sunrise to sunset time was calculated to be 14 hours and 40 minutes which corresponds to the dates April 29 and August 13. On these dates sunrise is at 0545 hours and sunset at 2025 hours and therefore the light cycle of the experimental room was set likewise. The heatlamps were set to turn on 1 hour, 40 minutes after the light came on and to turn off 12 hours later. This time gap simulated the short period after sunrise before the temperature rises significantly.

The arena set-up is illustrated in Fig. 2.9 and Plate 6. It measured 219 cm x 166 cm with 60 cm high galvanised sheet steel walls and a concrete base. A 12 cm overhang at the top of the walls helped to prevent any animals from escaping. The concrete base was covered by a 1-2 cm layer of yellow sand and fresh water was placed in a waterbath at the beginning of every experiment. A flowerpot and two wooden covers were placed in the arena as refuges for the snakes.

A single infra-red, 275 watt heatlamp (Thorn hard glass, red front) was placed at one end of the arena approximately 40 cm above the floor and a simple shade placed above it to cut out the glare on the video recording. During the 1988 season a shade was also placed around the lamp to produce a more defined heated area on the floor. Without the shade it had sometimes proved difficult to distinguish a definite basking area for the snakes. In conjunction with this, refuge 1 was moved 14 cm closer to the heatlamp so that snakes could still bask within the heated area with part of their body still under cover.

Snake behaviour was recorded with a Panasonic TV camera (Model WV-1550/B) fitted with a wide angle 8 mm lens and mounted 2 m above the arena. The lens aperture was automatically controlled. During the night phase the 'Trulight' was turned off but the arena remained lit with red or infra-red light. It was assumed that the snakes could not detect the red or infra-red light. However, the video camera was capable of detecting light in this part of the spectrum

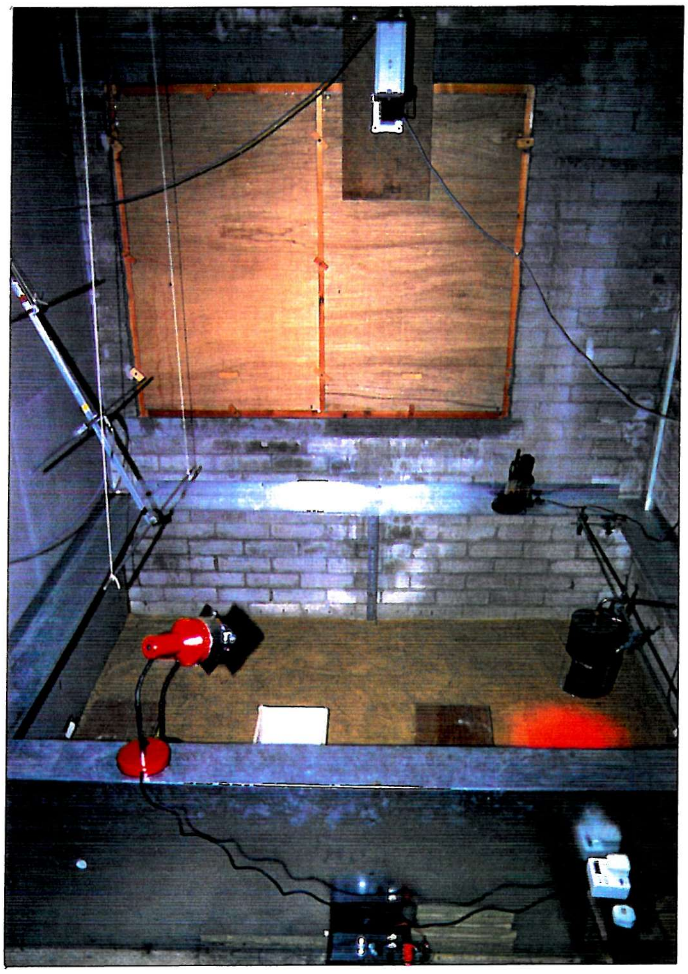


Plate 6. The laboratory indoor arena.

Note the video camera mounted on the wall. On the left is a 'Yagi' radio aerial suspended above the arena. The two anglepoise lights are fitted with infra-red filters. In the centre foreground is a Grant Temperature Recorder and to the right of that, an interval timer for the heatlamp.

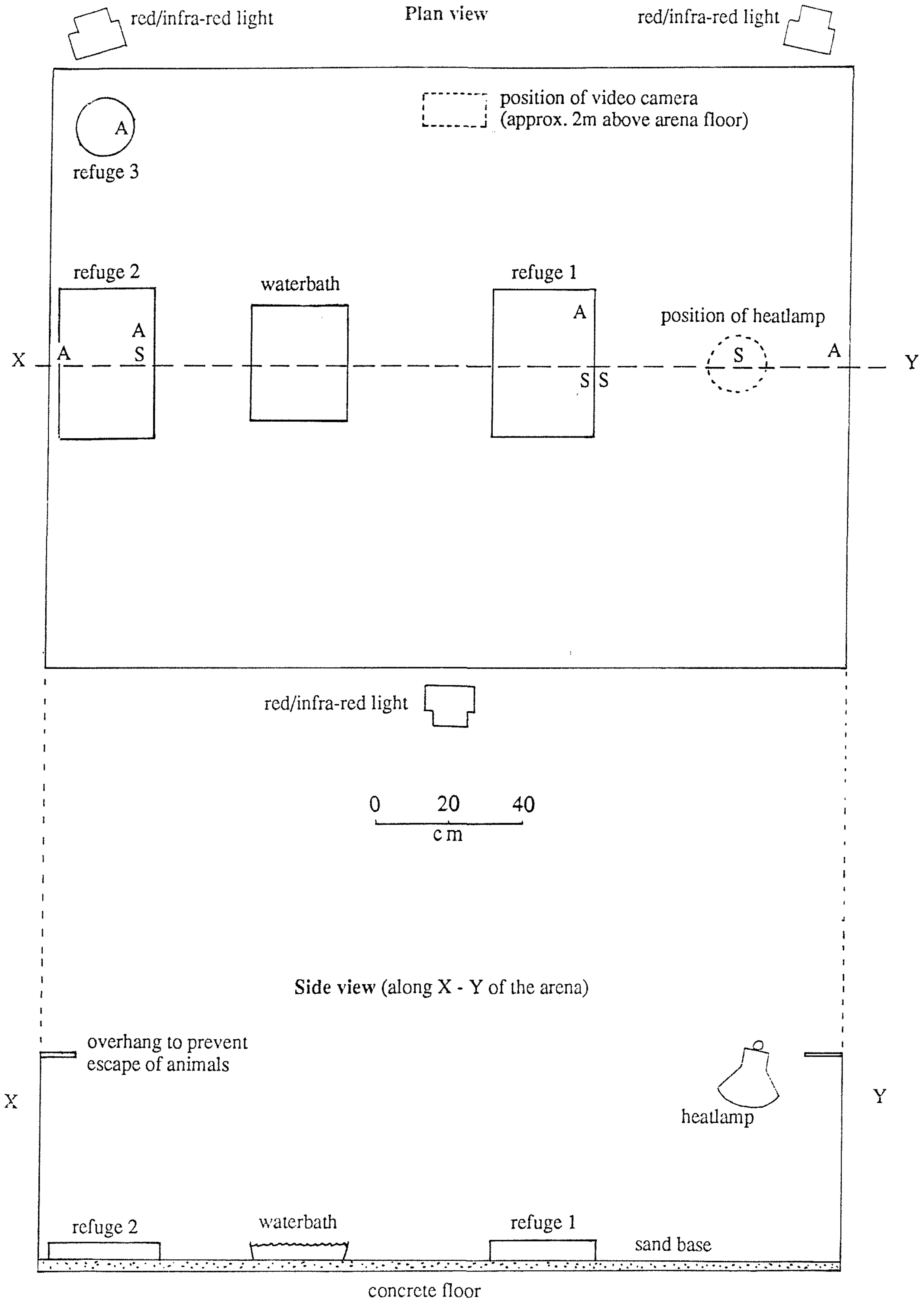


Fig. 2.9: Plan and side view of the laboratory arena.
Positions of shade air temperature (A) and sand temperature (S) probes are given.

and so nocturnal behaviour could also be monitored. The camera was connected to a Panasonic NV-8050 video recorder . The video recorder was fitted with a time/date generator and a time-lapse facility which allowed a record of up to 240 hours to be made on a 3 hour tape.

2.5.2. Data Recording

Each snake was usually kept in the tank overnight and placed in the arena the following midday. However, it was not possible to rely on being able to catch a snake on the day planned to be the start of an experiment so snakes were sometimes kept for up to 4 days in the tank. Snakes were measured and their feeding, breeding and sloughing condition assessed.

Body temperature data were collected using similar biotelemetric techniques as described in Section 2.4.2. During 1987 the receiver was connected to a chart recorder so that pulses were recorded as a series of peaks on a chart roll. Body temperatures were recorded once every 60 minutes in this way. In 1988 the chart recorder was abandoned in favour of a more efficient tape recorder system and body temperatures were recorded every 15 minutes.

Environmental temperatures were recorded using a Grant Temperature Recorder connected to nine temperature-sensitive probes positioned around the arena. Readings were taken automatically at hourly intervals in 1987 and half-hourly intervals in 1988. The position the probes were placed is shown in Fig. 2.9.

Once an animal had been placed in the video arena, the room in which the arena was situated was shut off and the snake was not disturbed until the end of the experiment. No data were collected for the first 24 hours to allow the snake to adapt to its new situation. Data were collected for the period (usually 72 hours) subsequent to the acclimitisation period. After the experiment had been completed the transmitter was removed from the snake and the animal released back into the wild as soon as possible.

Several different behavioural categories were identified and recorded when reviewing video recordings of snake activity;

B Basking - Heatlamp on and snake lying stationary (except for minor body adjustments) within area of heatlamp's influence for > 1 minute.

M Movement - Movement of snake for > 1 minute. Therefore excludes minor changes of position during basking etc.

R Refuge - Under a refuge for > 1 minute.

S Stationary - Snake lying stationary outside area of heatlamp's influence for > 1 minute.

RB Basking at refuge entrance - In refuge 1 at entrance closest to the heatlamp (i.e. within area of heatlamp's influence) with part of body outside basking for > 1 minute.

RS Stationary at refuge entrance - As above but at any other refuge entrance for > 1 minute.

ST Stationary and thigmothermy - Stationary for > 1 minute when heatlamp off and within area that had been warmed by the heatlamp.

SW Swimming

D Drinking

In addition to this the following details were collected:
1. Coiling posture of the snake when basking on a scale of one to five. The same scale applied as that used in the outdoor vivaria except that postures 5 and 6 were both categorised as 5. This was due to the resolution of the video preventing an accurate distinction being made between the two postures (see Fig. 2.7).
2. The refuge used by the animal; 1, 2 or 3.
3. The percentage body area of the animal exposed when at a refuge entrance. This was measured to the nearest of the following categories; head only, 25%, 50%, 75%.

2.6. Statistical Analysis

Data were accumulated and manipulated using the 'Lotus Symphony' spreadsheet package on an Amstrad PC-1640 microcomputer. The main data files generally consisted of character strings providing information on time (always in minutes), body temperature, environmental temperatures and behaviour. Data files could be exported from the spreadsheet software to the appropriate statistical programmes.

Details of the exact statistical methods used for each section are provided in the methods and results sections of each of the data chapters. It was decided to use non-parametric statistical tests for the majority of the analyses in the thesis. These techniques are distribution-free and are not dependent on a normal distribution of the data. They also operate on ranked data. Although the assumptions of the parametric statistical model were met for many of the analyses, it was felt that it was best to remain consistent throughout the study. The main exception to this was the use of mean temperature values which are presented in the text. Mean temperatures are used throughout many studies of reptilian thermal biology and so, to permit comparisons, they are presented in the text instead of median values. However, median values are provided in the summary statistics tables. An indication of the degree of variability of mean values is provided in the form of ± 1 standard deviation in the text and ± 1 standard error bars in the figures. A probability level of 5% has been used throughout the thesis as a level of significance (i.e. $p < 0.05$ indicates significance).

Tests between 2 independent samples were carried out using the Mann-Whitney U-test or the Wilcoxon two-sample test. These yield the same statistic and give the same results. The statistic quoted in the thesis is either 'U' or 'z' depending on what statistical package was used for the analysis. Tests between paired related samples were performed using the Wilcoxon matched-pairs signed-ranks test (statistic = z).

The Kruskal-Wallis test was employed for comparisons between more than 2 independent samples (statistic = chi-squared). Where a significant difference was found using the Kruskal-Wallis test, further analysis was continued using Mann-Whitney/Wilcoxon two-sample test between each pairwise combination. Strictly, this is not a proper procedure but there is no non-parametric equivalent to range tests (or 'comparison between sample means') available on statistical computer packages and so it is often used. Kolmogorov-Smirnov two-sample tests were used to compare frequency distributions (statistic = 'DN' or 'z' depending on the statistical package used). Comparisons of frequencies were performed using G-tests (statistic

= G). The main parametric tests used were regression analyses for which there is no non-parametric equivalent.

Three statistical packages were used during the analysis. ‘Statgraphics’ (version 2.0) was used on an Amstrad 1640 microcomputer. Data were transferred to the Southampton University mainframe computer (an IBM 3090-150) where the ‘Statistical Analysis System’ (SAS, version 5.16) and the ‘Statistical Packages for the Social Sciences’ (SPSS-X, version 3.0) programmes were used for further analysis. The list of references compiled for this thesis was aided by the ‘Paperbase De Luxe’ programme (Wight Scientific Programmes).

CHAPTER THREE

BODY TEMPERATURES

3.1. Introduction

Interest in the body temperatures of ectotherms was stimulated by the discovery that desert species used behavioural methods to thermoregulate (Cowles and Bogert, 1944). Since then there have been numerous studies into this particular aspect of reptilian biology and these have been reviewed by Brattstrom (1965) and Avery (1982). In the past, the emphasis seems to have been weighted towards studies of lizard thermal biology but Lillywhite (1987) was able to state that body temperature data were available for about 100 species of snakes representing at least 10 families. However, the usefulness of many of these studies is limited due to inadequate recording of environmental conditions and snake behaviour.

Many field studies involve the capturing of animals and measuring their body temperatures by hand, usually with the aid of a Schultheis thermometer. This means that continuous recording of body temperatures is not possible and measurements can only be made subject to being able to catch the animals. However, there have been a number of comprehensive studies using the technique in snake species (Gibson and Falls 1979, Gregory 1984, Hailey and Davies 1987).

One of the biggest advances in the methodology by which body temperatures can be recorded has been the refinement of biotelemetric equipment. The early radio transmitters could only be used on relatively large species such as iguanas and giant tortoises (Mackay 1964). McGinnis (1967) designed a transmitter measuring 8 mm by 4 mm for implantation into smaller lizards but it still required an external battery pack to be strapped to the animals tail. The temperature-sensitive transmitters presently available are smaller and can be implanted, fed or externally mounted to the study animals. The advantages and disadvantages of these different techniques are discussed in Section 2.3. There have been a number of biotelemetric experiments on snakes in the field (e.g. Brown and Parker 1976, Moore 1978, Shine and Lambeck 1985, Peterson 1987, Shine 1987) and in outdoor vivaria (e.g. Osgood 1970, Saint Girons 1978, Saint Girons and Bradshaw 1981). Biotelemetric techniques have also been used to monitor body temperatures of snakes in laboratory experiments (e.g. Greenwald and Kanter 1979, Gent 1988).

It should be emphasized at this point that cloacal temperatures were used throughout the study to represent body temperatures. Bartholomew (1982) and Avery (1982) noted that the elongate body shape of snakes could result in a variation of temperature between various points along the body. This could mean that a measured body temperature from the cloaca might differ from the internal 'true' body temperature. Peterson (1982) compared internal body temperatures with simultaneous head and cloacal temperatures of garter snakes (Thamnophis elegans vagrans) and found no significant difference between them. He did detect a significant variability between head and cloacal temperatures and suggested that the lower variances of oral temperatures may mean head temperatures were more precisely regulated. These factors should be taken into account especially when comparing studies where different body sites have been used to record 'body' temperature.

The aim of the work presented in this chapter was to undertake a comparative study of the body temperatures of the three British snake species. To do this, snakes were kept in an environment that was similar to field conditions (the outdoor vivaria) and in the constant and regulated environment of the laboratory. Comparisons were made between the body temperatures the 3 species selected during thermally unlimiting conditions. By knowing what their selected body temperatures were it was possible to estimate to what degree they were limited in maintaining them during varying environmental conditions. A comparison was also made between species of the temporal utilisation of thermally unlimiting conditions.

3.1.1. Definition of Thermoregulatory Terms

The vocabulary used with regards to reptilian thermoregulation is varied and often inconsistent. There have been many instances where workers have used similar or identical terms to describe different aspects of thermoregulation. In this thesis most of the thermoregulatory terminology is based on Pough and Gans (1982). It was their intention to reduce confusion by producing a unified set of terms. However, there are some items of terminology which need to be clarified for the purposes of the work undertaken here.

Selected body temperatures were defined by Pough and Gans as those 'maintained by an ectotherm in a laboratory temperature gradient or equivalent apparatus providing conditions that would permit an animal to extend its body temperature above and below the activity temperature range'. The mean selected temperature is the arithmetic mean of the temperatures measured in this way and is commonly used in intra- and inter-specific comparative work. The terms 'mean voluntary' (e.g. Spellerberg 1977b) or 'mean preferred' body temperature (or just 'preferred body temperature', Hammerson 1979) are synonymous in some studies. Pough and Gans make the point that the latter term has anthropomorphic connotations and that it should be avoided.

The terminology that should be employed in the case of non-laboratory based work seems to be less certain. Some form of mean body temperature measurement is frequently calculated in field or vivaria-based studies. These are often calculated from a collection of 'spot' body temperature recordings and are usually lower than corresponding mean selected temperatures obtained in the laboratory. Gent (1988) recorded a mean body temperature in the field for smooth snakes of 23.48°C ± 3.95 which compared with a mean selected body temperature of 29.6°C ± 3.15. As he pointed out, thermal conditions in the field were often limiting and therefore the snakes were sometimes simply unable to maintain higher body temperatures, unlike the situation in a laboratory temperature gradient. Other factors are also likely to contribute towards such a discrepancy but thermal limitation is likely to be of great import.

To allow a more realistic comparison between a mean selected body temperature and a mean field body temperature, field data should be used from conditions which are thermally unlimiting to the snake. Simple measurements of air and/or substrate temperatures are sometimes inadequate to judge when conditions are thermally limiting to a snake as numerous morphological, physiological and environmental factors contribute in determining its body temperature. The 'operative temperature' is a measurement of 'environmental temperature' which takes into account all such factors (see Section 2.4.3). Peterson (1982, 1987) used animal thermometers to estimate operative temperatures in the field and found that garter snakes, Thamnophis elegans vagrans, selected a mean body temperature of 29.9°C ± 1.32 when the thermal conditions were judged not to be limiting. This compared with a laboratory mean selected body temperature of 29.6°C (S.E. = 0.25).

Lillywhite (1980) and de Bont et al. (1986) described the snakes they were observing as maintaining 'thermal preferenda'. Lillywhite's study involved recording the body temperatures of seven elapid snake species in a laboratory thermal gradient. He observed that after an initial heating phase the snakes maintained their body temperatures at a relatively precise level. The 'thermal preferenda' were calculated from the body temperature values measured after the snakes' heating phase. The lowest 'thermal preferendum' for a species that Lillywhite recorded was 30.1°C. De Bont et al. (1986) studied smooth snakes in the field and they calculated the 'thermal preferenda' from body temperatures after the heating phase and before the cooling phase from sunny days only. They had to assume that sunny days were an indication that operative temperatures were higher than the body temperatures the snakes were attempting to maintain. They considered the 'thermal preferenda' of smooth snakes to be 29-33°C.

A similar definition to 'thermal preferenda' was used by Peterson (1982, 1987) in his study of garter snakes. On some days the snakes exhibited a distinct heating and cooling phase . After the heating phase the snakes maintained their body temperatures at a relatively precise level and this corresponds to the values used by the Lillywhite (1980) and de Bont et al. (1986) to calculate 'thermal preferenda'. Peterson called this the 'plateau phase' and calculated a mean 'plateau phase' body temperature of 29.9°C ± 1.32. As noted above, this was calculated when thermal conditions were considered to be unrestricting.

These examples demonstrate that care has to be taken to define exactly what is being described when body temperature data are being presented. In this volume, 'selected' body temperatures will be used for the description of laboratory and outdoor vivaria/field-based temperature data. Many workers employ the more commonly-used 'preferred' body temperature which Saint Girons (1978) described as a 'useful term and moreover a classic term' but the anthropomorphic reference is best avoided. 'Field selected body temperatures' will be used to describe body temperatures recorded in outdoor vivaria. These are maintained after an initial heating phase period and before a cooling phase period and when the thermal environment is considered not to be limiting. This corresponds to the 'plateau phase' body temperatures described by Peterson and the 'thermal preferenda' described by de Bont et al. and Lillywhite. 'Laboratory selected temperatures' describe the parallel values obtained from experimental work in the laboratory.

3.2. Methods

3.2.1. Outdoor Vivaria Experiments

The data used in the analysis for this chapter were obtained from the outdoor vivaria experiments undertaken during 1988 and 1989. Full details of the methods are given in Sections 2.3 and 2.4.

Seven separate experiments were carried out from April-September in 1988 and 4 from March-June in 1989. Each experiment lasted for approximately 2 weeks during which time from 3 to 6 individual snakes were studied. No more than 1 snake was kept in an individual vivarium at any time. Efforts were made to obtain data for all 3 snake species at the same time (by having one in each vivarium) but often this was not possible due to the supply of wild-caught specimens. Details of the 11 experiments are provided in Table 3.1. Periods in-between experiments were used for the return and capture of snakes, calibrating transmitters and fitting them with new batteries, reviewing body temperature recordings, maintaining the vivaria and working on laboratory experiments.

Comparison of Related Body Temperatures

There were 12 days when body temperatures were simultaneously recorded from all 3 species. This allowed a direct comparison of the data from snakes situated in similar environmental conditions. Direct comparison of body temperatures was also possible for 21 days between smooth snakes and grass snakes, 18 days between smooth snakes and adders and 24 days between grass snakes and adders.

Body temperatures were recorded at 15 minute intervals when I was present at the vivaria. Therefore, for the purpose of this particular comparison, only snake body temperature recordings from exactly corresponding times were used. This meant that a Wilcoxon matched-pairs signed-ranks test could be made between the paired data.

Calculation of Selected Body Temperatures

The criteria specified in Section 3.1.1 were used to calculate the field selected body temperatures for each of the 3 snake species. Recordings of model temperatures (which estimated operative temperatures) made it possible to identify when thermal conditions were sufficient to allow snakes the potential to achieve selected body temperature levels. A model temperature of >37°C was considered to represent such conditions. Body temperature records were examined from periods when model temperatures were approximately >37°C and it was possible to locate periods when the snakes were selecting body temperatures at a relatively precise level. Such periods were distinguished by a distinct 'plateau pattern' (Peterson 1982, 1987) of body temperatures which followed a heating phase and preceded a cooling phase (see

Experiment number and dates	Specimen number	Site of capture	SVL (mm)	TL (mm)	Weight (g)	Sex and reproductive condition	Slough condition	Dietary condition	Date placed in vivarium	T_b recording period	Behaviour recording period
1 12.4 - 27.4.88	Nn1	4	830	146	271.0	F, ?	Inter - S1	No bolus	12.4.88	19.4 - 27.4.88	15.4 - 27.4.88
	Nn2	3	525	115	54.0	F, ?	Inter - S1	Post - ab	13.4.88	--	15.4 - 20.4.88
	Nn3	other	625	160	86.5	M, ?	Inter - S1	No bolus	13.4.88	--	15.4 - 27.4.88
	Nn4	other	750	145	95.5	F, ?	Pre - S1	Post - ab	17.4.88	--	19.4 - 27.4.88
2 6.5 - 17.5.88	Nn5	4	605	155	168.5	M, ?	Inter - S1	No bolus	6.5.88	--	9.5 - 17.5.88
	Vb1	6	420	71	59.0	M, no sperm	Inter - S1	No bolus	6.5.88	9.5 - 17.5.88	9.5 - 17.5.88
	Vb2	5	500	70	58.0	M, sperm	Inter - S1	No bolus	15.5.88	16.5.88	16.5 - 17.5.88
3 22.5 - 6.6.88	Ca1	1	490	72	48.0	F, ?	Inter - S1	No bolus	22.5.88	24.5 - 27.5.88	24.5 - 27.5.88
	Nn6	other	640	133	59.0	F, ?	Inter/Pre-S1	No bolus	22.5.88	--	24.5 - 6.6.88
	Nn7	3	650	140	57.0	F, ?	Inter - S1	Post - ab	22.5.88	24.5 - 6.6.88	24.5 - 6.6.88
	Vb3	5	500	55	30.0	F, poss. gravid	Inter - S1	No bolus	1.6.88	2.6 - 6.6.88	2.6 - 6.6.88
4 20.6 - 1.7.88	Ca2	1	450	95	59.5	F, poss. gravid	Inter - S1	No bolus	21.6.88	22.6 - 1.7.88	22.6 - 1.7.88
	Nn8	4	540	145	80.5	M, ?	Pre - S1	No bolus	20.6.88	--	22.6 - 29.6.88
	Nn9	3	860	155	273.0	F, gravid	Inter - S1	No bolus	20.6.88	--	22.6 - 30.6.88
	Nn10	other	760	162	274.0	F, gravid	Pre - S1	No bolus	26.6.88	--	27.6 - 28.6.88
5 13.7 - 1.8.88	Ca3	2	355	108	39.5	M, ?	Inter - S1	No bolus	13.7.88	--	18.7 - 24.7.88
	Ca4	1	400	82	39.0	F, poss. gravid	Inter - S1	No bolus	24.7.88	25.7 - 1.8.88	25.7 - 29.7.88
	Nn10	other	760	162	271.0	F, gravid	Post - S1	No bolus	13.7.88	--	18.7 - 29.7.88
	Vb4	6	520	62	199.0	F, gravid	Pre - S1	No bolus	13.7.88	19.7 - 29.7.88	18.7 - 29.7.88
6 8.8 - 19.8.88	Ca5	1	420	86	52.0	F, poss. gravid	Inter/Pre-S1	No bolus	8.8.88	10.8 - 14.8.88	10.8 - 14.8.88
	Ca6	2	430	122	54.0	M, ?	Inter - S1	No bolus	9.8.88	14.8 - 19.8.88	11.8 - 19.8.88
	Nn10	other	760	162	170.5	F, poss. gravid	Inter - S1	No bolus	10.8.88	12.8 - 19.8.88	12.8 - 19.8.88
	Vb5	5	500	62	171.0	F, gravid	Post/Inter-S1	No bolus	16.8.88	17.8 - 19.8.88	17.8 - 19.8.88
7 11.9 - 25.9.88	Nn11	other	575	140	74.5	M, ?	Post - S1	No bolus	11.9.88	--	13.9 - 15.9.88
	Nn12	4	690	110	94.5	Unsexed	Inter - S1	No bolus	20.9.88	22.9 - 23.9.88	22.9 - 23.9.88
	Vb6	6	385	68	61.5	M, no sperm	Inter - S1	Possible bolus	11.9.88	13.9 - 23.9.88	13.9 - 23.9.88
	Vb7	6	525	65	114.0	F, post - gravid?	Inter - S1	No bolus	11.9.88	13.9 - 25.9.88	13.9 - 23.9.88

Table 3.1: Continued overleaf

Experiment number and dates	Specimen number	Site of capture	SVL (mm)	TL (mm)	Weight (g)	Sex and reproductive condition	Slough condition	Dietary condition	Date placed in vivarium	T_b recording period	Behaviour recording period
8 28.3 - 10.4.89	Nn13	3	640	140	74.0	Unsexed	Inter - S1	No bolus	28.3.89	31.3 - 10.4.89	31.3 - 10.4.89
	Vb6	6	385	68	55.0	M, no sperm	Inter - S1	No bolus	28.3.89	31.3 - 7.4.89	31.3 - 10.4.89
9 23.4 - 5.5.89	Ca7	1	390	117	31.5	M, no sperm	Post - S1	No bolus	23.4.89	24.4 - 30.4.89	24.4 - 28.4.89
	Nn14	4	600	165	179.0	F, *	Inter - S1	No bolus	23.4.89	24.4 - 28.4.89	24.4 - 28.4.89
	Nn15	4	790	125	338.5	F, gravid	Inter - S1	No bolus	30.4.89	1.5 - 5.5.89	2.5 - 5.5.89
	Vb8	5	500	80	98.0	M, no sperm	Post - S1	No bolus	23.4.89	24.4 - 28.4.89	24.4 - 28.4.89
	Vb9	5	440	75	73.5	M, no sperm	Pre - S1	No bolus	30.4.89	2.5 - 5.5.89	2.5 - 5.5.89
	Vb10	2	400	59	38.5	M, no sperm	Inter - S1	No bolus	2.5.89	3.5 - 5.5.89	3.5 - 5.5.89
10 15.5 - 29.5.89	Ca8	1	420	128	43.0	M, ?	Pre - S1	No bolus	15.5.89	16.5 - 21.5.89	16.5 - 19.5.89
	Nn16	4	630	142	115.5	F, ?	Imter - S1	Post - ab	15.5.89	16.5.89 - 19.5.89	16.5 - 19.5.89
	Nn17	4	750	177	258.0	Unsexed	Imter - S1	No bolus	21.5.89	24.5 - 26.5.89	23.5 - 25.5.89
	Vb11	5	490	80	94.5	M, ?	Inter - S1	No bolus	15.5.89	16.5 - 19.5.89	16.5 - 25.5.89
	Vb12	6	550	61	141.0	F, poss. gravid	Inter/Pre - S1	No bolus	21.5.89	26.5 - 29.5.89	23.5 - 25.5.89
11 11.6 - 22.6.89	Ca9	1	410	95	37.0	F, gravid	Post - S1	No bolus	11.6.89	12.6 - 16.6.89	13.6 - 16.6.89
	Ca10	1	420	95	45.0	F, gravid	Post - S1	No bolus	16.6.89	19.6 - 21.6.89	19.6 - 21.6.89
	Nn18	4	680	160	177.5	F, gravid	Post - S1	No bolus	11.6.89	13.6 - 16.6.89	13.6 - 16.6.89
	Vb13	7	400	50	78.5	F, not gravid	Inter - S1	No bolus	14.6.89	21.6 - 22.6.89	15.6 - 21.6.89

Table 3.1: **Details of the 11 experiments undertaken in outdoor vivaria during 1988 and 1989.**

Specimen numbers indicate species and individual snake number (prefix of Ca for *Coronella austriaca*, Nn for *Natrix natrix*, Vb for *Vipera berus*). Note that Nn10 was used in experiments 4, 5 and 6 and Vb6 was used in experiments 7 and 8. Under dietary condition, all the 4 snakes listed as post - absorptive regurgitated food items before they were placed in the vivaria.

Key for sex and reproductive condition.

M, sperm: male, spermatozoa detected
M, no sperm: male, no spematozoa detected
M, ?: male, not tested for presence of spermatozoa

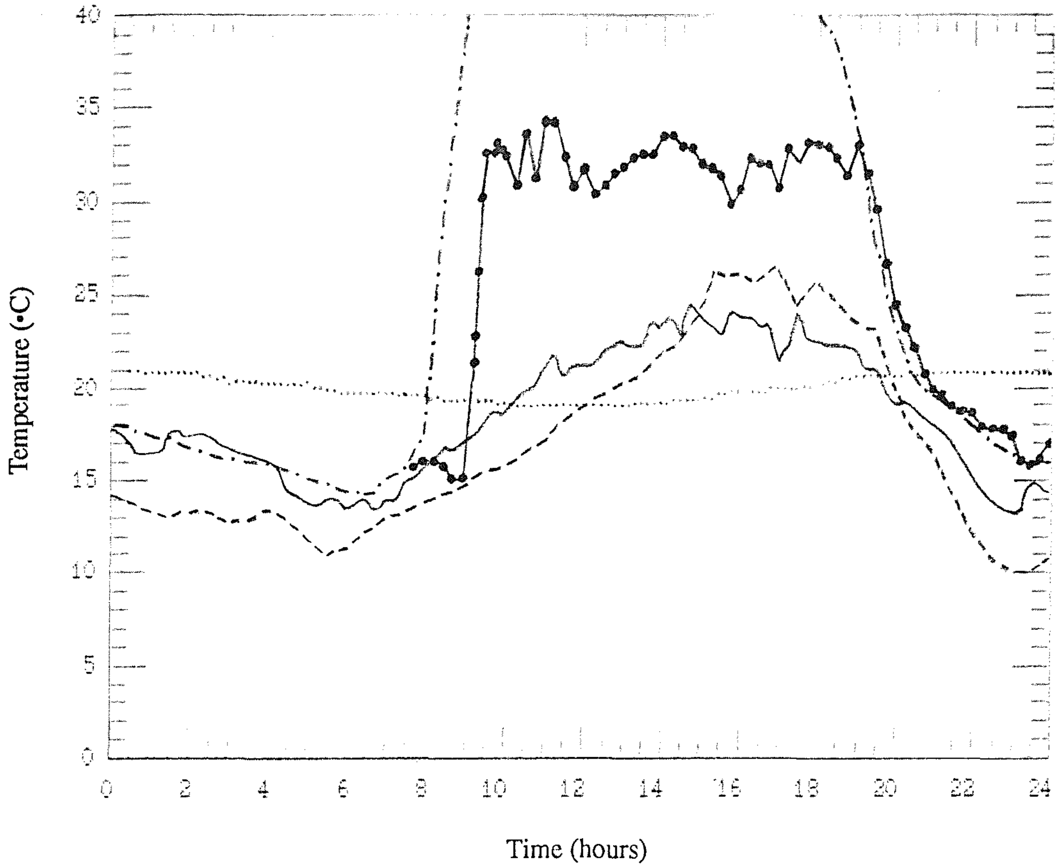
F, poss. gravid: female, possibly gravid
F, *: female, observed mating shortly before being captured
F, gravid: female, gravid
F, not gravid: female, definitely not gravid
F, post - gravid: female, recent parturition
F, ?: female, condition unknown

Fig. 3.1). These plateau phase temperatures were used to calculate the field selected body temperatures.

Thermal Conditions

Once the selected body temperatures for the 3 snake species had been calculated, it was possible to produce a better estimate of when conditions in the vivaria were such that the animals would not be able to maintain selected body temperatures. Peterson considered that when model temperatures were >30°C, the snakes he was studying were not limited by the thermal conditions and consequently were capable of maintaining body temperatures at selected levels. He had previously calculated the mean selected body temperatures of 9 specimens in a laboratory gradient to be 29.6°C and it was on the basis of this figure that he considered a model temperature of >30°C to indicate thermal conditions were not limiting. However, Peterson recorded selected temperatures in the laboratory gradient ranging from 28.6-34.6°C. Reptiles are believed to regulate their body temperatures between upper and lower set points rather than about a mean value (Barber and Crawford 1977, Huey 1982) and this should be remembered when considering mean selected body temperature values. In theory an operative temperature of about 30-31°C could actually be limiting to Peterson's snakes as they would be unable to reach the upper set point of their selected temperature range. The result of this would be a lower overall mean selected body temperature.

Taking the above factor into account, conditions considered not to be limiting to the snakes' ability to attain selected body temperatures were based on the spread of selected body temperature values rather than mean selected body temperatures. One option was to examine all the pooled selected body temperature data for each species and to use the maximum recorded values. However these maximum recorded values represented body temperatures that the snakes very rarely reached and were unrepresentative of the spread of selected body temperatures. Averaging the maximum recorded body temperature for each day was also unacceptable as the number of measurements greatly varied from day to day with the result that days with more measurements tended to have higher recorded maximum temperatures. In fact using maximum and minimum data is best avoided for this purpose as measurements were only recorded at 15 minute intervals and consequently it is impossible to state what the true extreme values were. Instead, 95% probability limits were calculated from the selected body temperature data. These values will be referred to as 'lower' and 'upper selected body temperatures'. The upper selected body temperature was used to represent the operative



Key

•—•—•— snake body temperature

———— shade air temperature

.... underground refuge temperature

—.—.—.— maximum model temperatures

– – – – minimum model temperatures

Fig. 3.1: **Body temperature pattern for a *Vipera berus* specimen (Vb13) on 21-6-89.** Note distinct heating phase, plateau phase and cooling phase of the snake's body temperature.

temperature above which snakes were considered to be capable of maintaining selected body temperatures.

Because the selected body temperatures of the 3 species varied, so did the conditions considered to be thermally limiting to each species. The model temperature data were analysed and it was possible to identify and quantify periods when the conditions prevented the different snake species from achieving selected body temperatures. When conditions were not limiting, the extent to which the snakes temporally utilised the thermal environment in attaining selected body temperatures was assessed. When calculating time periods during examination of temporal utilisation of the thermal environment, each model temperature measurement was considered to represent a 30 minute period (as they were recorded at 30 minute intervals) and each snake body temperature measurement represented a 15 minute period (recorded at 15 minute intervals).

Body temperatures were compared between species according to environmental conditions;

1. During periods when the floors of the vivaria were not in a position to receive the direct sun. This period covered the start of evening shadow on the arenas (varied from 1800 hours during experiment 7 to 1915 hours in experiment 3) until the following morning when the vivaria were no longer in shadow (varied from 0750 hours during experiment 3 to 0840 hours in experiment 7). From this point in the thesis it will be described as the '**unlit**' period. The phase when the vivaria were not in shadow will be described as the '**lit**' period (including periods when the sun was behind cloud). Table 3.2 gives times of lit and unlit periods for the 11 experiments. Conditions were always thermally limiting during the 'unlit' periods.

2. During the lit period when conditions were thermally unlimiting. As the conditions considered to be thermally unlimiting for each species varied, the highest upper selected body temperature between the 3 species was used to estimate the conditions for this category. Therefore, all 3 species could reach preferred body temperatures and a meaningful comparison between body temperatures measured during such conditions could be made.

3. During the lit period when conditions were thermally limiting. The conditions considered to be thermally limiting for each species also varied so the lowest upper selected body temperature between the 3 species was used as the extreme value. Therefore maximum model temperature values below the lowest upper selected body temperature were regarded as indicating conditions that were thermally limiting for all 3 species.

Experiment	Time Start	 Finish
1	0825	1825
2	0800	1915
3	0750	1915
4	0750	1915
5	0755	1915
6	0820	1830
7	0840*	1800
8	0825	1825
9	0825	1825
10	0800	1915
11	0750	1915

***Table 3.2:* Approximate times of the 'lit' periods during the outdoor vivaria experiments.**

The start time marked the end of the morning shadow on the floors of the vivaria when the direct sun began to shine on the north-west corners. The start of the evening shadow over the entire floors of the vivaria marked the finish time of the 'lit' period.

* For the 2 southerly vivaria, the start time began at 0900 due to the shade of a tree.

Although it is important for the purposes of analysis that the criteria for the calculation of the above factors should be firmly established, it should not be forgotten that the model temperatures measured in the vivaria were estimates of the operative temperatures. Also, the difference of a few degrees centigrade in the calculation of model temperatures which are considered to represent limits for the maintenance of selected body temperatures were only significant for relatively short periods of time. This was because on sunny days, model temperatures often rapidly increased to over 40°C for long periods and in such circumstances there is little doubt that conditions were adequate for the snakes to achieve selected body temperatures.

3.2.2. Laboratory Experiments

A total of thirty-one experiments on all species were undertaken in the laboratory. Fourteen took place during 1987 and 17 during 1988. Each experiment usually lasted 3 days although the duration varied from 1 up to 6 days. Details of the 31 experiments are provided in Table 3.3.

Calculation of Selected Body Temperatures

'Laboratory selected body temperatures' were calculated in the same way as the equivalent 'field selected body temperatures' in the outdoor vivaria. Thermally unlimiting conditions were considered to be available to the snakes during the periods when the heatlamp was on (0725 hours until 1925 hours). Sand temperatures directly under the heatlamp reached values of >38°C during these times. It was possible to distinguish periods when the snakes were selecting body temperatures at a relatively precise level. Such periods were marked by a distinct 'plateau phase' (see section 3.2.1) and it was these body temperatures that were used to calculate laboratory selected body temperatures.

Thermal Conditions

Two distinct periods were identified in terms of thermal conditions available to the snakes in the laboratory arena. As stated in the above section, once the heatlamp was on, thermally

Experiment number	Specimen number	Site of capture	SVL (mm)	TL (mm)	Weight (g)	Sex and reproductive condition	Slough condition	Dietary condition	Date placed in arena	T_b recording period	Behaviour recording period
1	Vb14	7	460	75	54.0	M, ?	Pre - S1	No bolus	10.4.87	--	11.4 - 14.4.87
2	Vb15	other	510	56	80.0	F, ?	Post - S1	No bolus	14.4.87	15.4 - 16.4.87	15.5 - 18.4.87
3	Vb16	5	435	72	58.0	M, ?	Post - S1	No bolus	27.4.87	28.4 - 1.5.87	28.4 - 1.5.87
4	Vb17	other	400	50	34.5	F, ?	Inter - S1	No bolus	7.5.87	8.5 - 9.5.87	8.5 - 11.5.87
5	Vb18	5	565	85	95.0	M, ?	Inter - S1	No bolus	11.5.87	12.5 - 13.5.87	12.5 - 15.5.87
6	Nn19	3	600	165	79.0	M, ?	Inter - S1	No bolus	21.5.87	--	22.5 - 25.5.87
7	Nn20	other	710	140	46.5	M, ?	Pre - S1	No bolus	28.5.87	29.5 - 31.5.87	29.5 - 1.6.87
8	Nn21	3	690	157	223.0	F, gravid	Inter - S1	No bolus	1.6.87	--	2.6 - 5.6.87
9	Ca11	1	420	130	52.5	M, ?	Pre - S1	No bolus	15.6.87	17.6 - 18.6.87	17.6 - 20.6.87
10	Ca12	1	560	104	30.5	F, ?	Post - S1	No bolus	24.6.87	--	25.6 - 28.6.87
11	Ca13	1	385	80	38.5	F, gravid	Post - S1	No bolus	30.6.87	2.7 - 5.7.87	2.7 - 5.7.87
12	Ca14	1	315	75	21.0	F, not gravid	Post - S1	Post - ab	16.7.87	--	17.7 - 20.7.87
13	Ca15	2	400	130	41.0	M, ?	Inter - S1	No bolus	26.8.87	--	27.7 - 30.8.87
14	Vb19	other	475	71	--	M, ?	Inter - S1	No bolus	2.10 87	--	3.10 - 6.10.87
15	Nn22	6	450	146	80.0	M, no sperm	Inter - S1	No bolus	23.3.88	24.3 - 28.3.88	24.3 - 28.3.88
16	Vb20	6	415	81	100.5	M, sperm	Inter - S1	No bolus	29.3.88	30.3.88	30.3 - 31.3.88
17	Nn5	4	605	155	168.5	M, ?	Inter - S1	No bolus	18.5.88	19.5 - 24.5.88	19.5 - 24.5.88
18	Vb2	5	500	70	58.0	M, sperm	Inter - S1	No bolus	24.5.88	--	26.5 - 29.5.88
19	Ca1	1	490	72	55.0	F, ?	Inter - S1	No bolus	30.5.88	--	31.5 - 3.6.88
20	Nn7	3	650	140	128.0	F, ?	Inter - S1	No bolus	6.6.88	7.6 - 10.6.88	7.6 - 10.6.88
21	Nn10	other	760	162	274.0	F, gravid	Inter - S1	No bolus	22.6.88	--	23.6 - 26.6.88
22	Nn8	4	540	145	69.0	M, ?	Post - S1	No bolus	30.6.88	1.7 - 4.7.88	1.7 - 4.7.88
23	Ca2	1	450	95	52.0	F, poss. gravid	Inter - S1	No bolus	4.7.88	5.7 - 8.7.88	5.7 - 8.7.88
24	Ca4	1	400	82	39.0	F, poss. gravid	Inter - S1	No bolus	14.7.88	15.7 - 17.7.88	15.7 - 19.7.88
25	Nn23	other	650	155	132.0	F, gravid	Inter - S1	Post - ab	21.7.88	22.7 - 23.7.88	22.7 - 24.7.88

Table 3.3: **Continued overleaf**

Experiment number	Specimen number	Site of capture	SVL (mm)	TL (mm)	Weight (g)	Sex and reproductive condition	Slough condition	Dietary condition	Date placed in arena	T_b recording period	Behaviour recording period
26	Ca3	2	355	103	36.5	M, ?	Inter - S1	No bolus	26.7.88	31.7 - 1.8.88	28.7 - 1.8.88
27	Vb4	5	510	65	126.0	F, gravid	Inter - S1	No bolus	17.8.88	18.8 -20.8.88	18.8 - 22.8.88
28	Ca16	1	455	105	37.5	F, ?	Inter - S1	No bolus	26.8.88	29.8 - 31.8.88	27.8 - 31.8.88
29	Nn11	other	575	140	74.5	M, ?	Post - S1	No bolus	5.9.88	6.9 - 9.9.88	6.9 - 9.9.88
30	Nn12	4	690	110	94.5	Unsexed	Inter - S1	No bolus	16.9.88	17.9 - 20.9.88	17.9 - 20.9.88
31	Vb22	6	450	70	79.0	M, ?	Inter - S1	No bolus	30.9.88	1.10 - 4.10.88	1.10 4.10.88

Table 3.3: **Details of the 31 experiments undertaken in the laboratory video arena during 1987 and 1988.**

Specimen numbers indicate species and individual snake number (prefix of Ca for *Coronella austriaca*, Nn for *Natrix natrix*, Vb for *Vipera berus*).

Key for sex and reproductive condition.

M, sperm: male, spermatozoa detected
M, no sperm: male, no spermatozoa detected
M, ?: male, not tested for presence of spermatozoa

F, poss. gravid: female, possibly gravid
F, gravid: female, gravid
F, not gravid: female, definitely not gravid
F, ?: female, condition unknown

unlimiting conditions were judged to be available to the snakes. This can be related to the 'lit' period / thermally unlimiting conditions category of the outdoor vivaria experiments. When the heatlamp was off, conditions were considered to be thermally limiting to the snakes and this situation can be related to the 'unlit' period of the outdoor vivaria (see section 3.2.1, Thermal Conditions).

In the outdoor vivaria experiments there was a third category distinguished by thermally limiting conditions during the 'lit' period. A parallel category did not exist in the laboratory arena. The effects of factors such as cloud cover and wind were not relevant in the laboratory and therefore conditions were similar between all days. This meant a more direct comparison between the body temperatures of the 3 snake species could be made without having to take account of the effects of varying environmental conditions.

The extent to which the snakes temporally utilised the thermal environment was assessed. Body temperatures in thermally limiting and thermally unlimiting conditions were compared between species.

3.3. Results

3.3.1. Outdoor Vivaria Experiments

A large amount of body temperature data was either lost or could not be used due to the breakdown of transmitter, reception and/or recording equipment. This was particularly the case in the earlier experiments when the techniques were being refined. However, the information that could be collected from the experiments is presented here.

Table 3.1 provides information on the snakes studied in the 11 outdoor vivaria experiments and the periods during which data were collected. A total of 10 smooth snakes, 18 grass snakes and 13 adders were used. Body temperature data were recorded from 9, 10 and all 13 of the respective individuals. The amount of usable body temperature data collected from each individual varied considerably. Body temperature data from one adder (specimen Vb2) came from only 1 day whereas another adder (specimen Vb7) contributed data on 13 days.

There was a total of 53 'snake days' on which at least some usable body temperature measurements were collected for smooth snakes. Grass snake data were recorded on 52 snake days. Adder data were collected on 66 separate days but on 6 of these, data were obtained from 2 different specimens which resulted in a total of 72 snake days. Snake body temperature data were collected on a grand total of 116 separate days and 177 snake days.

Comparison of Related Body Temperatures

Tables 3.4, 3.5 and 3.6 give the results of daily and the overall pooled body temperature comparisons. Frequency distributions of the pooled data are also presented (Fig. 3.2).

No significant difference was detected in the ranked comparison between smooth snakes and grass snakes (Wilcoxon matched-pairs signed-ranks, $z = 0.073$, $n = 592$, $p > 0.05$). A comparison of the 2 distributions using a Kolmogorov-Smirnov 2-sample test resulted in a highly significant difference ($DN = 0.127$, $n = 592$, $p < 0.001$). An inspection of the results from the 21 days reveals that on 9 days no significant difference was observed. On the days that a significant difference was observed, smooth snakes had higher median body temperatures on 8 days and grass snakes had higher median body temperatures on 4 days.

The difference between smooth snakes and adders was more pronounced than the last comparison ($z = 11.032$, $n = 516$, $p < 0.001$). A Kolmogorov-Smirnov 2-sample test revealed a highly significant difference ($DN = 0.277$, $n = 516$, $p < 0.001$). Paired body temperature recordings were taken on 18 days. On only 2 of the 15 days when a significant difference was observed did smooth snakes have higher median body temperatures than adders.

Adders were also found to have significantly different body temperatures compared to grass snakes ($z = 11.074$, $n = 640$, $p < 0.001$) and a highly significant difference was also observed in the body temperature distributions ($DN = 0.225$, $n = 640$, $p < 0.001$). There were 7 individual days when no significant difference was detected between the body temperatures of the 2 species, and of the 17 remaining days adders had higher median body temperatures on 15 of them.

During the 24 days that adders and grass snakes could be directly compared, there were 4 days when 2 adder specimens were available for comparison with a single grass snake. The adder specimens for which a larger number of body temperature recordings were available for comparison with the grass snake specimens were used in the above analysis. On 3 of the days

		Body temperatures (°C)							
		Coronella austriaca			*Natrix natrix*			Statistic	
Date	n	Median	Max	Min	Median	Max	Min	z	p
24.5.88	18	12.85	17.0	10.8	18.75	30.8	9.6	2.286	*
26.5.88	41	16.20	17.5	12.7	13.60	28.4	10.6	1.587	NS
27.5.88	35	17.10	20.8	9.0	26.50	34.7	8.9	4.152	***
12.8.88	27	21.80	28.5	13.2	23.70	29.9	14.8	1.586	NS
16.8.88	16	28.90	30.3	18.0	28.35	31.3	27.4	1.758	NS
17.8.88	40	23.70	31.8	10.0	28.75	33.4	13.4	4.814	***
18.8.88	36	14.45	27.8	9.4	23.25	32.9	14.5	5.059	***
19.8.88	26	19.50	27.8	12.4	20.10	27.5	12.4	1.009	NS
24.4.89	6	10.75	11.3	10.4	7.75	7.8	7.5	2.201	**
25.4.89	20	11.55	13.8	8.0	7.75	9.1	6.2	3.920	***
26.4.89	29	14.20	21.7	9.1	9.50	19.1	2.8	4.346	***
27.4.89	36	12.20	29.5	7.7	12.30	30.3	9.9	1.775	NS
28.4.89	7	25.80	32.6	9.8	26.00	33.8	20.1	1.014	NS
16.5.89	35	23.90	29.3	15.0	25.20	29.0	12.3	0.401	NS
17.5.89	46	24.00	32.7	16.1	20.50	32.3	11.8	3.685	***
18.5.89	45	27.40	32.4	13.4	25.70	33.3	9.7	3.128	**
19.5.89	22	27.50	32.2	15.5	27.50	35.0	11.3	0.503	NS
13.6.89	16	31.00	32.0	29.1	30.00	31.9	27.3	2.146	*
14.6.89	27	29.80	33.4	16.8	26.40	29.5	16.6	3.219	**
15.6.89	48	29.40	32.6	16.3	26.90	30.7	15.3	4.492	***
16.6.89	16	26.30	32.2	16.2	26.35	32.9	15.8	0.155	NS
All days	592	20.50	33.4	7.7	23.75	35.0	2.8	0.073	NS

Table 3.4: **Matched pairs comparisons of body temperatures recorded from *Coronella austriaca* and *Natrix natrix* specimens in outdoor vivaria.** The data presented here represents periods when simultaneous recording of the two species was possible. Daily and overall pooled results are presented with Wilcoxon matched-pairs signed-ranks test statistics (z) and their significance levels.

NS = $p > 0.05$
* = $p < 0.05$
** = $p < 0.01$
*** = $p < 0.001$

		Body temperatures (°C)							
		Coronella austriaca			*Vipera berus*			Statistic	
Date	n	Median	Max	Min	Median	Max	Min	z	p
25.7.88	3	19.00	19.0	18.7	20.50	22.5	20.5	1.604	NS
26.7.88	27	18.60	29.5	14.2	22.10	34.3	11.9	2.475	*
27.7.88	46	23.10	31.1	15.0	29.75	36.1	11.3	4.436	***
28.7.88	33	16.10	17.6	14.6	17.20	20.5	13.8	3.270	**
29.7.88	27	19.90	32.5	14.4	27.60	34.9	9.9	3.796	***
17.8.88	40	23.70	31.8	10.0	31.15	34.8	14.8	5.249	***
18.8.88	35	14.70	27.8	9.5	22.80	35.1	16.1	5.159	***
19.8.88	26	19.50	27.8	12.4	21.25	31.8	12.9	2.327	*
24.4.89	6	10.75	11.3	10.4	7.95	8.0	7.8	2.201	*
25.4.89	21	11.60	13.8	8.0	14.30	22.3	8.7	2.624	**
26.4.89	30	14.20	21.7	9.1	15.30	36.1	5.0	1.388	NS
27.4.89	36	12.20	29.5	7.7	11.65	38.5	7.0	1.728	NS
28.4.89	6	23.80	32.6	9.8	33.75	36.5	32.9	2.201	*
16.5.89	35	23.90	29.3	15.0	28.00	35.7	17.6	4.038	***
17.5.89	36	25.25	32.7	19.1	16.80	32.0	12.5	4.124	***
18.5.89	40	28.10	32.4	24.2	30.65	34.10	23.4	4.375	***
19.5.89	22	27.50	32.2	15.5	31.85	36.2	12.0	2.743	**
21.6.89	47	29.90	33.0	19.1	32.20	34.4	15.1	2.995	**
All days	516	21.05	33.0	7.7	24.85	38.5	5.0	11.032	***

Table 3.5: **Matched pairs comparisons of body temperatures recorded from *Coronella austriaca* and *Vipera berus* specimens in outdoor vivaria.** The data presented here represents periods when simultaneous recording of the two species was possible.Daily and overall pooled results are presented with Wilcoxon matched-pairs signed-ranks test statistics (z) and their significance levels.

NS = $p > 0.05$
* = $p < 0.05$
** = $p < 0.01$
*** = $p < 0.001$

		Body temperatures (°C)							
		Natrix natrix			*Vipera berus*			Statistic	
Date	n	Median	Max	Min	Median	Max	Min	z	p
2.6.88	19	14.30	15.1	12.7	15.30	16.1	14.5	3.823	***
3.6.88	41	15.60	22.2	13.6	17.10	21.5	12.8	2.942	**
6.6.88	17	14.80	22.8	12.9	16.10	23.9	10.8	0.426	NS
17.8.88	40	28.75	33.4	13.4	31.15	34.8	14.8	2.191	*
18.8.88	35	23.50	32.9	15.4	22.80	35.1	16.1	1.889	NS
19.8.88	26	20.10	27.5	12.4	21.25	31.8	12.9	0.940	NS
23.9.88	23	19.10	28.7	13.4	18.10	29.4	10.7	0.243	NS
31.3.89	38	13.35	27.5	7.2	29.90	35.0	7.6	5.373	***
3.4.89	21	14.70	28.2	7.9	26.90	33.7	11.5	3.883	***
7.4.89	15	9.60	20.2	8.6	9.20	20.1	8.2	0.248	NS
24.4.89	6	7.75	7.8	7.5	7.95	8.0	7.8	2.023	**
25.4.89	31	7.50	9.1	2.8	10.80	22.3	8.6	4.860	***
26.4.89	29	9.50	19.1	2.8	15.10	36.1	5.0	4.065	***
27.4.89	36	12.30	30.3	9.9	11.65	38.5	7.0	1.245	NS
28.4.89	17	21.50	33.8	6.5	34.10	36.9	9.0	3.621	***
2.5.89	9	26.40	27.8	19.1	11.40	11.9	10.7	2.666	**
3.5.89	19	25.80	28.4	14.6	32.50	39.9	16.4	2.213	*
4.5.89	45	26.50	33.1	11.8	28.70	35.6	9.0	0.397	NS
5.5.89	17	13.20	32.5	11.7	31.10	35.6	8.2	2.533	*
16.5.89	35	25.20	29.0	12.3	28.00	35.7	17.6	4.710	***
17.5.89	36	20.95	32.3	14.2	16.80	32.0	12.5	4.095	***
18.5.89	41	27.10	33.3	11.5	30.70	34.1	23.4	4.931	***
19.5.89	22	27.50	35.0	11.3	31.85	36.2	12.0	3.667	***
26.5.89	22	17.60	31.9	15.2	32.65	35.0	14.9	4.042	***
All days	640	19.10	35.0	2.8	21.05	39.9	5.0	11.074	***

***Table 3.6:* Matched pairs comparisons of body temperatures recorded from *Natrix natrix* and *Vipera berus* pecimens in outdoor vivaria.** The data presented here represents periods when simultaneous recording of the two species was possible. Daily and overall pooled results are presented with Wilcoxon matched-pairs signed-ranks test statistics (z) and their significance levels.

NS = $p > 0.05$
* = $p < 0.05$
** = $p < 0.01$
*** = $p < 0.001$

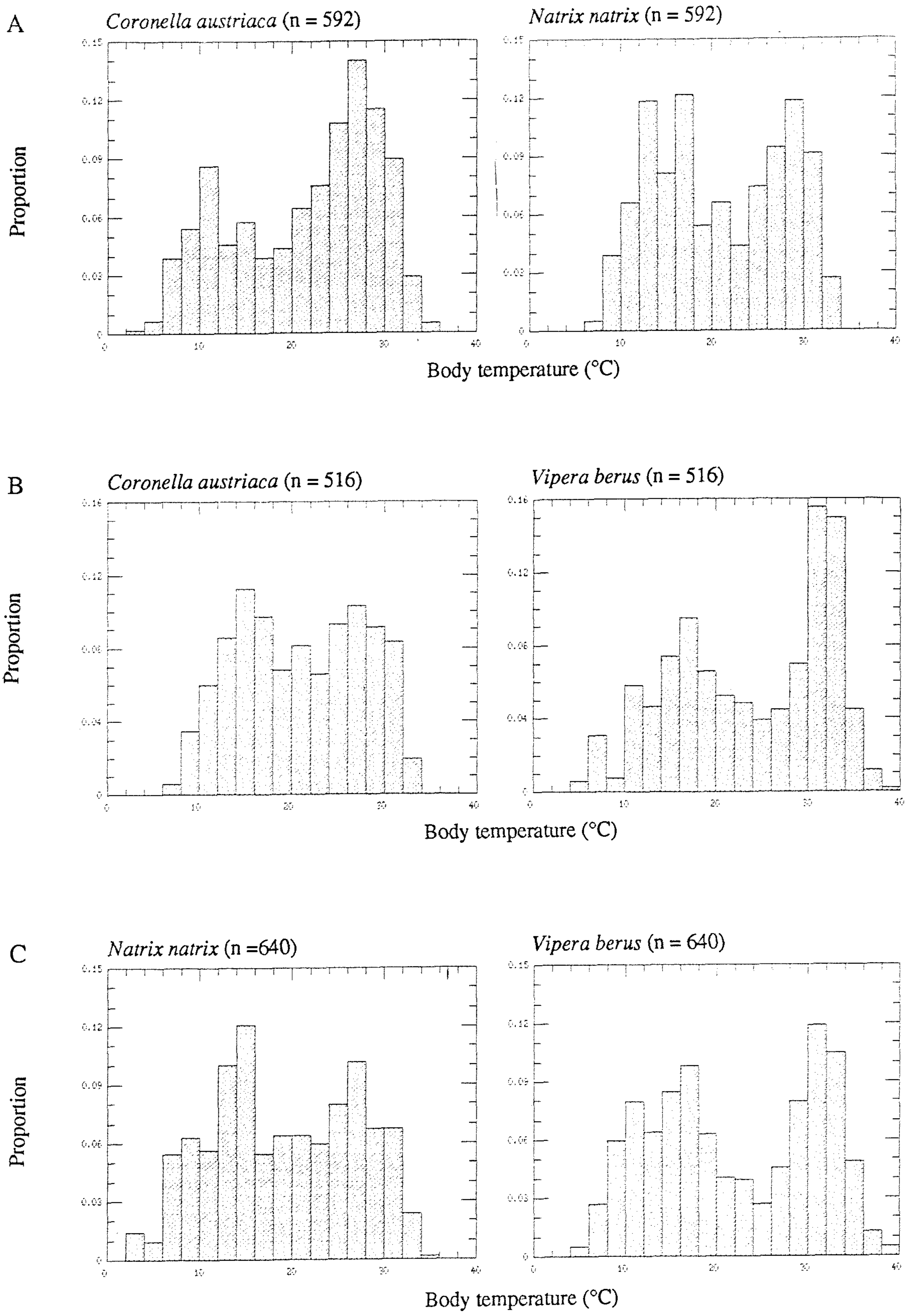


Fig. 3.2: **Relative frequency distributions of snake body temperatures recorded in the outdoor vivaria for matched pairs species comparisons.**
For each paired comparison, body temperatures of snakes in neighbouring vivaria were simultaneously measured.

	Coronella austriaca	*Natrix natrix*	*Vipera berus*
n	310	310	310
Mean	20.47	20.20	22.76
SD	7.106	8.074	8.752
Median	21.05	20.70	23.00
Max	32.7	35.0	38.5
Min	7.7	2.8	5.0
Skewness	- 0.053	- 0.161	- 0.208
t_s	- 0.381	- 1.157	- 1.495
p	NS	NS	NS
Kurtosis	-1.367	- 1.171	- 1.274
t_s	- 4.913	- 4.208	- 4.579
p	***	***	***

Table 3.7: **Summary statistics of body temperature data for the periods when measurements were simultaneously recorded for all 3 species in the outdoor vivarium.**

Details of skewness and kurtosis of the data are provided with tests of significance (Sokal and Rohlf, 1981).

NS = $p > 0.05$
* = $p < 0.05$
** = $p < 0.01$
*** = $p < 0.001$

concerned the body temperatures of the adder specimen that was not used were particularly low as the animal stayed under cover. However, even when the data from the adder specimen not used in the above comparison are substituted, there still remains a highly significant difference between the 2 species ($z = 6.626$, $n = 630$, $p < 0.001$)

There were also 12 days when body temperatures were recorded simultaneously for all 3 species. Table 3.7 summarises the data. A Kruskal-Wallis test was carried out on the data and a highly significant difference between the three species was detected (chi-squared = 21.49, $n = 310$, $p < 0.001$). This data recorded simultaneously between the three species were also incorporated into the 3 matched-pairs comparisons examined above. It was therefore not unexpected to find that the smooth snake and grass snake body temperature data from the 12 days were not significantly different (Wilcoxon matched-pairs signed-ranks, $z = 1.369$, $n = 310$, $p > 0.05$) but that there was a significant difference between smooth snakes and adders ($z = 7.118$, $n = 310$, $p < 0.001$) and adders and grass snakes ($z = 8.158$, $n = 310$, $p < 0.001$).

Field Selected Body Temperatures

There were 17 smooth snake days, 20 grass snake days and 21 adder days during which there were periods when thermal conditions were judged to be unlimiting and the snakes appeared to be maintaining selected body temperatures. These body temperatures were used to calculate the selected body temperature results. If there was any uncertainty that the thermal conditions were limiting, even if body temperatures were high and appeared to be precisely maintained at the same time, then the body temperature data in question were not used.

The mean field selected body temperature for smooth snakes was calculated to be 30.3°C ± 1.64 ($n = 377$, median = 30.3°C), for grass snakes 29.3°C ± 2.63 ($n = 291$, median = 29.1°C) and for adders 33.2°C ± 1.86 ($n = 491$, median = 33.4°C). A Kruskal-Wallis test was used to compare the 3 sets of data. A highly significant variation between the selected body temperatures among the 3 species was found (chi-squared = 512.609, $n = 1159$, $p < 0.001$). A series of Mann-Whitney/Wilcoxon tests was performed on each pairwise species combination and significant differences detected in each case ($z = 5.540$, $n_1 = 377$, $n_2 = 291$, $p < 0.001$ for smooth snakes and grass snakes, $z = 19.495$, $n_1 = 377$, $n_2 = 491$, $p < 0.001$ for smooth snakes and adders, $z = 17.968$, $n_1 = 291$, $n_2 = 491$, $p < 0.001$ for grass snakes and adders).

Upper and lower mean selected body temperatures were calculated from the 95% probability limits of the selected body temperature data. The lower and upper selected body temperatures of smooth snakes were worked out as 27.1°C and 33.5°C, grass snakes as 24.2°C and 34.5°C and adders as 29.5°C and 36.8°C.

Thermal Conditions

The values calculated to be the upper mean selected body temperatures for the 3 snake species were used to represent the operative temperatures above which the environmental conditions were considered thermally unlimiting and would therefore allow snakes to maintain selected temperatures. Model temperatures ≥ 34°C for smooth snakes, ≥ 35°C for grass snakes and ≥ 37°C for adders estimated these conditions in the vivaria.

Of the 53 snake days on which body temperatures were recorded for smooth snakes, there were 33 days on which at least one model temperature measurement of ≥ 34°C was recorded (62% of the days). The average duration of model temperatures ≥ 34°C for each day (excluding the measurements of 1 day when recording finished early, therefore $n = 52$) was 221.5 mins ± 239.6.

Twenty-nine of the snake 52 days on which grass snake body temperatures were recorded produced one or more model temperature measurements of ≥ 35°C (56% of days). The average duration of model temperatures ≥ 35°C (excluding the measurements of 3 days when recording finished early, therefore $n = 49$) was 183.1 mins ± 196.0.

For adders, 38 of 72 snake days resulted in model temperatures ≥ 37°C (53% of days). The average duration of model temperatures ≥ 37°C, and therefore of conditions judged to be thermally unlimiting for adders, (excluding the measurements of 3 days when recording finished early, therefore $n = 69$) was 142.2 mins ± 183.7.

Table 3.8 provides details of the amount of time thermal conditions were monitored in the outdoor vivaria and the extent to which conditions were utilised by the snakes. Fig. 3.3 gives a graphical version of the results for thermally unlimiting conditions. Note that, for example in the case of smooth snake recording, there is a category for total time when maximum operative temperatures available to the snakes (estimated by the model temperatures) in the vivaria were actually recorded (29,130 minutes). During this time, there was a total of 11,490

	Coronella austriaca	*Natrix natrix*	*Vipera berus*
(a) Total time that maximum model temperatures available to the snakes in the outdoor vivaria were monitored during the 'lit' phase	29130 mins	26220 mins	33540 mins
(b) Total time during (a) that conditions were considered to be thermally unlimiting	11490 mins	8970 mins	10440 mins
Proportion of time	0.39	0.34	0.31
(c) Total time during (b) that body temperatures were monitored	8865 mins	6150 mins	8730 mins
(d) Total time during (c) that body temperatures > mean field selected body temperatures were recorded	3225 mins	1845 mins	3660 mins
Proportion of time	0.36	0.30	0.42
(e) Total time during (a) that conditions were considered to be thermally limiting	17640 mins	17250 mins	23100 mins
Proportion of time	0.61	0.66	0.69
(f) Total time during (e) that body temperatures were monitored	12375 mins	10995 mins	15885 mins
(g) Total time during (f) that body temperatures > mean field selected body temperatures were recorded during thermally limiting conditions	90 mins	465 mins	1425 mins
Proportion of time	0.007	0.04	0.09

Table 3.8: Overall results of the duration that thermal conditions were monitored in the outdoor vivaria and the extent to which such conditions were utilised by the snakes.

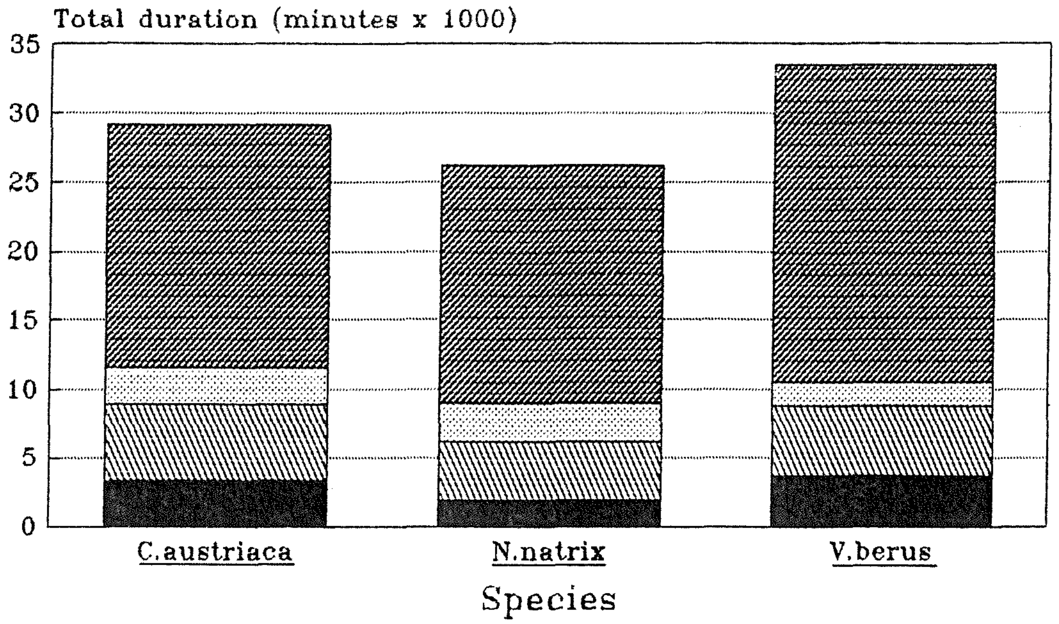


Fig. 3.3: **Overall results of the duration that thermal conditions were monitored in the outdoor vivaria and the extent to which such conditions were utilised by the snakes.**

▨ **Duration (a):** total time that maximum model temperatures available to the snakes in the outdoor vivaria were monitored during the 'lit' phases.

░ **Duration (b):** total time during (a) that conditions were considered to be thermally unlimiting (i.e. maximum model temperatures ≥ 34°C for *Coronella austriaca*, ≥ 35°C for *Natrix natrix*, ≥ 37°C for *Vipera berus*).

▧ **Duration (c):** total time during (b) that body temperatures were monitored.

■ **Duration (d):** total time during (c) that body temperatures ≥ mean field selected body temperatures were recorded.

minutes when model temperatures were ≥34°C and therefore indicated that conditions were thermally unlimiting for the smooth snakes. Out of the 11,490 minutes, body temperature measurements were recorded for 8,865 minutes. During the 8,865 minutes that body temperatures were monitored while conditions were thermally unlimiting, smooth snakes maintained temperatures at or above the mean field selected body temperature for 3,225 minutes.

It was noted in Section 2.4.3 that during 1988 the models were placed so that they could not always record the maximum model temperatures available in the vivaria. The models did not receive the last direct sun of the day when some parts of the vivaria were still 'lit' nor, in the case of the first 3 experiments, the first direct sun in the morning. There were also problems with the Squirrel recorder during experiment 7 when no readings were obtained from model 4, and experiment 8 when none were obtained from models 5, 6 and 7. It was possible to calculate the amount of time when the models were not in a position to receive the direct sun and were therefore unable to record maximum model temperatures. Returning to the above example, maximum model temperatures were recorded during a total of 29,130 minutes over the 53 days of smooth snake body temperature recording. However, there were 4,560 minutes when model temperatures were recorded but may not have been measuring the maximum values in the vivaria (i.e. the models were not in the direct sun). During the periods when grass snake and adders were studied, there were 5,490 minutes and 9,000 minutes respectively when maximum model temperatures may not have been measuring the maximum values available in the vivaria. These periods of unknown maximum model temperatures were not used in the analysis that follows in this chapter nor in the analyses of Chapters Four and Five.

The following analysis is based on the periods when the maximum model temperatures available to the snakes in the vivaria were recorded. An indication of the proportion of time when environmental conditions were suitable for the snakes to reach selected temperatures can be made. For smooth snakes, model temperatures of ≥34°C were actually recorded during 39% of the time that model temperatures had the potential of reaching ≥34°C had conditions been sufficient (i.e. during the 'lit' phase). The proportions were 34% for grass snakes and 31% for adders. Thus a large proportion of the period over which experiments were undertaken was considered to be limiting for the snakes as they were restricted in being able to maintain selected temperatures.

Utilisation of the Thermal Environment

It was not always possible to record body temperatures when conditions were thermally unlimiting for the snakes. There were 33 days when at least one model temperature measurement of ≥34°C (and therefore conditions judged to be thermally unlimiting) was recorded for smooth snakes. However, body temperature recording coincided with thermally unlimiting conditions on only 30 days. For grass snakes the proportion was 28 of the 29 days and for adders it was 36 of the 38 days. For the purposes of this analysis and to allow a meaningful comparison, the body temperatures of snakes during periods of thermally unlimiting conditions were examined.

Fig. 3.3 and Table 3.8 incorporate results which indicate the overall duration of thermally unlimiting conditions when the snakes were able to maintain body temperatures equal or above their mean field selected body temperatures. Figs. 3.4, 3.5 and 3.6 illustrate the results on a daily basis. For example, on 27.5.88 the smooth snake did not achieve mean selected body temperatures at all during the 315 minutes when conditions were thermally unlimiting (≥34°C) and body temperatures were being monitored. However, on 15.8.88, a smooth snake was recorded maintaining body temperatures equal or above mean field selected body temperatures during 255 minutes of 300 minutes of thermally unlimiting conditions. Note that for smooth snakes, equal or above mean field selected body temperatures were recorded on 21 of the 30 days (proportion of 0.70), for grass snakes it was 20 out of 28 days (proportion of 0.71) and for adders, 27 out of 36 days (proportion of 0.75). It also should be noted that mean field selected body temperatures (or higher values) were also recorded, although to a lesser extent, when conditions were 'thermally limiting' (see Table 3.8).

The vertical axes for Figs. 3.4, 3.5 and 3.6 give actual times rather than relative values. The amount of data varied a great deal between each day and each individual either due to the weather conditions and/or the amount of body temperature recording that was possible. Because of this it could be misleading to compare relative values. For example, in the above paragraph it was noted that a smooth snake achieved greater or equal to mean body temperatures for 255 minutes out of the 300 minutes of thermally unlimiting conditions. This is a proportion of 0.85. However, on 29.7.88 the conditions were thermally unlimiting for only 30 minutes when body temperatures were being recorded and during this time the smooth snake was at or above the mean field selected body temperature for 30 minutes, resulting in a proportion of 1.0.

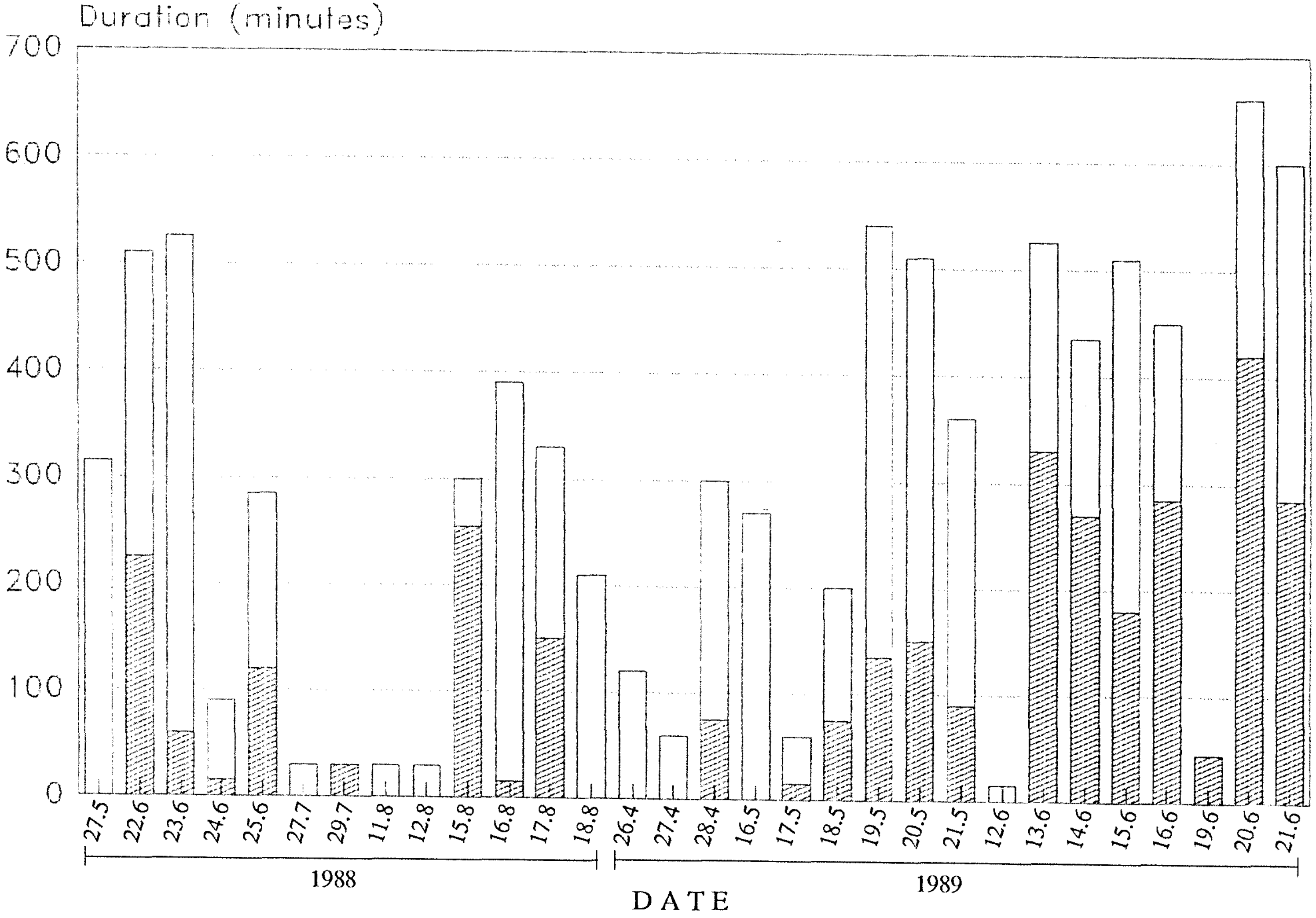


Fig. 3.4: **Daily records of temporal utilisation of thermally unlimiting conditions for *Coronella austriaca* in the outdoor vivaria.** The columns indicate the duration that body temperatures were monitored during thermally unlimiting conditions. The shaded areas represent the proportion of time when body temperatures ≥ mean field selected body temperatures were recorded.

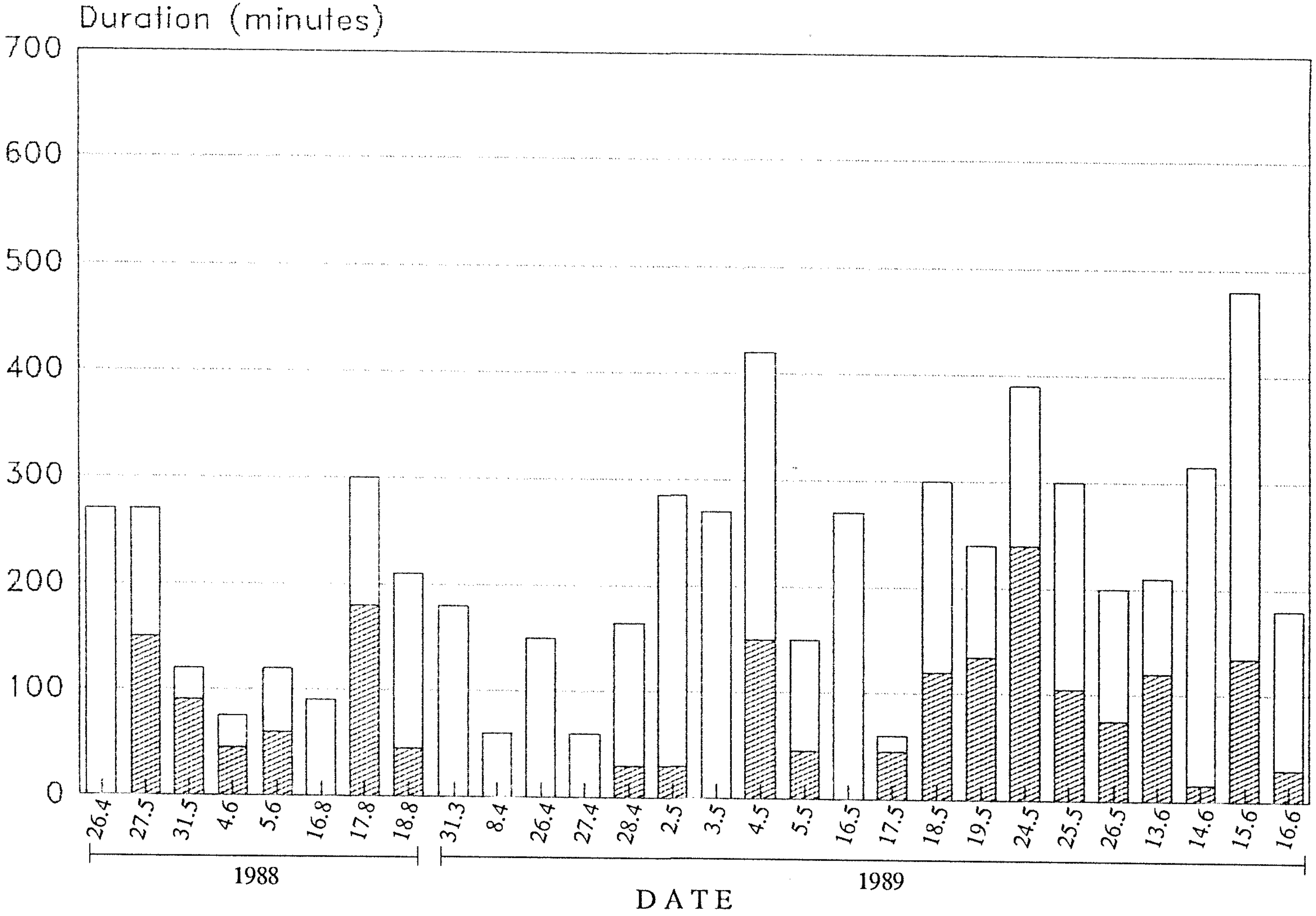


Fig. 3.5: **Daily records of temporal utilisation of thermally unlimiting conditions for *Natrix natrix* in the outdoor vivaria.** The columns indicate the duration that body temperatures were monitored during thermally unlimiting conditions. The shaded areas represent the proportion of time when body temperatures ≥ mean field selected body temperatures were recorded.

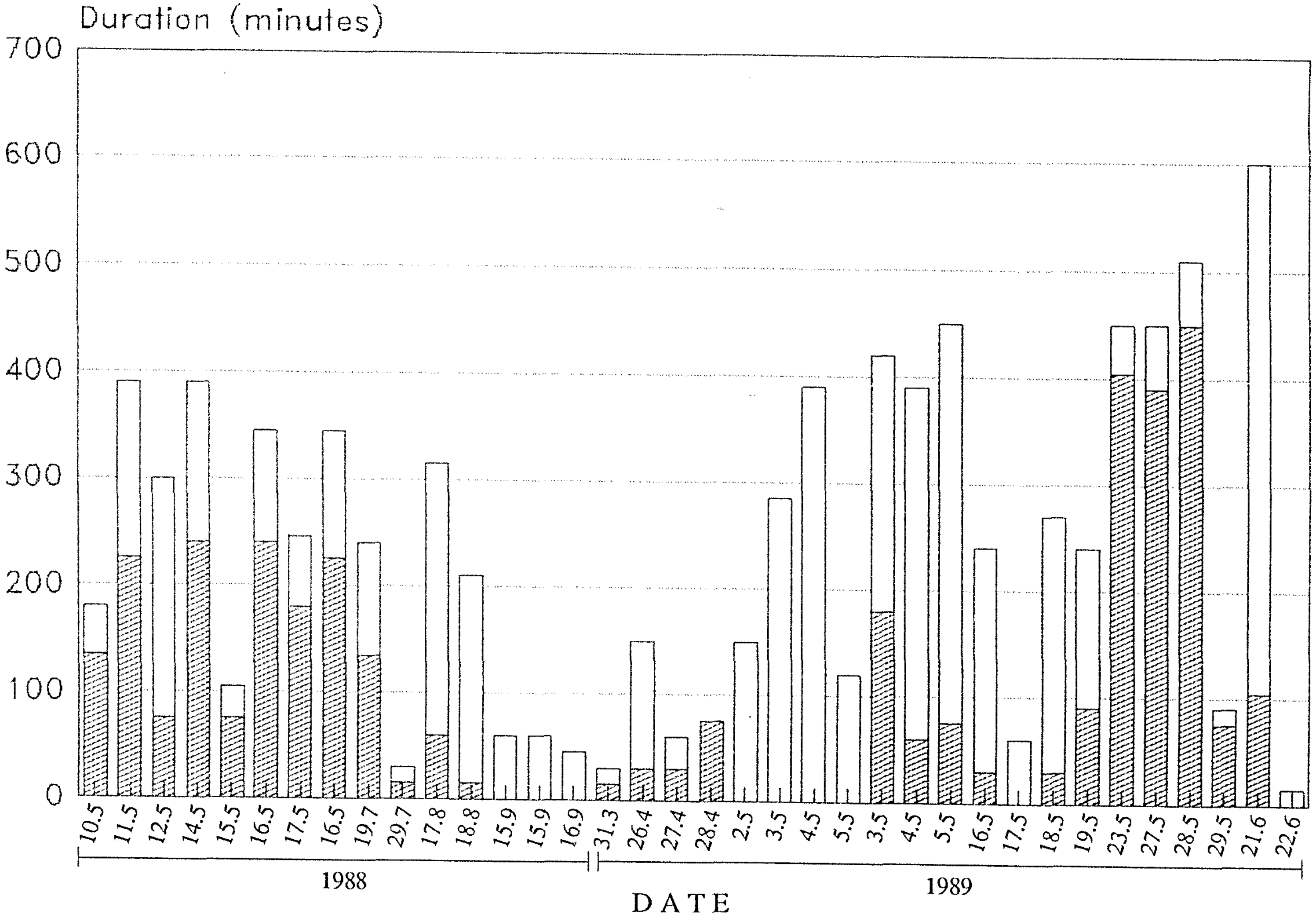


Fig. 3.6: **Daily records of temporal utilisation of thermally unlimiting conditions for *Vipera berus* in the outdoor vivaria.** The columns indicate the duration that body temperatures were monitored during thermally unlimiting conditions. The shaded areas represent the proportion of time when body temperatures ≥ mean field selected body temperatures were recorded.

In total, there were 8,865 minutes when conditions were thermally unlimiting and body temperatures were being monitored at the same time for smooth snakes. Out of this total, smooth snakes maintained body temperatures at or above the mean field selected body temperature for 3,225 minutes (a proportion of 0.36). For grass snakes the respective values were 6,150 minutes and 1,845 minutes (a proportion of 0.3) and for adders, 8,730 minutes and 3,660 minutes (a proportion of 0.42). G-tests were carried out on the number of body temperature records measured during the above times and a significant difference was detected between smooth snakes and grass snakes ($G = 4.435$, 1 d.f., $p < 0.05$), and between grass snakes and adders ($G = 14.842$, 1 d.f., $p < 0.001$) but no significant difference was detected between smooth snakes and adders ($G = 3.788$, 1 d.f, $p > 0.05$).

There was one particular adder specimen (specimen Vb9) which never reached mean field selected body temperatures even though conditions were suitable for long periods of time (see Fig. 3.6, for the days 2.5.89 - 5.5.89). In fact this snake was never observed above cover and always maintained relatively low body temperatures although the weather conditions were hot and sunny. If the results for this specimen are removed then the respective values for adders stated above become 6,450 minutes and 3,660 minutes (a proportion of 0.57).

An examination of the slopes of regression lines using the above data allows a comparison between species with regards to their utilisation of thermally unlimiting conditions. The closer the regression coefficients approach a value of 1, the greater the proportion of time the snakes maintain mean selected body temperatures (or above) during periods of thermally unlimiting conditions (Fig. 3.7). The regression equations for the daily records are as follows;

Smooth snakes: $y = -1.770 + 0.454x$

(Slope significantly different from zero, $t_s = 6.32$, $p < 0.001$)

Grass snakes: $y = -0.722 + 0.349x$

(Slope significantly different from zero, $t_s = 3.67$, $p < 0.001$)

Adders: $y = -1.317 + 0.501x$

(Slope significantly different from zero, $t_s = 5.09$, $p < 0.001$)

Adders (without the data of specimen Vb9):

$$y = -0.890 + 0.525x$$

(Slope significantly different from zero, $t_s = 5.41$, $p < 0.001$)

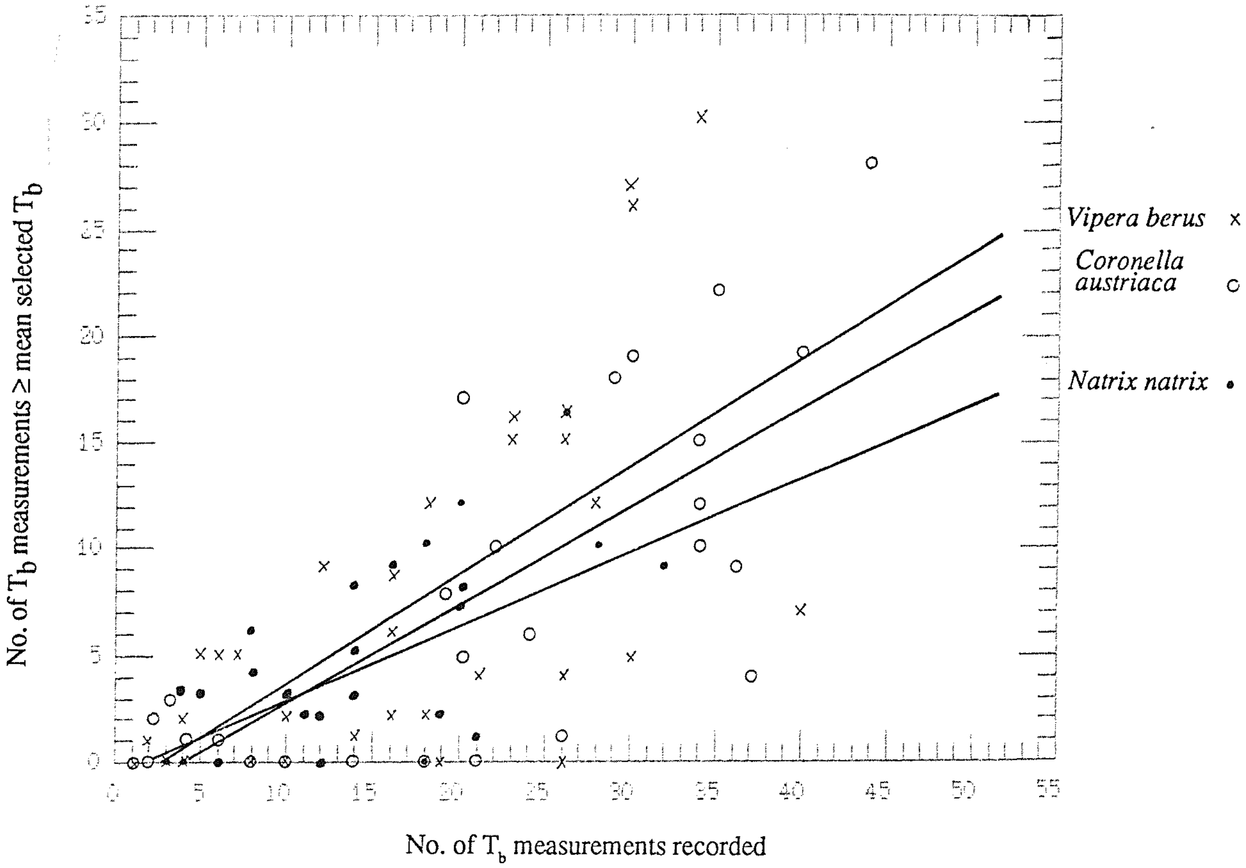


Fig. 3.7: **Regression lines of temporal utilisation of thermally unlimiting conditions for the 3 snake species in the outdoor vivaria.**
The daily number of body temperature measurements recorded during thermally unlimiting conditions is related to the number of those that were greater or equal to the mean field selected body temperature.

n = 30 for *Coronella austriaca* n = 28 for *Natrix natrix* n= 36 for *Vipera berus*

In these equations the independent (x) variable represents the number of body temperature measurements recorded during thermally unlimiting conditions and the dependent variable the number of those body temperature measurements that were equal or above mean field selected body temperatures. As can be seen the adders have the highest regression coefficient value of 0.501 (0.525 if the data for specimen Vb9 are excluded). A comparison of regression coefficients revealed significant differences between smooth snakes and grass snakes ($t = 4.207$, 54 d.f., $p < 0.001$), smooth snakes and adders ($t = 2.254$, 62 d.f., $p < 0.05$) and grass snakes and adders ($t = 4.938$, 60 d.f., $p < 0.001$).

Body Temperatures During 'Unlit' Conditions

The relative frequency distributions of the pooled body temperature data for each of the 3 snake species during 'unlit' conditions are illustrated in Fig. 3.8. Table 3.9 summarises the basic statistical information of the data.

Significant differences between the distributions of the data were detected using a Kolmogorov-Smirnov two-sample test between smooth snakes and grass snakes ($z = 4.989$, $n_1 = 1075$, $n_2 = 486$, $p < 0.001$), smooth snakes and adders ($z = 7.973$, $n_1 = 1075$, $n_2 = 1068$, $p < 0.001$) and adders and grass snakes ($z = 4.668$, $n_1 = 486$, $n_2 = 1068$, $p < 0.001$).

A Kruskal-Wallis test between the data of the 3 species indicated significant differences between data (chi-squared = 295.2, $n = 2629$, $p < 0.001$). The latter test was followed-up with a comparison between each pair of species and significant differences were found in all 3 combinations (Mann-Whitney/Wilcoxon test, smooth snakes and grass snakes, $U = 178712.5$, $n_1 = 1075$, $n_2 = 486$, smooth snakes and adders, $U = 340386.0$, $n_1 = 1075$, $n_2 = 1068$, grass snakes and adders, $U = 210659.5$, $n_1 = 486$, $n_2 = 1068$, $p < 0.001$ in all 3 cases).

The average of the daily means for the smooth snake data was 15.4°C ± 3.97 ($n = 41$) which compares with 14.3°C ± 3.04 ($n = 33$) for grass snakes and 12.2°C ± 4.35°C ($n = 52$) for adders.

	'Unlit 'conditions			Thermally limiting conditions			Thermally unlimiting conditions		
	Coronella austriaca	*Natrix natrix*	*Vipera berus*	*Coronella austriaca*	*Natrix natrix*	*Vipera berus*	*Coronella austriaca*	*Natrix natrix*	*Vipera berus*
n	1075	486	1068	825	733	1059	525	375	576
Mean	15.68	13.51	12.25	18.93	18.24	19.07	27.24	26.56	29.32
SD	4.23	3.00	4.78	5.47	6.71	8.19	5.84	5.78	7.60
Median	15.00	13.40	12.05	17.80	17.70	17.60	29.70	28.00	32.70
Max	34.7	23.8	35.1	34.5	34.8	36.6	35.5	37.1	39.9
Min	7.0	6.0	2.0	7.7	2.8	2.2	9.1	2.8	4.8
Skewness	0.500	0.338	0.234	0.435	0.049	0.245	−1.422	−1.297	−1.510
t_s	6.693	3.042	3.122	5.100	0.542	3.255	−13.302	−10.254	−14.795
p	***	**	**	***	NS	**	***	***	***
Kurtosis	0.207	0.955	0.963	−0.627	−0.809	−0.748	0.817	1.510	0.966
t_s	1.385	4.477	6.424	−3.676	−4.471	−4.969	3.821	5.969	4.732
p	NS	***	***	***	***	***	***	***	***

***Table 3.9:* Summary statistics of snake body temperatures recorded in the outdoor vivarium**

The table is divided into 'unlit' conditions, thermally limiting conditions (when maximum recorded model temperature < 34° C during 'lit' conditions) and thermally unlimiting conditions (when maximum recorded model temperature ≥37° C during 'lit' conditions). Details of skewness and kurtosis of the data are provided with tests of significance (statistic = t_s, Sokal and Rohlf, 1981).

NS = $p > 0.05$
* = $p < 0.05$
** = $p < 0.01$
*** = $p < 0.001$

Body Temperatures During Thermally Limiting Conditions.

The results presented in this section are analysed in the same way as those in the previous section and the section to follow. Fig. 3.9 and Table 3.9 provide information on the frequency distribution and summary statistics of the pooled body temperature data recorded during thermally limiting conditions. Maximum model temperatures of <34°C were regarded as indicating conditions that were thermally limiting to all 3 species of snakes. Data for this category were only collected during 'lit' periods.

The distributions of the smooth snake data and grass snake data were significantly different (Kolmogorov-Smirnov two-sample, $z = 2.796$, $n_1 = 825$, $n_2 = 733$, $p < 0.001$). So too were the distributions of smooth snake and adder, and grass snake and adder body temperature data ($z = 2.825$, $n_1 = 825$, $n_2 = 1059$, and $z = 2.498$, $n_1 = 733$, $n_2 = 1059$ respectively, $p < 0.001$ in both cases). However, a Kruskal-Wallis test between the 3 species showed no significant differences in the data sets (chi-squared = 4.354, $n = 2617$, $p > 0.05$).

The average of the daily means for smooth snake data was 19.3°C ± 4.72 ($n = 48$), for grass snakes 18.6°C ± 5.88 ($n = 48$) and for adders, 19.5°C ± 6.41 ($n = 63$).

Body Temperatures During Thermally Unlimiting Conditions

Fig. 3.10 and Table 3.9 present the relative frequency distributions and summary statistics of pooled snake body temperature data during thermally unlimiting conditions (for all 3 species indicated by maximum model temperatures of ≥37°C in the vivaria). The distributions of data between the 3 species were found to be significantly different (Kolmogorov-Smirnov two-sample test, $z = 3.369$, $n_1 = 525$, $n_2 = 375$ between smooth snakes and grass snakes, $z = 7.941$, $n_1 = 525$, $n_2 = 576$ between smooth snakes and adders, $z = 7.268$, $n_1 = 375$, $n_2 = 576$ between grass snakes and adders, $p < 0.001$ in all 3 cases).

Significant variation between species data was detected with a Kruskal-Wallis test (chi-squared = 223.3, $n = 1476$, $p < 0.001$) and a comparison between each pairwise combination showed significant differences in each of the 3 cases (Wilcoxon/ Mann-Whitney test, smooth snakes and grass snakes, $U = 82744.5$, $n_1 = 525$, $n_2 = 375$, smooth snakes and adders, $U = 83335.0$, $n_1 = 525$, $n_2 = 576$, grass snakes and adders, $U = 58318.5$, $n_1 = 375$, $n_2 = 576$ and $p < 0.001$ in all cases).

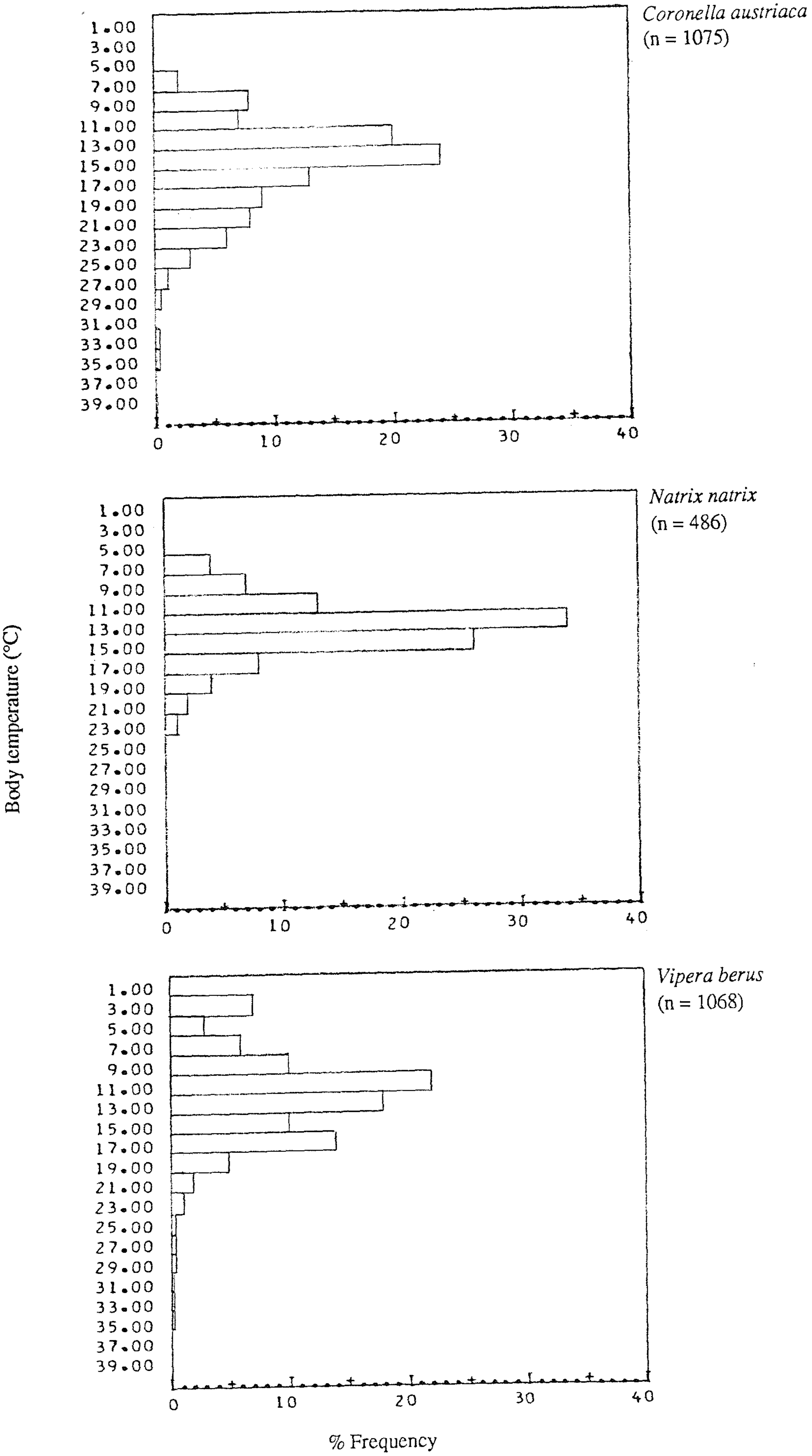


Fig. 3.8: Relative frequency distributions of snake body temperatures recorded in the outdoor vivaria during 'unlit' periods.

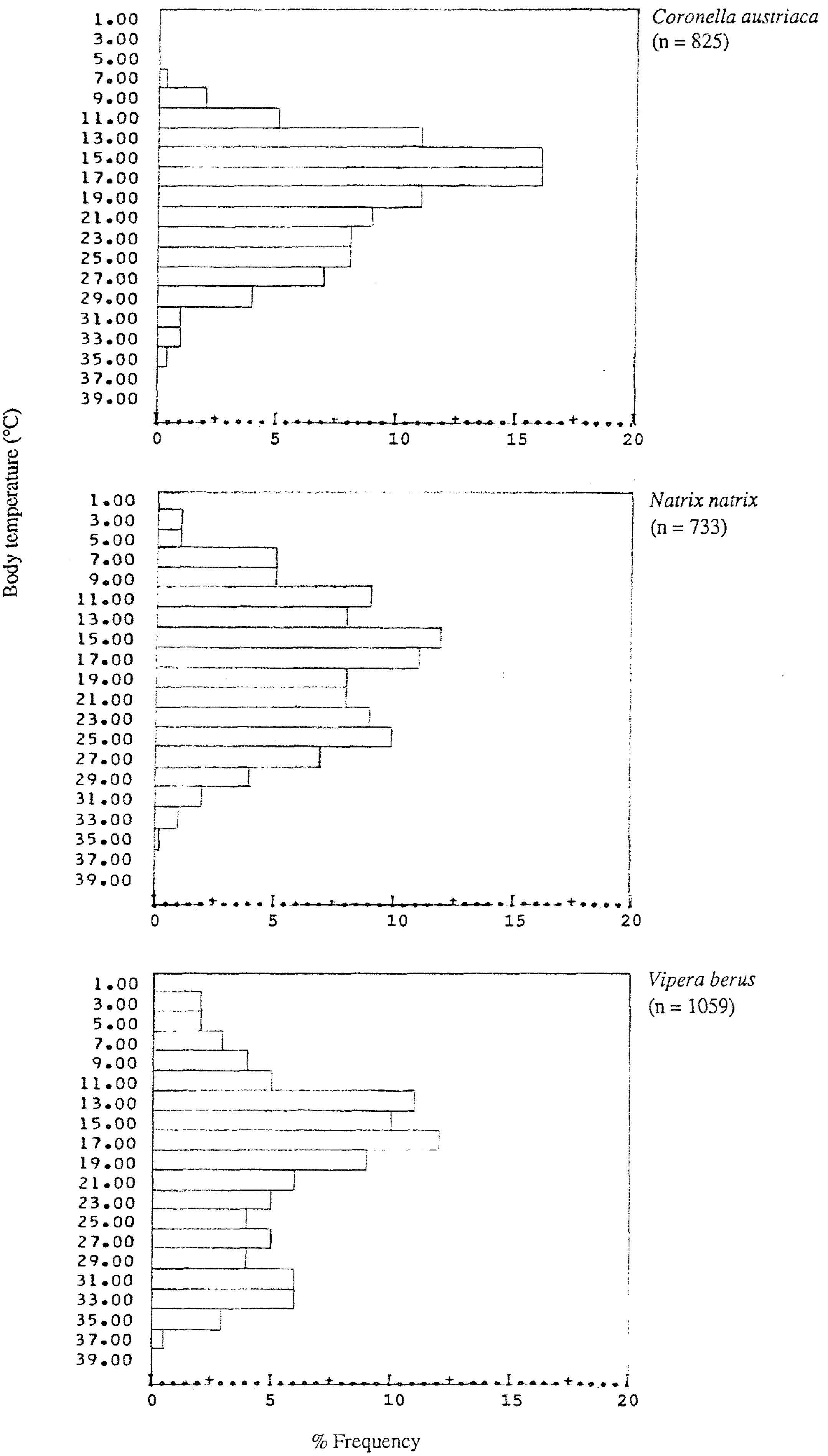


Fig. 3.9: Relative frequency distributions of snake body temperatures recorded in the outdoor vivaria during thermally limiting conditions (i.e. when maximum recorded model temperatures were < 34°C during 'lit' periods).

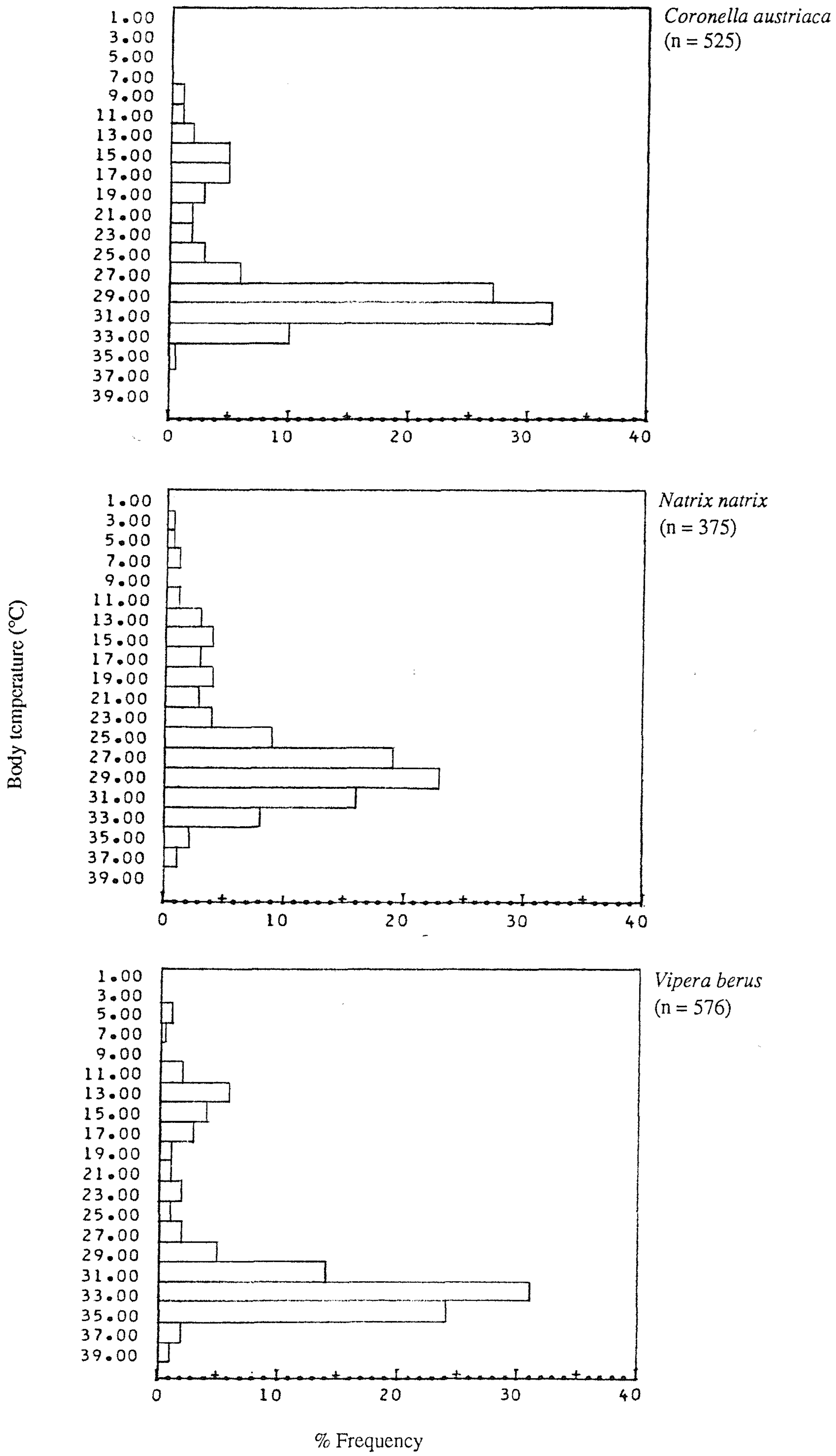


Fig. 3.10: Relative frequency distributions of snake body temperatures recorded in the outdoor vivaria during thermally unlimiting conditions (i.e. when maximum recorded model temperatures were≥ 37°C).

The average value of the daily mean body temperatures for smooth snakes was 26.4°C ± 5.31 (n = 27), for grass snakes it was 25.9°C ± 4.92 (n = 26) and for adders, 28.7°C ± 7.07 (n = 35).

3.3.2. Laboratory Experiments

Table 3.3 provides details of the 31 individual laboratory experiments. Ten smooth snake specimens, 11 grass snake specimens and 10 adder specimens were studied. There were problems with the body temperature recording apparatus in this series of experiments as well as those of the outdoor vivaria and so some data were lost or could not be used. Body temperature data were recorded from 6 of the smooth snake specimens (on a total of 18 days), 8 of the grass snake specimens (on a total of 31 days) and 7 of the adder specimens (a total of 17 days). Therefore a total of 66 days of snake body temperature data were amassed from the laboratory experiments. The amount of body temperature data that were obtained on each day varied considerably.

Laboratory Selected Body Temperatures

There were 10 smooth snake days, 11 grass snake days and 11 adder days when relatively complete body temperature recordings were available and which indicated selected levels were being maintained. This data were used to calculate the overall laboratory selected body temperature of each species.

The mean laboratory selected body temperature for smooth snakes was calculated to be 30.8°C ± 1.25 (n = 241, median 30.6°C), for grass snakes 31.0°C ± 2.10 (n = 189, median 30.8°C) and for adders 32.5°C ± 2.27 (n = 159, median 32.6°C). The distributions of the 3 sets of data were all found to be significantly different from eachother when compared with Kolmogorov-Smirnov two-sample tests (DN = 0.018, n_1 = 241, n_2 = 189 between smooth snakes and grass snakes, DN = 0.475, n_1 = 241, n_2 = 159 between smooth snakes and adders, DN = 0.384, n_1 = 189, n_2 = 159 between grass snakes and adders, $p < 0.001$ in all cases).

A Kruskal-Wallis test was used on the data and a significant difference between species found (chi-squared = 76.62, n = 589, $p < 0.001$). A series of Wilcoxon/Mann-Whitney tests between the 3 pairs was also carried out (no significant difference between smooth snakes and grass snakes, $z = 0.055$, $n_1 = 241$, $n_2 = 189$, but a significant difference between smooth snakes and adders, $z = 8.750$, $n_1 = 241$, $n_2 = 159$, $p < 0.001$, and between grass snakes and adders, $z = 6.548$, $n_1 = 189$, $n_2 = 159$, $p < 0.001$).

Thermal Conditions

Once the heatlamp switched on, the thermal conditions were considered to be thermally unlimiting for the snakes. Trials were undertaken before the laboratory experiments were started to assess the thermal conditions in the arena. These indicated that sand temperatures directly beneath the heatlamp could reach 37°C within 10 minutes and over 40°C in 23 minutes. When the heatlamp turned off, sand temperatures beneath the heatlamp remained slightly higher than temperatures elsewhere in the arena. By the end of the thermally limiting period they were often up to 1.5°C higher than sand temperatures recorded at other locations.

Attempts were made to keep the thermal conditions as constant as possible between experiments. However, there was a degree of variation throughout the study periods. In the Spring and Autumn, the concrete floor of the arena was slightly colder which had some effect on the sand and ambient temperatures. The minimum temperature recorded in the arena was 14°C during the early morning of experiments 15 and 16 (shade air temperature in refuge 3) which were undertaken in March 1988. The average minimum temperature recorded in the arena throughout the laboratory experiments was 17.9°C ± 1.74 ($n = 31$ experiments).

Utilisation of the Thermal Environment

When body temperatures were monitored when the heatlamp was on, conditions were judged to be thermally unlimiting for all 3 snake species. The proportion of body temperatures during such conditions that were equal or above the calculated mean laboratory selected body temperature was considered to represent an index of the temporal utilisation of the thermal environment by the snake species.

A total of 416 body temperature measurements were taken from smooth snake specimens during thermally unlimiting conditions. Of this total, 115 measurements were equal or above the mean laboratory selected body temperature (30.8°C), which represents a proportion of 27.6%. For grass snake specimens, 122 of the 983 measurements were equal or above the mean selected body temperature (31.0°C), a proportion of 12.4%. In the case of adders, 99 of the 228 measurements were ≥32.5°C, a proportion of 43.4%. Inter-specific comparisons of these frequencies were made using G-tests and significant differences found in all 3 combinations (G = 45.101 between smooth snakes and grass snakes, G = 16.271 between smooth snakes and adders, G = 101.388 between grass snakes and adders, 1 d.f. and $p < 0.001$ in all cases).

Figs. 3.11, 3.12 and 3.13 illustrate the daily results. Note that for the smooth snake results, 10 of the 17 days (59%) had at least 1 body temperature result equal or above the mean selected body temperature. In the case of grass snakes the respective values were 17 of 31 days (55%) and for adders, 13 of 16 days (81%). However on some days very few recordings were taken (a minimum of 2 measurements). Therefore it is possible that mean selected body temperatures could have been maintained by the snakes when body temperature recording was not undertaken.

An overall examination of the extent to which snakes temporally utilised their thermal environments was examined using the same methods as Section 3.3.1., 'Utilisation of the Thermal Environment'. The relationship between the number of body temperature measurements made during thermally unlimiting conditions and the number of those that were greater or equal to the laboratory mean selected body temperature is illustrated in Fig. 3.14 for the 3 snake species. The regression equations for the daily records were as follows;

Smooth snakes: $y = -0.072 + 0.279x$
(Slope significantly different from zero, $t_s = 2.792$, $p < 0.05$)

Grass snakes: $y = -0.210 + 0.131x$
(Slope not significantly different from zero, $t_s = 1.794$, $p > 0.05$)

Adders: $y = 0.905 + 0.371x$
(Slope significantly different from zero, $t_s = 4.377$, $p < 0.001$)

A comparison of regression coefficients revealed significant differences between smooth snakes and grass snakes ($t = 5.939$, 44 d.f., $p < 0.001$), smooth snakes and adders ($t = 2.736$, 29 d.f., $p < 0.05$) and grass snakes and adders ($t = 3.403$, 43 d.f., $p < 0.01$).

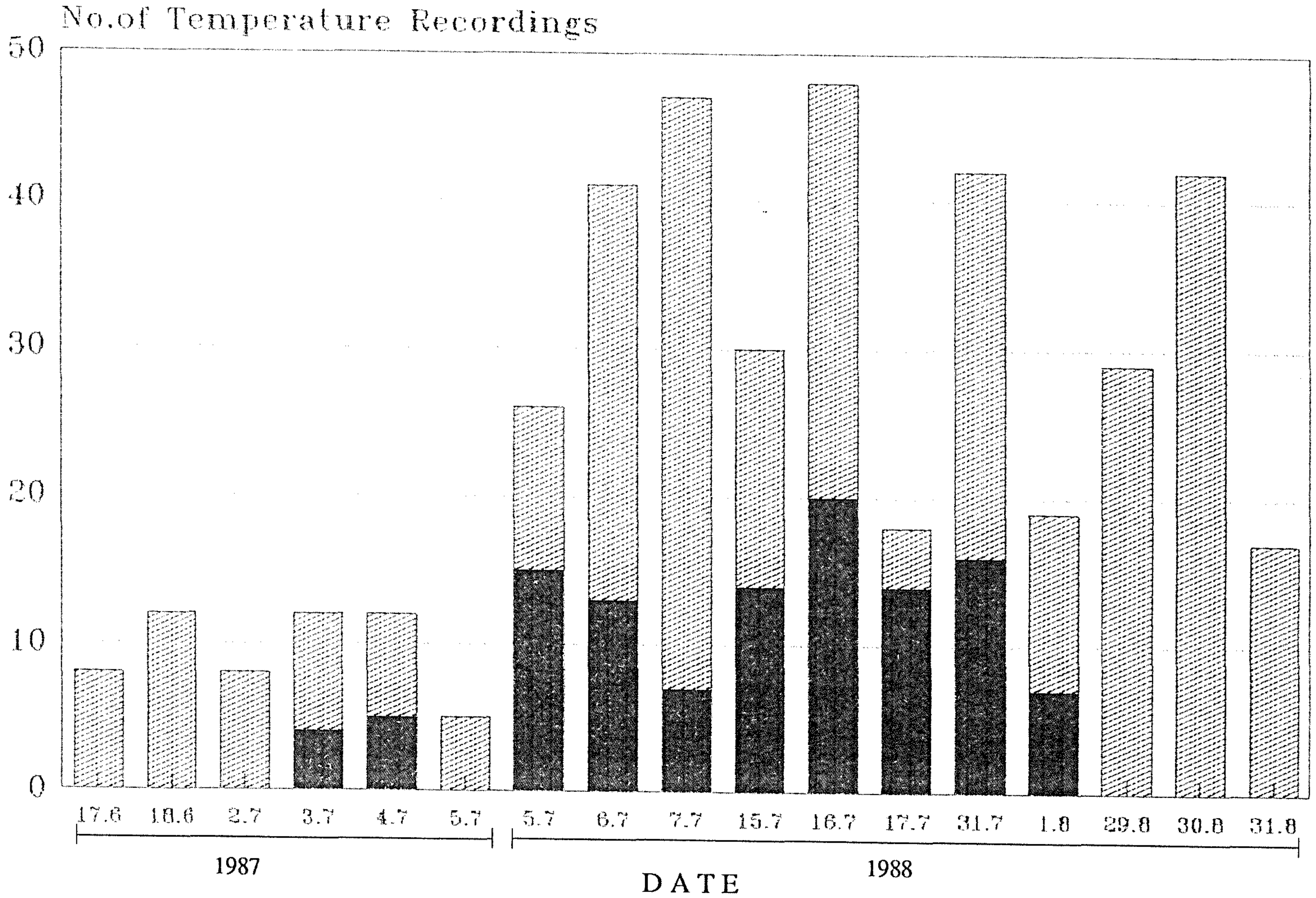


Fig. 3.11: **Daily records of temporal utilisation of thermally unlimiting conditions (i.e. periods when the heatlamp was on) for *Coronella austriaca* in the laboratory.** The columns indicate the number of body temperature measurements that were recorded during thermally limiting conditions. The shaded areas represent the proportion of body temperature measurements that were ≥ mean laboratory selected body temperature.

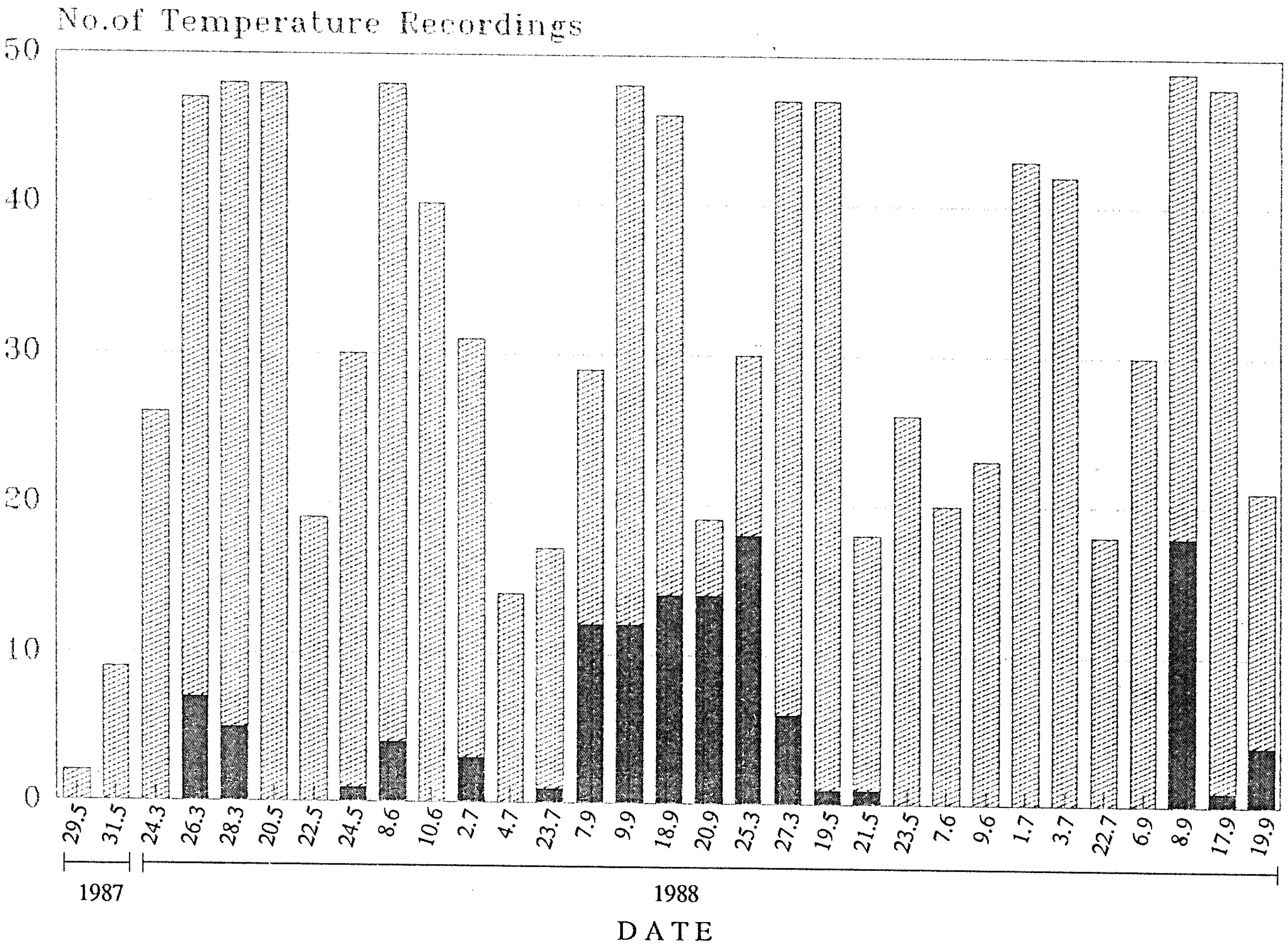


Fig. 3.12: **Daily records of temporal utilisation of thermally unlimiting conditions (i.e. periods when the heatlamp was on) for *Natrix natrix* in the laboratory.** The columns indicate the number of body temperature measurements that were recorded during thermally limiting conditions. The shaded areas represent the proportion of body temperature measurements that were ≥ mean laboratory selected body temperature.

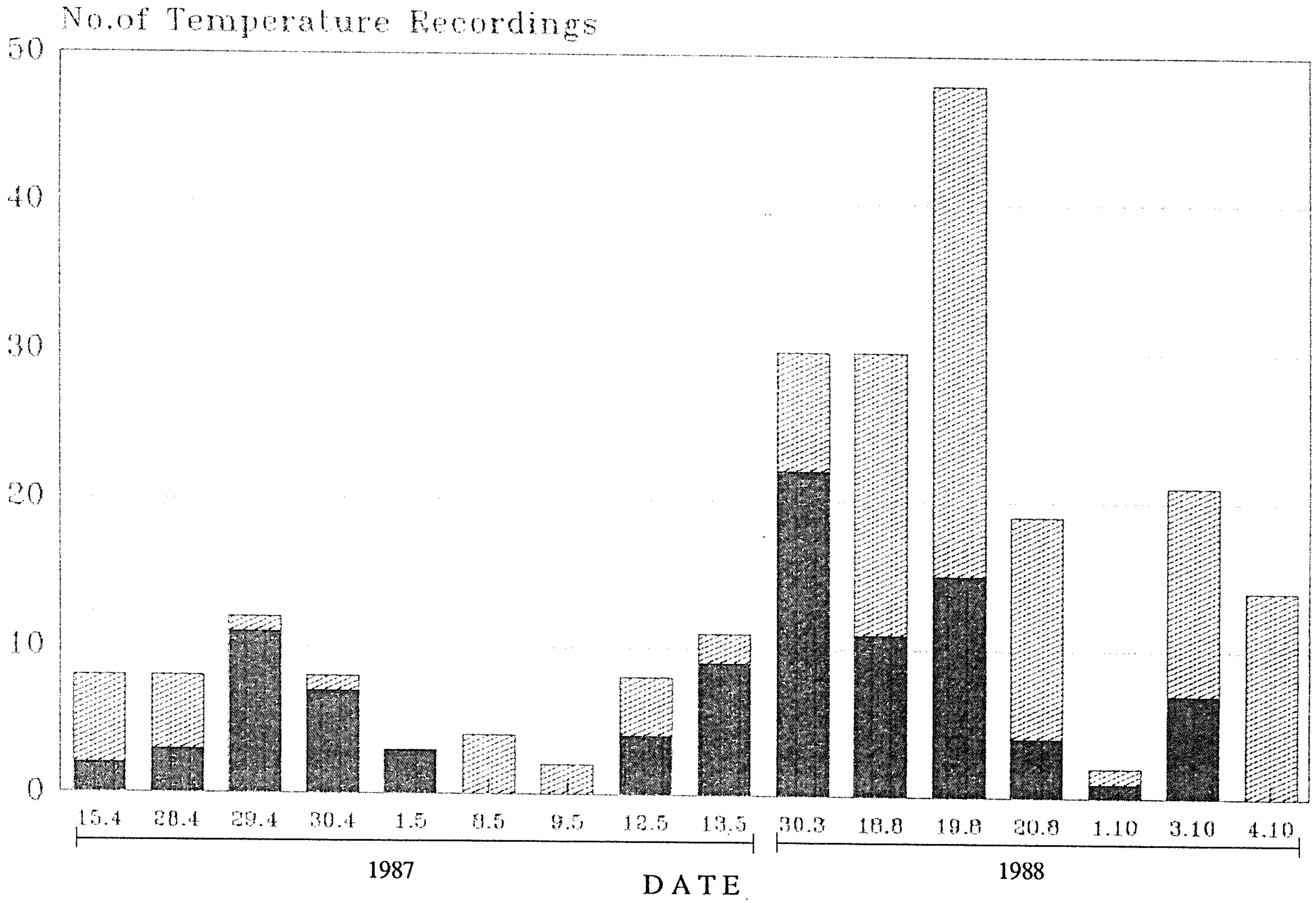


***Fig. 3.13:* Daily records of temporal utilisation of thermally unlimiting conditions (i.e. periods when the heatlamp was on) for *Vipera berus* in the laboratory.** The columns indicate the number of body temperature measurements that were recorded during thermally limiting conditions. The shaded areas represent the proportion of body temperature measurements that were ≥ mean laboratory selected body temperature.

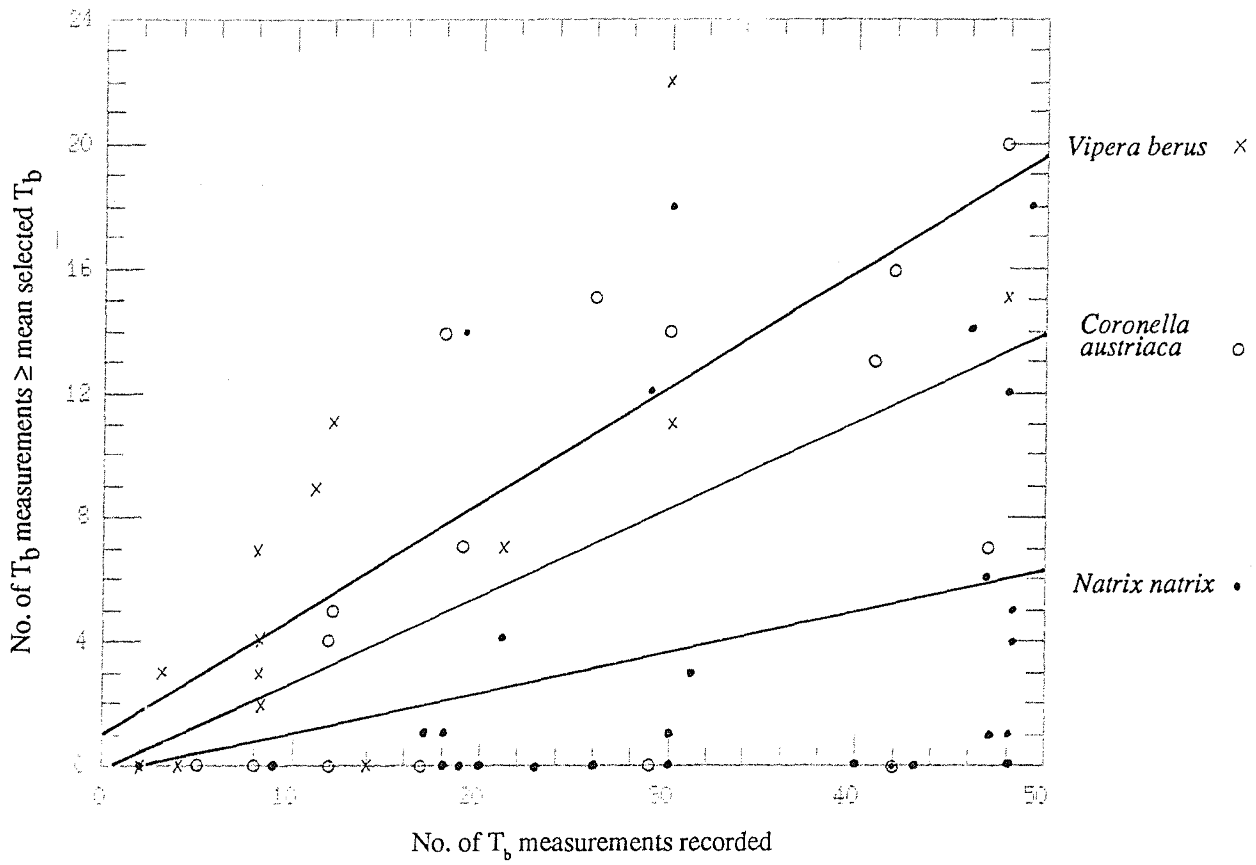


Fig. 3.14: **Regression lines of temporal utilisation of thermally unlimiting conditions for the 3 snake species in the laboratory.**
The daily number of body temperature measurements recorded during thermally unlimiting conditions is related to the number of those that were greater or equal to the mean laboratory selected body temperature.

n = 17 for *Coronella austriaca* n = 31 for *Natrix natrix* n= 16 for *Vipera berus*

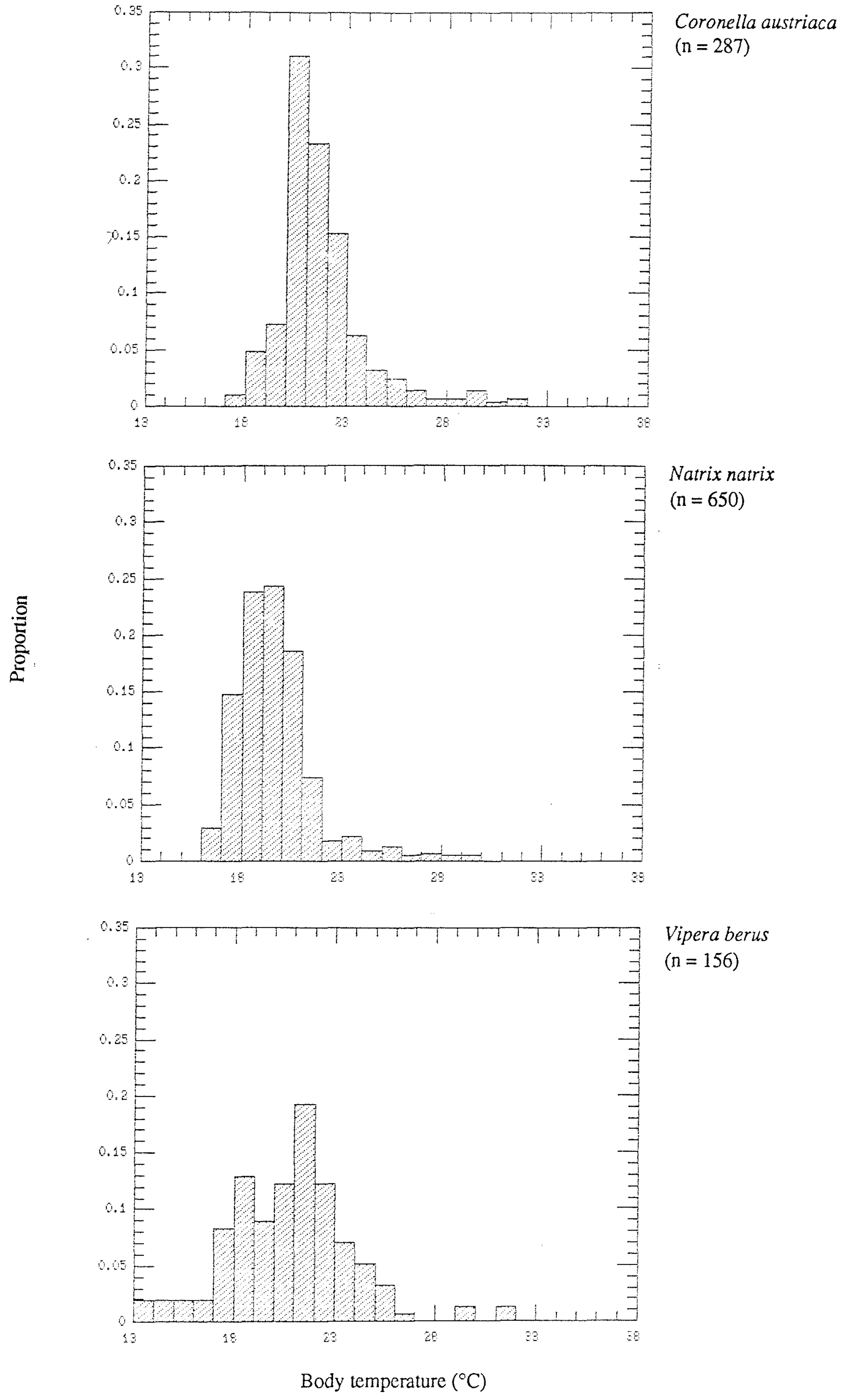


Fig. 3.15: Relative frequency distributions of snake body temperatures recorded in the laboratory arena during thermally limiting conditions (i.e. when the heatlamp was off).

	Thermally limiting conditions			Thermally unlimiting conditions		
	Coronella austriaca	*Natrix natrix*	*Vipera berus*	*Coronella austriaca*	*Natrix natrix*	*Vipera berus*
n	287	650	156	416	983	228
Mean	21.74	19.70	20.84	27.44	23.19	31.09
SD	2.21	2.03	3.08	4.63	5.15	3.84
Median	21.20	19.40	21.00	29.80	21.20	32.00
Max	31.4	29.4	31.9	35.3	37.1	37.2
Min	17.7	16.5	13.6	18.0	16.5	18.4
Skewness	1.748	1.798	0.507	- 0.660	0.797	- 1.157
t_s	12.088	18.710	2.585	- 5.496	10.196	- 7.133
p	***	***	**	***	***	***
Kurtosis	4.404	4.912	1.666	- 1.069	- 0.692	1.098
t_s	15.229	25.564	4.247	-4.449	-4.431	3.384
p	***	***	***	***	***	***

Table 3.10: **Summary statistics of snake body temperatures recorded in the laboratory.** The table is divided into thermally limiting conditions (when the heatlamp was off) and thermally unlimiting conditions (when the heatlamp was on). Details of skewness and kurtosis of the data are provided with tests of significance (statistic = t_s, Sokal and Rohlf, 1981).

NS = $p > 0.05$
* = $p < 0.05$
** = $p < 0.01$
*** = $p < 0.001$

Body Temperatures During Thermally Limiting Conditions

The pooled body temperature data recorded for each species during thermally limiting conditions in the laboratory arena are presented as relative frequency distributions in Fig. 3.15. Summary statistics of the data are given in Table 3.10.

The distributions of the 3 species were compared via a series of Kolmogorov-Smirnov two-sample Tests. A highly significant difference was found between smooth snakes and grass snakes ($z = 7.447$, $n_1 = 287$, $n_2 = 650$, $p < 0.001$), smooth snakes and adders ($z = 2.687$, $n_1 = 287$, $n_2 = 156$, $p < 0.001$) and grass snakes and adders ($z = 3.986$, $n_1 = 650$, $n_2 = 156$, $p < 0.001$).

A Kruskal-Wallis test was performed on the data and a significant difference was detected (chi-squared = 222.2, $n = 1093$, $p < 0.001$). A series of Wilcoxon/Mann-Whitney tests between each pair of species indicated that there was a significant difference for each combination ($U = 35543.0$, $n_1 = 287$, $n_2 = 650$, $p < 0.001$ between smooth snakes and grass snakes, $U = 18548.0$, $n_1 = 287$, $n_2 = 156$, $p < 0.01$ between smooth snakes and adders, $U = 35721.0$, $n_1 = 650$, $n_2 = 156$, $p < 0.001$ between grass snakes and adders).

The average of the daily mean body temperatures for smooth snakes was calculated as 21.8°C ± 1.60 ($n = 18$), for grass snakes 19.8° ± 1.79 ($n = 29$) and for adders 20.6°C ± 2.38 ($n = 16$).

Body Temperatures During Thermally Unlimiting Conditions.

Fig. 3.16 and Table 3.10 respectively present the relative frequency distributions and summary statistics of pooled snake body temperatures during thermally unlimiting conditions in the laboratory arena (i.e. when the heatlamp was on).

A Kolmogorov-Smirnov two-sample test was performed between each pair of species and significant differences in the distributions were detected in each case ($z = 7.056$, $n_1 = 416$, $n_2 = 983$ between smooth snakes and grass snakes, $z = 5.015$, $n_1 = 416$, $n_2 = 228$ between smooth snakes and adders, $z = 8.378$, $n_1 = 983$, $n_2 = 228$ between grass snakes and adders, $p < 0.001$ in all 3 cases).

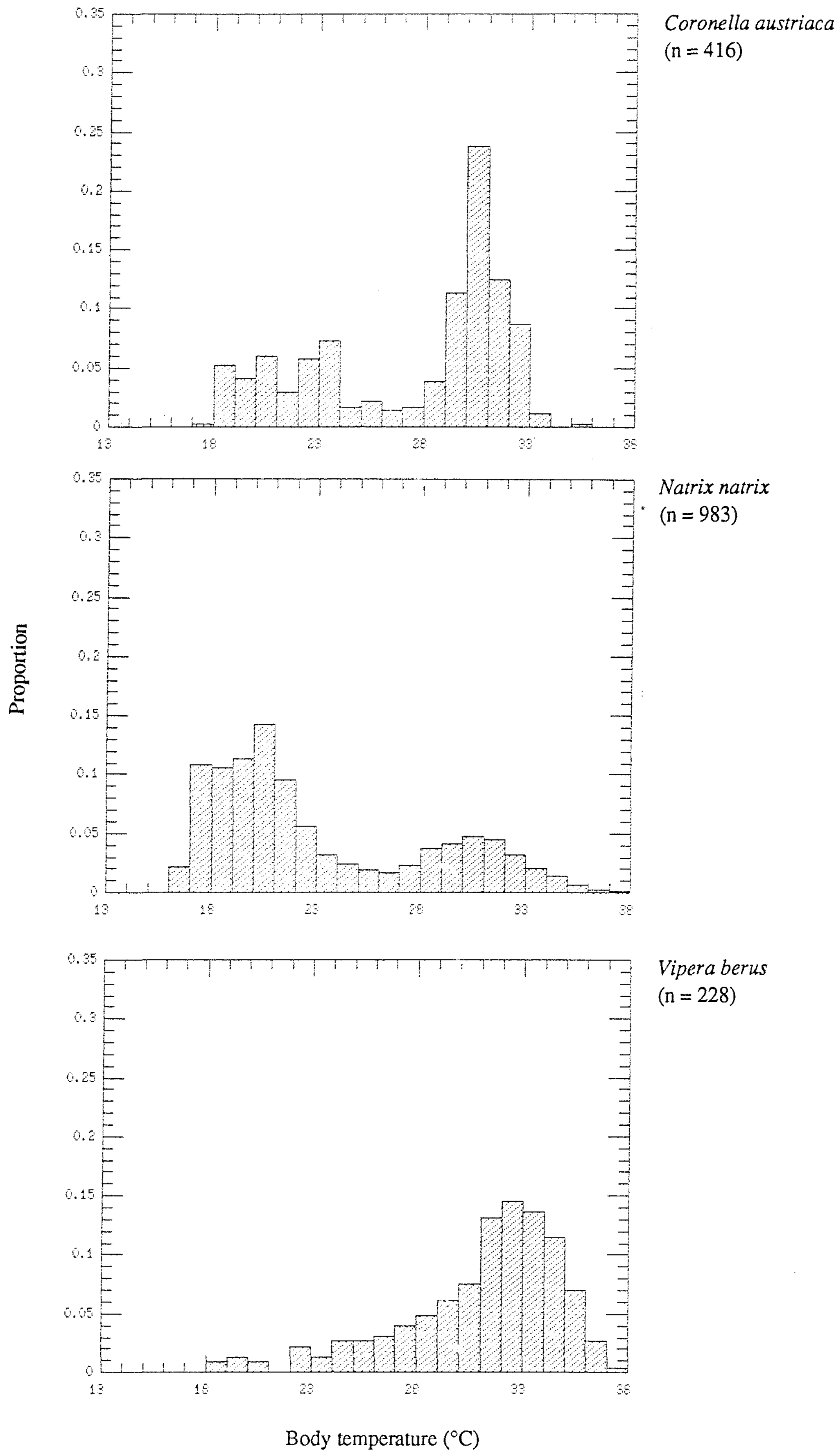


Fig. 3.16: Relative frequency distributions of snake body temperatures recorded in the laboratory arena during thermally unlimiting conditions (i.e. when the heatlamp was on).

A significant difference was detected when a Kruskal-Wallis test was applied to the body temperature data (chi-square = 425.3, $n = 1627$, $p < 0.001$) and this was followed up by a series of Wilcoxon/Mann-Whitney tests on the 3 pairwise combinations. Significant differences between the species was detected in each case ($U = 110789.0$, $n_1 = 416$, $n_2 = 983$ between smooth snakes and grass snakes, $U = 23660.5$, $n_1 = 416$, $n_2 = 228$ between smooth snakes and adders, $U = 28760.5$, $n_1 = 983$, $n_2 = 228$ between grass snakes and adders, $p < 0.001$ in all 3 cases).

The average of the daily means for the smooth snake data during thermally unlimiting conditions was 26.2°C ± 4.44 ($n = 17$), for grass snakes it was 22.9°C ± 3.41 ($n = 31$), and for adders, 30.7°C ± 3.45 ($n = 16$).

3.4. Discussion

3.4.1. Categorisation of Thermal Conditions and Body Temperatures

Simultaneous body temperature recording of the 3 species of snakes in neighbouring outdoor vivaria allowed a direct comparison between smooth snakes, grass snakes and adders to be made. Each vivarium was designed in exactly the same way, the aim being to provide a range of microhabitats and microclimates for the snakes. The assumption was made that each of the 3 vivaria had similar microclimates.

The number of occasions when direct comparisons were possible was limited. This was especially the case during 'unlit' periods when the automatic recording equipment was restricted to receiving temperature-sensitive radio-transmitter pulses from only 1 animal at a time. Therefore body temperature data were also compared between species from periods when the data were not recorded simultaneously. However, the effects of the variable thermal environment had to be taken into account when making such comparisons. In the case of one snake species having a lower mean body temperature than another, it was difficult to determine whether this was due to a difference in the behaviour or physiology of the 2 species, or if it was the result of more body temperatures being recorded during thermally limiting conditions and therefore preventing the snakes of the first species from achieving higher body temperatures.

For example, if all the body temperature measurements from the 'lit' periods (see Section 3.2.1, 'Thermal Conditions') of the outdoor vivaria experiments are averaged, the mean body temperature of smooth snakes is found to be 22.0°C ± 6.90 (range 7.7 - 38.6°C, n = 1586), for grass snakes 20.6°C ± 7.42 (range 2.8 - 37.1°C, n = 1435) and for adders 21.9 ± 9.35 (range 2.2 - 39.9°C, n = 2178). However, it is difficult to state whether the lower body temperature result of grass snakes is an indication of behavioural or physiological differences between the species or the result of a greater proportion of measurements taken during thermally limiting conditions. The use of animal thermometers to estimate operative temperatures meant that it was possible to identify periods when the snakes would or would not be limited in maintaining selected body temperatures in the vivaria.

The definitions of the thermoregulatory terminology used in this chapter have been described in Section 3.1.1. The categorisation of environmental conditions are described in Section 3.2.1 for the outdoor vivaria experiments and Section 3.2.2 for the laboratory experiments. At this point it is worth considering some of the definitions more carefully. As stated before, 'laboratory' and 'field selected body temperatures' were calculated from the 'plateau phase' patterns (Peterson, 1982, 1987) exhibited by the snakes when they were maintaining their body temperatures at relatively precise levels during thermally unlimiting conditions. Lillywhite (1980) and de Bont et al. (1986) also used similar criteria to describe selected body temperatures (or 'thermal preferenda' as they described the selected temperatures). However, it should be noted that Pough and Gans (1982) defined the mean selected temperature as the arithmetic mean of body temperatures measured in a laboratory temperature gradient or equivalent apparatus providing conditions that would permit an animal to extend its body temperature above and below the activity range.

During the outdoor vivaria experiments, mean body temperatures were calculated from periods when conditions were considered to be thermally unlimiting. This being the case, these temperatures might be considered to be a better representation of selected body temperatures (than 'plateau' temperatures) as defined by Pough and Gans. In fact, there were several reasons why it was decided that they differed from the results that might be expected from a laboratory thermal gradient. In the outdoor vivaria conditions were described as thermally unlimiting when maximum model temperatures indicated that the snakes could reach selected body temperatures. However, those conditions only applied to certain areas within the vivaria (generally those areas in the direct sun) and the snakes had to be in those areas to achieve the selected temperatures.

For example, in early spring the nights were often cold and the model temperatures sometimes dropped to below 0°C. Snake body temperatures also dropped considerably during such conditions, the minimum body temperature recorded was 2.0°C in the case of a adder specimen (Vb6 on 3.4.89). In a laboratory thermal gradient snakes never 'voluntarily' select such low temperatures. In the morning, if the day was clear and sunny, the model temperatures in the sunny areas of the vivaria could increase to 37°C or more. Therefore at such times the conditions were described as thermally unlimiting as there was the potential situation for snakes to bask in the sun and achieve selected body temperatures. However, the snake first had to reach the 'hot' area to maintain such body temperatures. Model temperatures in other parts of the vivaria still in the shade could still be comparatively low. A snake in a 'cold' area of a vivarium could only raise its body temperature by moving to the 'hot' areas if it was capable of detecting such environmental conditions were available or coming across the area during foraging/exploratory activity.

It is possible that if the animals had been more familiar with their environments, then the snakes might have basked in thermally unlimiting areas (i.e. sunny areas) more often. An analysis of shell temperatures of the tortoise Testudo hermanii was made by Chelazzi and Calzolai (1986). They discovered that tortoises resident in the authors' study area behaved as homoiotherms whereas animals imported from a similar microenvironment appeared relatively poikilothermic. This supported the view that a familiarity with the microenvironment facilitated the behavioural thermoregulation of the tortoises. The snakes in the present study were only in the vivaria for a maximum period of 12 days and so would have been relatively unfamiliar with their microenvironment. However, the vivaria were relatively small areas for the snakes to explore.

Thus body temperature data recorded during thermally unlimiting conditions included measurements of snakes which might have been in 'cold' areas of the vivarium and may not have been aware of the 'hot' areas available. Although a thermal gradient of sorts was available at such times it was not a gradual thermal gradient that might be expected in a laboratory situation. Instead the operative temperatures were often more 'patchy' between microhabitats, especially during times of great thermal contrasts (e.g. sunny April morning after a cold night). The effect of these factors would be to decrease overall mean body temperature values as it would be unlikely that snakes were always aware when thermally unlimiting conditions existed, especially in the mornings.

The problem of varying thermal conditions was not as severe when comparing species body temperatures from the laboratory experiments. The thermal regime was kept as similar as possible between the 31 experiments. Minimum recorded shade air temperatures ranged from only 15 - 21.5°C (during the 31 experiments) and the maximum sand temperatures directly beneath the heatlamp (when it was on) indicated that thermally unlimiting conditions were available for the snakes. The thermal conditions were still 'patchy' with a hot spot directly underneath the heatlamp. The same criteria used to describe 'field selected body temperatures' were used to describe 'laboratory selected body temperatures' to allow comparisons to be made.

3.4.2. Related Body Temperature Recording

During the periods when it was possible to simultaneously record data from 2 or all 3 species in the outdoor vivaria, environmental conditions varied considerably. However, at any one time, the snakes in neighbouring vivaria were subject to the same environmental conditions and therefore direct comparison could be made.

It was not possible to make direct comparisons between snake body temperatures during nocturnal periods but data from 0700 hours until 1915 hours were available. Higher body temperatures were recorded from adder specimens than from either grass snakes or smooth snakes. This result was found in the series of 3 comparisons when data from 2 species were available (Tables 3.4, 3.5, 3.6) and in the tests involving data recorded from all 3 species simultaneously (Table 3.7).The maximum body temperatures that adder attained on a daily basis and overall were also higher than the other 2 species . However, there did not appear to be a significant difference between the body temperatures of smooth snakes and grass snakes.

The overall median body temperatures were low when compared with field selected body temperatures. The highest overall median body temperature was that of adders (24.85°C) from the comparison with smooth snakes. Overall median body temperatures were low due to limiting thermal conditions on some occasions. For instance on 24.4.89, the maximum recorded model temperature in the vivaria was 11°C and the median body temperatures recorded on that day were 10.75°C for the smooth snake, 7.75°C for the grass snake and 7.95°C for the adder.

Most of the frequency distributions of pooled body temperatures from the above tests are bimodal to a degree. The distribution of pooled adder data in the comparison with smooth snakes is bimodal and skewed to the left. (Fig. 3.2). The lower peak probably corresponds to body temperatures recorded during thermally limiting conditions, the upper peak to body temperatures recorded when conditions were not so limiting and the snakes could maintain selected body temperatures. Note that the mode category of the upper peak lies between 30-32°C, which is close to the mean field selected body temperature (33.2°C). The distribution of smooth snake body temperatures taken simultaneously is also slightly bimodal but not skewed. The mode category of the upper peak lies between 26-28°C but is more flattened suggesting that the snakes did not maintain body temperatures as precisely as adder during the more thermally unlimiting periods.

3.4.3. Selected Body Temperatures and Body Temperatures Recorded During Thermally Unlimiting Conditions

The mean selected body temperature of smooth snake was calculated as 30.3°C ± 1.64 (n = 377) in the outdoor vivaria and 30.8°C ± 1.25 (n = 241) in the laboratory. These results are similar to the observations of de Bont et al. (1986) who described smooth snakes as having a 'thermal preferendum' (equivalent to 'selected body temperature' in this study) of 29-33°C. They used radio telemetry to monitor the stomach temperatures of free-ranging snakes. Gent (1988) calculated a mean selected body temperature of 29.6°C ± 3.15 (range 19.0 - 38.0°C, n = 324) in a laboratory thermal gradient. The larger standard deviation of Gent's results could be attributable to the fact that he calculated a mean body temperature from all available measurements in the gradient rather than from 'plateau phase' body temperatures which are maintained by the snakes with relatively greater precision.

The standard deviation values of the mean selected body temperatures give an indication of the precision with which the snakes maintained body temperatures during the 'plateau' phase of body temperatures. In both the outdoor vivaria and the laboratory experiments, these values were smallest for smooth snakes suggesting that they maintained body temperatures with the greatest degree of precision at such times. This aspect is discussed further in Chapter Five.

Spellerberg and Phelps (1975) investigated the selected body temperatures of 2 individual smooth snake specimens. The first specimen maintained mean body temperatures of 25.8°C (range 11.0 - 36.0°C) during the day and 25.8°C (range 10.0 - 34.0°C) during the night.

Mean temperatures for the second specimen were 28.4°C (range 23.0 - 33.0°C) during the day and 19.8°C (range 10.0 - 31.0°C) during the night. In another study, a selected mean body temperature of 27.0°C (range 20 - 34°C, n = 3 snakes) was recorded by Spellerberg (1976). These values were lower than those recorded in the later studies described in the above paragraph. As Gent (1988) pointed out, in the Spellerberg and Phelps (1975) study, the body temperatures were recorded using thermistor probes implanted above the heart. Bartholomew (1982) has noted that thermal gradients can exist along the body lengths of snakes and so a direct comparison between the results reported in this study and those of Spellerberg and Phelps (1975) should be made cautiously.

When conditions that were considered to be thermally unlimiting were available to smooth snakes, mean body temperatures of 27.2°C ± 5.84 (range 9.1 - 35.5°C, n = 525) were recorded from the outdoor vivaria and 27.4°C ± 4.63 (range 18.0 - 35.3°C, n = 416) from the laboratory experiments. Minimum environmental temperatures in the laboratory arenas (sand and ambient air temperatures) were not as low as minimum model temperatures recorded in the outdoor vivaria. Therefore snake minimum body temperatures varied considerably between the laboratory and outdoor studies. However, in both situations maximum environmental temperature were high (≥37°C). Therefore it was to be expected that similar maximum body temperatures were recorded from the laboratory and outdoors as snakes were able to maintain selected body temperatures. Note that the mean body temperature values are lower than the mean selected body temperature values as was predicted in Section 3.4.1.

The selected body temperatures of grass snakes were found to differ significantly from those of smooth snakes in the outdoor vivaria (mean 29.3°C ± 2.63, n = 291) and in the laboratory (mean 31.0°C ± 2.10, n = 189). A previous study by Spellerberg (1976) found that grass snakes in a laboratory thermal gradient selected mean body temperatures of 26.0°C (range 15 - 36°C, n = 3 snakes). The discrepancy is again likely to be due to my values being calculated from 'plateau' temperatures and Spellerberg's values /from all body temperature measurements while the snakes were in the thermal gradients.

When conditions were considered to be thermally unlimiting, a mean body temperature of 26.6°C ± 5.78 (range 2.8 - 37.1°C, n = 375) was recorded in the vivaria and 23.2°C ± 5.15 (range 16.5 - 37.1°C, n = 983) in the laboratory. Once again, minimum environmental temperatures that were also available during these periods were sometimes much colder in the vivaria than in the laboratory, hence the lower minimum body temperatures from the former experiments. Hailey and Davies (1986) reported a mean body temperature of 26.0°C ± 3.1 (range 23.2 - 30.4°C, n = 6) of basking grass snakes in Spain although conditions might not have been thermally unlimiting when these measurements were recorded.

In both the outdoor vivaria and laboratory, mean selected body temperatures of adders were higher and significantly different to those of the other 2 species (mean 33.2°C ± 1.86, n = 491 and 32.5°C ± 2.27, n = 159 respectively). This was also the case for mean body temperatures calculated from thermally unlimiting conditions (29.3°C ± 7.60, range 4.8 - 39.9°C, n = 576 and 31.1°C ± 3.84, range 18.4 - 37.2°C, n = 228 respectively). A selected mean body temperature of 30.0°C (range 20 - 38°C, n = 2 snakes) was measured for adder specimens in a thermal gradient in the study of Spellerberg (1976). Saint Girons (1978) recorded the body temperatures of adder specimens in outdoor vivaria in relation to the stage of food digestion. He took measurements during sunny periods only and therefore assumed that conditions were probably sufficiently unlimiting to allow the snakes to attain selected body temperatures on most if not all of the occasions. Mean body temperatures of 31.84°C (n = 21) and 33.24°C (n = 17) were recorded on the day that the snakes were fed with mice, and 31.92°C (n = 21) 4 days later. Snakes in an absorptive condition have often been observed to display a thermophilic response (Greenwald and Kanter 1979, Regal 1966). As none of the adder specimens in the present study were thought to be in an absorptive condition, the results are not directly comparable with those of Saint Girons (1978).

3.4.4. Body Temperatures from Thermally Limiting Conditions During Lit and Unlit Periods

In the outdoor vivaria it was possible to define periods which were thermally limiting for the snakes during the 'lit' phase of the day. There was no equivalent category in the laboratory experiments as whenever the heatlamp was on (the 'lit' phase) conditions were always considered to be thermally unlimiting. Mean body temperatures were much lower during such conditions in the outdoor vivaria than when conditions were limiting. The mean body temperature of smooth snakes was 18.9°C ± 5.47 (range 7.7 - 34.5°C, n = 825), for grass snakes 18.2°C ± 6.71 (range 2.8 - 34.8°C, n =733) and for adders 19.1°C ± 8.19 (range 2.2 - 36.6°C, n = 1059). No significant difference was found between the results although care should be taken making comparisons. Although model temperatures were always <34°C in this category, there may have been a disproportionate number of body temperatures of one species recorded during periods when model temperatures were significantly higher than those when another species' body temperatures were measured.

Although conditions were considered to be thermally limiting, the body temperatures that were recorded during these periods were sometimes higher than the mean selected body temperatures for all 3 species (although the maximum body temperatures were not as high as those recorded in thermally unlimiting conditions). This could partly be a result of the limitations of the models which estimated operative temperatures. In Section 2.4.3 it was stated that the 'Squirrel' loggers averaged 100 model readings over the previous 30 minutes and recorded that value. It may have been that there were brief spells of thermally unlimiting conditions of only a few minutes in duration resulting in high body temperatures. However, when the model readings were averaged out over 30 minutes the overall recorded value would have indicated that conditions were thermally limiting. In addition, periods of unlimiting thermal conditions could have been followed by periods of limiting thermal conditions and snakes that had been maintaining high body temperatures during the former period may have used behavioural means to conserve body heat and keep body temperatures relatively high. Insulation of body heat could have been achieved through body coiling. Staying in contact with a warm substrate could also have kept body temperatures high.

During unlit conditions, body temperatures were monitored in the outdoor vivaria and the laboratory. Mean body temperatures of the 3 species were lower in the outdoor vivaria (15.7°C ± 4.23, range 7.0 - 34.7°C, n = 1075 for smooth snakes, 13.5°C ± 3.00, range 6.0 - 23.8°C, n = 486 for grass snakes, 12.2°C ± 4.78°C, range 2.0 - 35.1°C, n = 1068 for adders) than in the laboratory (21.7°C ± 2.21, range 17.7 - 31.4°C, n = 287 for smooth snakes, 19.7°C ± 2.03, range 16.5 - 29.4°C, n = 650 for grass snakes, 20.8°C ± 3.08, range 13.6 - 31.9°C, n = 156 for adders). Once again comparison between species from the outdoor vivaria experiments should be treated cautiously as thermal conditions varied between occasions on which body temperatures were monitored. Maximum body temperatures were relatively high as there were occasions when snakes maintained high body temperatures during thermally unlimiting conditions until the vivaria moved into shadow or the heatlamp turned off in the laboratory. These changes meant that conditions were then categorised as unlit but body temperatures remained relatively high before eventually decreasing.

3.4.5. The Ecological Significance of Body Temperatures

Adders selected higher body temperatures than the other 2 species investigated in this study. Mean selected body temperatures were higher as were maximum recorded body temperatures of the adders. The maximum body temperatures recorded in the laboratory and the outdoor vivaria during thermally unlimiting conditions can be compared to voluntary maximum (or 'maximum tolerated') temperatures measured in thermal gradients (the temperature at which an animal moves to seek a site where cooler body temperatures can be maintained)

The highest body temperature for adders of 39.9°C was recorded on 3.5.89 (specimen Vb10). In fact all the data used in the analysis for this chapter have come from the measurements taken at 15 minute intervals. Five minutes after the measurement of 39.9°C was recorded, the body temperature was measured at 40.4°C, the highest recorded body temperature for this species. However, 5 minute intervals were not used in the overall analysis and therefore the body temperature of 40.4°C was not included. This temperature probably represented the maximum tolerated temperature as the snake must have moved away around the time the measurement was taken. Within an hour its body temperature was down to 29.8°C before increasing again and levelling off around 32 - 34°C. Maximum model temperatures were >40.0°C throughout this period.

The highest body temperature recorded for smooth snakes during unlimiting thermal conditions in the vivaria or in the laboratory was 35.5°C. There was another occasion when the maximum model temperatures were unknown in the outdoor vivaria and so the data were not used in the analysis. On 14.8.88, specimen Ca6 reached a body temperature of 38.6°C at 1745 hours and 1815 hours. This is thought to be the highest recorded body temperature for this species. Maximum operative temperatures available in the vivaria were known up until 1630 hours and the highest value had only been around 24°C until then. Presumably there was a sunny period later in the afternoon when a snake basking in the south-eastern area of the vivarium could have raised its body temperature. Unfortunately there were no models in a position to estimate operative temperatures in this microhabitat at the time.

The maximum recorded body temperatures of 37.1°C for grass snakes were also the highest recorded temperatures for the species. It should not be totally unexpected that the highest maximum body temperatures recorded have been observed in this study. The number of body temperature measurements recorded during the project have been very large. Because maximum recorded temperatures are likely to represent maximum tolerated temperatures, they are usually not maintained for very long periods before the snakes move to sites where cooler body temperatures can be maintained. It follows that the probability of measuring a body temperature when a snake is close to its maximum tolerated temperature increases with the number of samples that are taken.

Not only was the overall maximum recorded temperature of the adder higher than that of the other species but maximum temperatures were also higher on a daily basis. For example, in the paired comparison tests, the maximum body temperatures recorded for adders were higher than smooth snakes on 15 of the 18 days (83% of days, Table 3.5) and higher than grass snakes on 20 of the 24 days (83% of days, Table 3.6). The difference between smooth snakes and grass snakes was not so evident with the latter having higher maximum body temperatures than the former on 12 of the 21 days (57% of days, Table 3.4).

Minimum temperatures recorded in the experiments of the present study could not be so readily related with voluntary minimum temperatures measured in a laboratory gradient. The reasons for this have already been explained in this discussion. There was also a problem with the reliability of transmitters at very low temperatures. They were usually calibrated down to about 7°C as below that level some transmitters ceased to function. Therefore the minimum temperatures that the snakes might have reached were not recorded on some occasions. For instance, the minimum recorded body temperature of smooth snakes was 7.0°C (Specimen Ca7 on 26.4.89 in the outdoor vivaria). The body temperature of this particular specimen probably decreased even lower that night as surface model temperatures dropped to -5.0°C. However, the reliability of the particular transmitter that was attached to the snake could not be relied upon below 7.0°C and so measurements lower than 7.0°C were not used. The minimum recorded body temperature of grass snakes was 2.8°C and for adders 2.0°C. However, on both the occasions that these were recorded, although the reliability of the transmitters could be relied upon down to those temperatures, their accuracy could not be relied upon at lower levels. It is therefore possible that the snakes' true minimum body temperatures could have been lower.

Gent (1988) determined the mean critical temperature of smooth snakes as 1.98°C. Using a different methodology, the mean critical temperature of the same species in a study by Spellerberg (1976) was recorded as 3.5°C. Critical minimum temperatures are those body temperatures at which ectotherms lose their power of locomotion and they reflect the degree to which ectotherms are adapted to cold climates. Body temperatures were not recorded as low as the critical temperatures for smooth snakes in the present study although they might have occurred on cold, early Spring nights.

Spellerberg (1976) also recorded mean critical temperatures of 3.9°C for grass snakes and 3.0°C for adders. Minimum body temperatures lower than these temperatures were recorded in the outdoor vivaria. The snakes which were determined as having these low body temperatures would have probably lost their power of locomotion. If their body temperatures had dropped further to the 'lethal minimum temperatures', they would have run the risk of suffering physiological damage. They would also be unable to escape predators and so the minimum critical temperature has been described as an ecologically lethal temperature for an animal that has not found shelter (Pough and Gans 1982).

A distinct pattern emerges in the distributions of body temperature data examined in the laboratory and outdoor vivaria. Distributions of body temperature data from periods when environmental conditions varied tended to be bimodal. This was observed in the paired comparison test data of the outdoor vivaria and has been mentioned before in the discussion. One peak of the bimodal distribution tends to correspond to body temperatures recorded during thermally limiting periods, the other to body temperatures maintained during thermally unlimiting periods. This can be seen more clearly when the body temperature distributions of thermally limiting and unlimiting conditions are viewed separately.

Distributions from thermally unlimiting conditions tend to have a modal category in the 29 - 33°C zone, are heavily skewed to the left, and are leptokurtic (Figs. 3.10, 3.16). This type of pattern has been observed in thermal studies of lizards and attributed to the observation that optimal temperatures are apparently close to the critical maximum and upper lethal limits (Dawson 1975). Distributions from thermally limiting conditions during lit periods (outdoor vivaria only) were skewed to the right in the case of smooth snake and adder data, platykurtic but with a modal category in the 15 - 17°C zone (Fig. 3.9). The distributions of data from the unlit periods were all skewed to the right, leptokurtic with modal categories in the 19 - 20°C zone for the video experiments and 11 - 15°C zone in the outdoor vivaria experiments (Figs. 3.8, 3.15). The body temperatures of snakes during low temperature conditions have been largely ignored in the past as there has been a bias towards recording from active snakes on warm days (Peterson 1987). However, thermally limiting conditions were found to occur for most of the time that monitoring was undertaken in the present study and so play an important part in snake ecology.

The body temperature distribution data of adders during thermally unlimiting conditions were more skewed to the left than that of the other 2 species in both outdoor and laboratory situations. The modal category was also higher in the case of adders (32 - 34°C in the outdoor vivaria, 31 - 33°C in the laboratory). This again reflects the higher body temperatures that adders were observed to maintain. The body temperature distribution of smooth snakes in turn was more skewed than that of grass snakes. In the laboratory investigation, the distribution of the grass snake data was actually positively skewed and slightly bimodal, with the modal category in the 20 - 21°C zone (and the modal category of the upper temperature region of the distribution at 30 - 31°C). It is difficult to say why this should be the case in the laboratory compared to the outdoor vivaria situation where the grass snake data were negatively skewed. Grass snake specimens were observed to forage on many occasions (Chapter Four) and during such behaviour in the open, they would have been exposed to thermally unlimiting conditions in a great proportion of the vivarium, especially during midday periods. Therefore their body temperatures would be relatively high although they would not actually be basking in a stationary position. In the laboratory, the only thermally unlimiting area was underneath the heatlamp and so during foraging, a snake would be in cooler areas of the arena throughout most of its journey. The result of this might be that in the outdoor vivaria, foraging grass snakes could maintain relatively higher body temperatures than foraging grass snakes in the laboratory, hence the difference in distributions.

An important question to raise is what is the actual significance of the temperatures that were recorded? Physiological performances of snakes will vary with body temperature. At a certain 'optimal' temperature, a particular physiological function will perform at maximal levels. This will affect the overall performance of the 'whole-animal' and therefore the fitness of the snake. To assess optimal temperatures for the purposes of an ecological study, it is better to examine the performances of the whole-animal rather than specific cellular or biochemical processes (Huey 1982). For example, an examination of animal sprint speeds at varying temperatures will probably give a more realistic impression of the ecological importance of temperature than a study of muscle fibre action.

Where information on thermal performance has not been available, optimal temperatures have been estimated from the mean selected body temperatures measured in laboratory thermal gradients. Dawson (1975) concluded that the information available for lizards suggested that many physiological processes (e.g. auditory sensitivity, digestion, immunological response) proceeded optimally near the mean selected body temperature in many species.

The temperature range for mid-level performance has been described as the 'thermal performance breadth' (Huey 1982). Estimates of this can be gained from activity temperatures. For example, the 'activity temperature range' (Pough and Gans 1982) was described as the body temperatures at which a free-ranging animal engages in its ordinary routine. The latter term was derived from the 'normal activity temperature range' of Cowles and Bogert (1944). Another similar term, the 'voluntary temperature range', was used by Spellerberg (1976, after Brattstrom 1965) and defined as the range of body temperatures between the voluntary minimum and voluntary maximum temperature. Huey (1982) described several indirect estimates of thermal performance breadth, for example the variance of activity temperatures or the range among mean activity temperatures.

The mean selected body temperatures of smooth snakes, grass snakes and adders were all relatively high. There are few records where performances of these species have been directly measured at varying temperatures. Hailey and Davies (1986) measured the burst speeds of grass snakes at 5°C intervals and found them to be greatest at 30°C. This is close to the mean selected body temperatures of the grass snakes studied in this project but it should be noted that Hailey and Davies used the subspecies Natrix natrix persa (from Greece) in their study. The influence of varying temperatures on the gastric digestion of grass snakes (from Warsaw, Poland) was investigated by Skoczylas (1970). Digestion rates were measured at 5°C, 15°C, 25°C and 35°C. The fastest rates were found at 25°C. At 35°C digestion occurred at the same or a slightly slower rate. The body temperature categories were rather broad but they do suggest that digestion was fastest in the region of the mean selected body temperatures measured in the current study.

Many physiological performance parameters are therefore likely to be greatest when the snakes are able to maintain body temperatures at selected levels. However, to examine the relationship of body temperature to activity, the body temperatures that the snakes exhibited while engaged in different types of behaviour in the outdoor vivaria are investigated in more detail in Chapter Four.

3.4.6. Temporal Utilisation

A noticeable aspect of the data collected regarding the estimated operative temperatures available to the snakes in the outdoor vivaria was the proportion of time that conditions were considered to be thermally limiting for the 3 species of snakes. For example on the days that body temperatures were collected for smooth snakes, conditions were judged to be thermally unlimiting for the snakes during only 39% of the time. These values are calculated from only the 'lit' periods and do not take account of the 'unlit' periods (which includes night time) which were always recorded as being thermally limiting. For grass snakes and adders, conditions were thermally unlimiting for 31% of the time. These values varied on a daily basis throughout the experiments (from 0% to 100%). During the experimental period, body temperatures were recorded irrespective of the weather conditions and so the overall data probably gives a fair representation of operative temperatures in the 1988 and 1989 snake activity seasons.

Peterson (1987) noted that the garter snakes he was studying (Thamnophis elegans vagrans) were also constrained by the thermal conditions that were available to them. He considered a model temperature of >30°C to indicate conditions were thermally unlimiting but such conditions were measured on only 23 of 39 days of monitoring. Because of such constraints, mean body temperature records of ectotherms studied in the field are often likely to be underestimates of selected body temperatures. Gent remarked on this when commenting on the discrepancy between the mean body temperature of 23.48°C ± 3.95 (n = 327) of smooth snake in the field and the selected body temperature of 29.6°C ± 3.15 (n = 324) in a laboratory thermal gradient. This was also observed in the present study when overall mean body temperatures during 'lit' conditions were found to be considerably lower than mean selected body temperatures. Measurements of the body temperatures of captured ectotherms in the field are also likely to be biased towards those animals that are easy to catch. Ectotherms that are relatively hot tend to be more difficult to catch as they have quicker reactions and are faster. They may also be hidden from view away from extreme environmental temperatures that would otherwise cause them to overheat. During cold conditions ectotherms would again be more likely to be under cover. Biotelemetric studies permit a constant monitoring of body temperatures throughout varying environmental conditions.

When conditions were thermally unlimiting, mean body temperatures were markedly higher as has already been discussed. Because conditions usually were limiting in the outdoor vivaria, the opportunities for the snakes to maintain selected body temperatures were restricted. Therefore, the ability to utilise thermally unlimiting conditions when they did occur is a potentially important factor in snake thermoregulation. Adders select higher body temperatures than either of the other 2 species, and therefore the duration of conditions that this particular species finds thermally unlimiting (>37°C) is less. Grass snakes were considered to be thermally unlimited at temperatures >35°C and smooth snakes at >34°C.

The temporal thermal utilisation of the snakes was compared by calculating the proportion of body temperatures recorded during thermally unlimited conditions that were equal or above the mean selected body temperature for each species. An analysis of the overall data suggested that adders were able to maintain selected body temperatures during these periods for the greatest proportion of time (43% of the time in laboratory experiments, 42% in the outdoor vivaria). This was followed by smooth snakes (28% in the laboratory, 36% in the outdoors) and finally grass snakes (12% in the laboratory, 30% in the outdoors). Adders also attained selected body temperatures (i.e. ≥ mean selected body temperature) for greater proportions of time when conditions were thermally limiting in the outdoor vivaria. The big difference between the laboratory and outdoor values of grass snakes was again probably due to the extensive foraging behaviour that the species displayed. Foraging in the laboratory arena was more likely to take place in thermally limiting areas than foraging in the outdoor vivaria.

Therefore, although adders had a higher mean selected body temperature than the other species and conditions were usually thermally poor, it made more use of the periods when operative temperatures were high and maintained selected body temperatures for longer periods. The daily data analysed in the regressions (Fig. 3.7) reinforced the above conclusion. How the adders and other snakes achieved such body temperatures, and the relationship between the thermal environment and overall behaviour and ecology, is investigated in the next two chapters.

3.5. Summary

(i) Selected body temperatures were considered to be those temperatures maintained at relatively precise levels after an initial heating phase and before a cooling phase (the 'plateau phase', Peterson 1982, 1987) by the snakes during thermally unlimiting periods. The mean selected body temperature of smooth snakes was 30.3°C ± 1.64 (n = 377) in the outdoor vivaria and 30.8°C ± 1.25 (n = 241) in the laboratory. The mean selected body temperature of grass snakes was 29.3°C ± 2.63 (n = 291) outdoors and 31.0°C ± 2.10 (n = 189) in the laboratory. For adders the results were 33.2°C ± 1.86 (n = 491) outdoors and 32.5°C ± 2.27 (n = 159) in the laboratory. The body temperatures of adders were significantly different and higher than those of the other 2 species.

(ii) Estimates of maximum operative temperatures available to the snakes in the outdoor vivaria suggested that for much of the time the animals were restricted from being able to maintain selected body temperatures. Thermally unlimiting conditions were measured during a total of only 31-39% of the 'lit' periods.

(iii) When periods were thermally unlimiting, adders maintained body temperatures ≥ mean selected body temperatures for longer periods than the other 2 species. Smooth snakes in turn, maintained body temperatures ≥ mean selected body temperatures for longer periods than grass snakes.

(iv) A direct, interspecific comparison of body temperatures was carried out for those days when simultaneous recording from 2 or more species was undertaken in the outdoor vivaria. The body temperatures of grass snakes and smooth snakes were not found to differ significantly. However, the body temperatures of adders were higher and significantly different from those of the other 2 species.

(v) When conditions were thermally unlimiting, the snakes maintained higher body temperatures than during periods of thermally limiting conditions. Adders had higher body temperatures than the other 2 species during thermally unlimiting conditions and smooth snakes had higher body temperatures than grass snakes. Significant differences were detected between the data of all 3 species. The data distributions were all negatively skewed, except for that of grass snakes in the laboratory. This was probably due to the extensive foraging behaviour exhibited by this species. During such behaviour, it would have been exposed to thermally unlimiting conditions in a greater proportion of the outdoor vivarium than in the laboratory.

(vi) The maximum body temperature recorded (equivalent to maximum tolerated body temperatures) for adders was 40.4°C, grass snakes 37.1°C and smooth snakes 38.6°C. The minimum body temperatures that were recorded were higher than the true values as the transmitter reliability restricted accurate monitoring on some occasions. However, a body temperature of 2.0°C was recorded for an adder specimen, 2.8°C for grass snakes and 7.0°C for smooth snakes.

CHAPTER FOUR

GENERAL BEHAVIOUR

4.1. Introduction

Relatively few detailed behavioural studies of free-ranging snakes have been undertaken. Most snakes tend to be relatively cryptic and are difficult or even dangerous to capture. Those studies that have been carried out were originally biased towards 'active' animals but with the advent of suitable biotelemetrical equipment, it is now possible to obtain information about the behaviour of snakes that are hidden from view.

The use of temperature-sensitive transmitters on free-ranging snakes has meant that much information on body temperatures and thermoregulation has been acquired (Montgomery and Rand 1978, Peterson 1982, 1987, Shine and Lambeck 1985, de Bont et al. 1986, Shine 1987). Direct observation of snake behaviour has sometimes been used to supplement such studies but the frequency of records has to be limited to avoid disturbing the animals and disrupting their behavioural patterns. Tracking snakes with non-temperature-sensitive transmitters has been used in studies concentrating more on aspects of movement biology and habitat selection although behavioural observations were incorporated into some of the studies (Barbour et al. 1969, Brown and Parker 1976, Madsen 1984, 1987, Gent 1988).

In addition to studying the interspecific differences of body temperatures for the 3 British snake species, a detailed record of snake behaviour was required for the purposes of the present study. Continuous monitoring of behaviour in the field was judged not to be feasible and so snakes were kept in the outdoor vivaria and laboratory arena. Direct observation and video recording techniques meant that the behaviour of the snakes could be studied without the risk of disturbing them. In the outdoor vivaria the 3 species could be studied simultaneously which would have been impossible in a field situation. Each vivarium was identically landscaped so interspecific differences in behaviour could not be attributed to responses to different environments. Conditions in the laboratory were kept as similar as possible between experiments to permit direct interspecific comparisons.

In this chapter, the general behavioural categories exhibited by smooth snakes, grass snakes and adders are investigated. Detailed records of thermoregulatory behaviour were also made but these are discussed in the Chapter Five. There have already been some investigations into various aspects of the behaviour of the 3 British species but no full comparative study has been undertaken. Previous studies on smooth snakes have indicated that they appear to be a relatively sedentary species (Breeds 1973, Spellerberg and Phelps 1977, Goddard 1981, Gent 1988) although the latter author noted that they occasionally engaged in relatively large-scale movements. They have also been described as a particularly secretive snake although overt heliothermic behaviour is sometimes displayed. In contrast to smooth snakes, studies by Madsen (1984, 1987) and Brown (pers.comm.) have indicated that grass snakes are relatively wide-ranging. Hailey and Davies (1986) supported this view by describing grass snakes as 'widely foraging' predators.

The mating behaviour of adders has been the subject of several studies (Andrén 1976, 1981, Andrén and Nilson 1981, Kelleway 1982) although this aspect was not investigated in the present study. Saint Girons (1978) carried out a detailed study on the thermoregulation of European vipers, including adders, in an outdoor vivarium but quantitative data on behaviour were not recorded (apart from emergence and submergence behaviour). The most detailed ecological study on adders in the U.K. published to date has been that of Prestt (1971). He recorded adders making relatively large-scale movements between summer and winter sites but only local movements at other times. Basking behaviour was commonly observed in adders during Prestt's study and appears to form an important part of their daily activity.

Although the confines of the outdoor vivaria and the laboratory arena prevented the snakes from making wide-ranging movements it was nevertheless possible to obtain information on movement activities. The behaviour of snakes during the outdoor vivaria studies were related to the thermal conditions available (measured by the models which in turn estimated operative temperatures). An investigation was made into the significance of behavioural thermoregulation in overall snake behaviour by examining time budgets. How thermoregulatory behaviour relates to overall snake behaviour is discussed in Section 4.4 but a detailed investigation of specific thermoregulatory strategies is left for Chapter Five. Records were also made of the body temperatures that the snakes attained during different categories of behaviour and thermal conditions. It was therefore possible not only to make interspecific comparisons of the frequency that the snakes displayed certain behavioural actions, but also of the body temperatures that they maintained during such times. Similar comparisons were made from the data of the laboratory experiments although recording also took place during nocturnal phases.

4.2. Methods

4.2.1. Daily Emergence

Outdoor Vivaria Experiments

As the environmental conditions varied on a daily and seasonal basis, it was difficult to make meaningful interspecific comparisons of daily emergence behaviour during the outdoor vivaria experiments. This problem was solved by using observations recorded simultaneously for different snake species.

Interspecific comparisons were made between smooth snakes and grass snakes, smooth snakes and adders, and grass snakes and adders. The possible role of environmental factors in providing a stimulus for emergence was investigated by recording ambient temperatures (usually model ambient temperatures) and body temperatures on emergence. The times of emergence were also estimated and interspecific comparisons made.

Times of emergence were estimated using 2 methods. The time of the first daily siting of a snake was considered to represent one estimate. Where body temperatures were recorded, a distinct rise in temperature was also considered to indicate that a snake had emerged from cover, even when it could not be observed. This was particularly useful for smooth snakes which were highly cryptic. Often a rise in body temperature occurred in conjunction with the first behavioural observation of a snake. However, sometimes a rise in body temperature occurred some time before the first siting of a snake in which case the earlier body temperature record was taken as indicating the daily emergence time. Body temperatures were not always monitored during the outdoor vivaria experiments which meant that in those cases emergence times were estimated from direct observations alone. There is therefore a possibility that some snakes may have actually emerged before they were first seen and this should be taken into account when examining the data.

The body temperature and ambient temperature recorded immediately prior to emergence have been included in the analysis. Pre-emergence temperatures were used as the snakes had often heated-up to a certain degree by the time they were first observed. Interspecific comparisons of emergence temperatures were made using Wilcoxon matched-pairs signed-ranks tests. Records of emergence are only included for those days when behaviour was monitored during the morning periods in the outdoor vivaria. Sometimes snakes were not observed to emerge at all during behavioural monitoring and those records have also been included.

Laboratory Experiments

The environmental conditions that existed in the laboratory indoor arena remained relatively constant between different experiments. The light switched on at 0545 hours and the heatlamp switched on at 0725 hours for each day.

A certain degree of nocturnal activity was observed on some of the nights when behavioural monitoring was undertaken. In those cases it was not possible to identify a distinct emergence time and therefore the data were not used in the present analysis. Emergence time was always ascertained from the video recordings of snake behaviour. Two main forms of emergence were identified. The first was when only the head region of the snake was exposed from beneath one of the 3 refuges ('head emergence'). The second was when the snakes fully emerged from cover ('full emergence').

Times of head and full emergence were related to when the light turned on and when the heatlamp turned on. It should be noted that when the heatlamp switched on, it was an additional possible stimulus for emergence as the light was already on. A record of the refuge utilised by the snake prior to emergence was also recorded. This was because if a snake was in the refuge next to the heatlamp, the animal would be more likely to detect the heatlamp switching on than if it was in one of the 2 refuges at the opposite end of the arena. Records of ambient temperatures were recorded for emergence times.

4.2.2. Behaviour Time Budgets

The method of sampling used in the outdoor vivaria was 'point' or 'on-the-dot' recording. Behavioural observations were usually made at 15 minute intervals although more frequent observations were made during the heating phases of the snakes. Only data from the 15 minute records have been used in this chapter. Detailed records were also made of behaviour and basking site utilisation such as coiling postures, amount of body exposed and substrate types. However, the main aim of the work presented in this chapter is to examine the general behaviour displayed by the snakes. Therefore, only records of the main behavioural categories are discussed; basking, mosaic basking, moving and hidden from view. Swimming and drinking records are also included in the summary but not in the statistical comparisons as each of the 2 behavioural categories was only seen on 1 occasion.

Summary statistics have been provided for all the behavioural observations from the outdoor vivaria. However, to permit more meaningful comparisons of data, records were divided into those collected during thermally limiting conditions and those from thermally unlimiting conditions. The same criteria as described in Section 3.2.1. of the previous chapter has been used to define such conditions. When maximum model temperatures indicated that there were conditions available in the vivaria which would allow a snake to attain selected body temperatures, conditions were described as thermally unlimiting (maximum model temperature $\geq 37°C$ for all 3 species). Maximum model temperatures $<34°C$ were considered to indicate that conditions were thermally limiting for all 3 species. Summary statistics are also provided for the 'unlit' periods (also thermally limiting) but relatively few behavioural records were made for these. Comparisons of observed behavioural frequencies were made using G-tests.

Unlike the outdoor vivaria experiments, behavioural data were continuously recorded using time-lapse video techniques. The earliest behavioural observations were made at 0645 hours and the latest at 2000 hours in the outdoor vivaria whereas recording of behaviour from nocturnal periods was possible in the laboratory. Eight main behavioural categories were identified in the laboratory; basking, refuge basking, moving, in refuge, stationary, refuge stationary, thigmothermy and refuge thigmothermy. Swimming and drinking behaviour are also included in the summary statistics but were not used in statistical comparisons.

Basking and refuge basking were only recorded when the heatlamp was on (thermally unlimiting conditions) and thigmothermy and refuge thigmothermy were only recorded when the heatlamp was off (thermally limiting conditions). Therefore if a snake was basking under the heatlamp, when the heatlamp switched off the snake was then recorded as displaying thigmothermy. Behavioural time budgets in the laboratory were calculated from the total time durations that each species was observed exhibiting each behaviour. General summary statistics for the durations that the snakes engaged in each behavioural category were also calculated from the overall data.

4.2.3. Related Samples Time Budgets

To allow the direct comparison of behaviour between the 3 species, an analysis of data from periods of simultaneous recording in the outdoor vivaria was performed. On 23 days, behavioural observations were made on a smooth snake, grass snake and an adder, one in each of the adjacent vivaria. As stated above, behavioural recordings were made at 15 minute intervals. At any one recording, the behaviour was observed for each of the 3 species. Therefore, exactly the same number of behavioural recordings was made for each species. The frequency of observations for each of the 4 main behavioural categories (basking, mosaic basking, moving, hidden) was calculated for each of the 23 days. These frequencies were then compared between each species for each of the 4 behavioural categories using Wilcoxon matched-pairs signed-rank tests. Mosaic basking and basking were combined to form a fifth behavioural category. The data of 5 individual smooth snakes, 5 grass snakes and 5 adders were used over the 23 days. Finally, a G-test was carried out on the overall frequencies between species.

4.2.4. Observed Behaviour and Body Temperatures.

The same statistical techniques were used in the analysis of body temperature data from the outdoor vivaria and the laboratory experiments. In the outdoor vivaria, body temperatures were recorded whenever behavioural observations were made (subject to the biotelemetric equipment functioning). For the laboratory experiments, behavioural data recorded on video were matched to automatically recorded body temperature data.

Summary statistics are provided for the body temperatures of the main behavioural categories. Interspecific comparisons were carried out for each behavioural category using Kruskal-Wallis tests on the body temperature data. When a significant difference was found between the body temperatures of the 3 species for a particular behavioural category, a series of pairwise Wilcoxon/Mann-Whitney tests was performed. These tests identified between which pairs of species the differences were significant.

The same method was used during intraspecific tests. A Kruskal-Wallis test was first performed on the body temperature data between each behavioural category within each species. If this test revealed a significant difference between the body temperatures of the main behavioural categories, a series of Wilcoxon/Mann-Whitney tests was made.

Using the above data it was possible to define activity temperatures (see Section 3.4.5 for a definition of the term) from the outdoor vivaria experiments. These were calculated from any period when a snake was observed to be 'active', which was considered to be when a snake was out or partially out of a retreat but not necessarily moving. Activity temperatures were calculated from when snakes were observed engaged in basking, mosaic basking and moving (but not 'hidden'). Thus, the body temperatures of these behavioural categories were combined to give the activity temperatures.

In the text, mean body temperature values are often given. Non-parametric statistical tests have been performed on the data throughout this chapter and so strictly, median values should be stated. However, it was considered that mean body temperatures should be stated as they are most commonly used in reptilian thermoregulatory studies and therefore provide a simple value to allow comparisons. Nonetheless, median body temperature values are provided in the results tables.

4.3. Results

4.3.1. General Results

Behavioural observations were made on 10 individual smooth snakes in the outdoor vivaria during 1988 and 1989. There were 45 days when more than 1 behavioural observation was recorded for a smooth snake (although on some days more than 1 smooth snake was examined, therefore a total of 47 'snake days'). Eighteen individual grass snakes (specimen Nn10 during 3 separate experiments) were observed over a total of 70 days (98 snake days). Thirteen adders (specimen Vb6 during 2 separate experiments) were observed over a total of 56 days (71 snake days). Overall, 1378 behavioural observations were made on smooth snakes, for which body temperature data were also available for 1250 observations. Of the 2687 observations on grass snakes, body temperature data were also recorded on 1267 occasions. Of the 2076 observations on adders, body temperature data were recorded on 1981 occasions. Details of the animals that were studied and dates of observations are provided in Table 3.1.

In the laboratory arena, snake behaviour could be monitored continuously with the aid of video equipment. Smooth snake behaviour was monitored over a total of 40377 minutes. During this time, 10 individual snakes were studied over a total of 37 days. A total of 703 body temperature measurements were recorded over the period. The behaviour of grass snakes was monitored over a total of 47572 minutes. Eleven individual grass snakes were studied over 45 days and 1627 body temperature measurements recorded. The behaviour of 10 adder specimens was monitored during a total of 40332 minutes from 38 days and 383 body temperature measurements were recorded. Details of the laboratory experiments are provided in Table 3.3.

4.3.2. Daily Emergence

Outdoor Vivaria Experiments

Interspecific comparisons of emergence data between smooth snakes and grass snakes were possible for 31 days (see Table 4.1). On 1 of the days, 2 smooth snakes were studied (therefore a total of 32 'snake days') and on 2 days, 2 grass snakes were studied (therefore a total of 33 'snake days'). Of the 32 snake days on which smooth snakes were studied, the snakes did not appear to emerge on 10 of them (31.2%). Grass snakes did not appear to emerge on 9 of the 33 snake days (27.3%).

Smooth snakes emerged before grass snakes on 10 snake days (including 6 days when grass snakes did not appear to emerge at all). Grass snakes emerged before smooth snakes on 17 days (including 9 days when smooth snakes did not appear to emerge at all). The median time of emergence for days when both smooth snakes and grass snakes emerged, was 0945 hours for smooth snakes (n = 16, range 0815 - 1645 hours) and 0945 hours for grass snakes (n = 16, range 0800 - 1440 hours).

The median model ambient temperature of emergence for smooth snakes was 16.2°C (n = 13, range 12.6 - 20.2°C, mean 16.4°C ± 2.61) and for grass snakes on the same days, 14.8°C (n = 13, range 10.0 - 19.4°C, mean 14.9°C ± 2.51). There was no significant difference between the emergence model ambient temperature data (Wilcoxon matched-pairs signed-ranks, n_1 and n_2 = 13, z = 1.937, $p > 0.05$). The median body temperatures for smooth snakes was 14.7°C (n = 10, range 10.0 - 19.5°C, mean 14.3°C ± 3.12) and for grass snakes on the same days, 14.4°C (n = 10, range 9.9 - 16.9°C, mean 14.1°C ± 2.25). No significant difference existed between the latter sets of data (n_1 and n_2 = 10, z = 0.306, $p > 0.05$).

Interspecific comparisons of emergence data between smooth snakes and adders were possible for 23 days (see Table 4.2). Smooth snakes did not appear to emerge on 6 days (26.1%), adders on 1 day (4.3%). On 6 days smooth snakes emerged before adders (including 1 day when an adder did not appear to emerge) whereas adders emerged before smooth snakes on 15 days (including 6 days when smooth snakes did not appear to emerge). The median emergence time for days when both species emerged was 0930 hours for smooth snakes ($n = 15$, range 0815 - 1645 hours) and 0915 hours for adders ($n = 15$, range 0830 - 1300 hours).

The median model ambient temperature measured at emergence for smooth snakes was 15.8°C ($n = 13$, range 12.6 - 20°C, mean 16.1°C ± 0.74) and 14.8°C for adders over the same days ($n = 13$, range 11.6 - 17.6°C, mean 15.0°C ± 1.78). A significant difference was found between the model ambient temperature data (n_1 and $n_2 = 13$, $z = 2.178$, $p < 0.05$). The median body temperature measured at emergence for smooth snakes was 15.4°C ($n = 8$, range 10 - 19.1°C, mean 15.2°C ± 2.54) and 12.6°C for adders over the same days ($n = 8$, range 7.9 - 19.5°C, mean 12.9°C ± 3.44). There was no significant difference between the latter body temperature data (n_1 and $n_2 = 8$, $z = 1.750$, $p > 0.05$).

The final comparison of emergence data was between grass snakes and adders. Data were available for 40 days (43 'snake days' for grass snakes and 49 'snake days' for adders). Grass snakes did not appear to emerge on 14 of the 43 snake days (32.5%) and adders did not appear to emerge on 9 of the 49 snake days (18.4%). Grass snakes emerged before adders on 10 snake days (including 3 snake days when adders did not appear to emerge) and adders emerged before grass snakes on 30 snake days (including 8 snake days when grass snakes did not appear to emerge). The median emergence time for days when both species emerged was 1015 hours for grass snakes ($n = 31$, range 0815 - 1515 hours) and 0945 hours for adders ($n = 31$, range 0800 - 1300 hours).

The median model ambient temperature at the time of emergence was 15.4°C for grass snakes ($n = 25$, range 5.2 - 23.4°C, mean 16.1°C ± 3.82) and 15.8°C for adders over the same days, with the adder data more negatively skewed ($n = 25$, range 5.2 - 18.2°C). There was a significant difference between the model ambient temperature data (n_1 and $n_2 = 25$, $z = 2.403$, $p < 0.05$). The median body temperature at the time of emergence was 13.4°C for grass snakes ($n = 17$, range 7.5 - 17.6°C, mean 12.5°C ± 2.88) and 12.6°C for adders over the same days ($n = 17$, range 3.4 - 19.5°C, mean 12.3°C ± 4.14). There was no significant difference between the body temperature data of grass snakes and adders (n_1 and $n_2 = 17$, $z = 0.473$, $p > 0.05$).

	Coronella austriaca			*Vipera berus*		
Date	Emergence time	T_a	T_b	Emergence time	T_a	T_b
26.5.88}	} Hidden (1930)			1700	17.6	-
26.5.88}	}			1145	18.8	-
27.5.88}	} Hidden (1545)			1015	14.4	-
27.5.88}	}			0930	15.0	-
22.6.88	1000	16.4	14.4	Hidden (1617)		
23.6.88	0930	16.6	14.0	Hidden (1900)		
24.6.88	1030	19.4	17.9	Hidden (1245)		
27.6.88	1050	14.8	16.4	Hidden (1347)		
28.6.88	1300	16.2	13.9	Hidden (1700)		
29.6.88	Hidden (1703)			1115	22.4	-
30.6.88	Hidden (1130)			Hidden (1130)		
18.7.88	1645	20.0	-	1045	19.4	-
20.7.88	Hidden (1849)			1415	21.4	-
21.7.88	Hidden (1700)			Hidden (1700)		
22.7.88	1430	18.6	-	1145	19.0	-
26.7.88	0830	14.4	14.9	1440	18.2	-
27.7.88	0845	15.0	15.2	1030	15.2	-
28.7.88	1245	15.8	16.3	Hidden (1700)		
29.7.88	0930	13.2	14.5	0945	13.2	-
12.8.88}	0945	16.2	13.8	} 0945	16.2	16.3
12.8.88}	Hidden (1535)			}		
17.8.88	0915	16.0	10.3	0915	14.8	14.4
18.8.88	1015	19.8	10.9	0825	14.2	14.5
25.4.89	Hidden (1700)			Hidden (1700)		
26.4.89	Hidden (1730)			1030	2.6	2.8
27.4.89	1115	-	10.0	1100	-	9.9
28.4.89	1145	-	<7.0	1015	5.2	7.6
16.5.89	1045	-	16.3	1000	14.8	13.3
17.5.89	Hidden (1918)			1015	19.6	12.3
18.5.89	0900	12.6	13.9	0930	11.6	11.5
19.5.89	0845	13.8	15.5	0900	13.8	12.7
14.6.89	0945	20.2	19.5	0815	16.2	16.9
15.6.89	0815	16.8	16.5	0815	16.0	15.7
16.6.89	0915	16.4	16.3	0800	14.6	15.8

Table 4.1: **Comparison of emergence times recorded during the outdoor vivaria experiments for *Coronella austriaca* and *Natrix natrix*.** Times of emergence are provided with model ambient temperature (T_a °C) and body temperature (T_b °C) immediately prior to emergence. Where snakes were not observed to emerge and remained 'hidden', the time of the last observation is recorded.

	Coronella austriaca			*Vipera berus*		
Date	Emergence time	T_a	T_b	Emergence time	T_a	T_b
18.7.88	1654	20.0	-	0900	15.4	-
19.7.88	Hidden (1600)			1130	20.2	15.3
20.7.88	Hidden (1849)			1200	18.2	17.1
21.7.88	Hidden (1700)			0930	17.8	14.6
22.7.88	1430	18.6	-	1145	17.6	18.0
26.7.88	0830	14.4	14.9	0900	-	13.4
27.7.88	0845	13.8	15.2	0915	14.4	12.5
28.7.88	1245	15.8	16.3	0830	14.4	12.6
29.7.88	0930	13.2	14.5	0845	11.6	9.9
17.8.88	1115-1300	19.6	15.3	0930	16.0	15.0
18.8.88	1015	19.8	-	0915	17.0	16.4
25.4.89	Hidden (1700)			1215	-	8.7
26.4.89	Hidden (1730)			1115	-	6.1
27.4.89	1115		10.0	1100	-	7.9
28.4.89	1145		<7.0	1000	5.2	9.2
16.5.89	1045	-	16.3	0945	13.4	19.5
17.5.89	Hidden (1918)			1115	(19.0)	16.6
18.5.89	0900	12.6	13.9	0900	12.6	-
19.5.89	0845	13.8	15.5	0845	13.8	12.6
15.6.89	0815	16.8	16.5	1300	15.8	-
16.6.89	0915	16.4	16.3	Hidden (1132)		
20.6.89	0845	16.6	16.5	0915	17.4	-
21.6.89	0845	14.2	19.1	0915	14.8	15.1

Table 4.2: **Comparison of emergence times recorded during the outdoor vivaria experiments for *Coronella austriaca* and *Vipera berus*.** Times of emergence are provided with model ambient temperature (T_a °C) and body temperature (T_b °C) immediately prior to emergence. Ambient temperature values in parentheses are shade air temperatures rather than model ambient temperatures. Where snakes were not observed to emerge and remained 'hidden', the time of the last observation is recorded. On 17.8.88 the *Coronella austriaca* specimen emerged at some time between 1115-1300 hours and the body temperature measurement provided was recorded at 1115 hours.

	Natrix natrix			*Vipera berus*		
Date	**Emergence time**	**T_a**	**T_b**	**Emergence time**	**T_a**	**T_b**
9.5.88	Hidden (1700)			Hidden (1700)		
11.5.88	Hidden (1400)			0815	9.0	10.2
16.5.88}	Hidden (1545)			0900	13.0	11.6
16.5.88}				0930	14.6	15.4
17.5.88}	Hidden (1215)			1045	14.2	10.8
17.5.88}				0945	11.4	-
2.6.88}	Hidden (1130)			Hidden (1130)		
2.6.88}	Hidden (1130)					
3.6.88}	1515	17.4	-	1015	16.6	16.3
3.6.88}	0915	13.4	13.6			
6.6.88}	Hidden (1100)			1015	15.2	16.3
6.6.88}	0915	14.6	13.4			
18.7.88	1045	19.4	-	0900	15.4	-
20.7.88	1415	21.4	-	1200	18.2	17.1
21.7.88	Hidden (1700)			0930	17.8	14.6
22.7.88	1145	19.0	-	1145	17.6	18.0
26.7.88	1440	18.2	-	0900	14.6	13.4
27.7.88	1030	15.2	-	0915	14.4	12.5
28.7.88	Hidden (1700)			0830	14.4	12.6
29.7.88	0945	13.2	-	0845	11.6	9.9
17.8.88	0915	14.8	14.4	0932	16.0	15.0
18.8.88	0825	14.2	14.5	0915	17.0	16.4
13.9.88}	Hidden (1046)			Hidden (1046)		
13.9.88}				0930	12.4	9.8
14.9.88}	Hidden (1300)			Hidden (1300)		
14.9.88}				1230	14.6	11.7
22.9.88	1031	15.4	14.1	1145	16.2	13.6
23.9.88	0930	12.6	13.4	1130	13.2	12.6
31.3.89	1300	(9.0)	10.5	1030	(9.0)	9.7
3.4.89	1215	(7.0)	7.9	0845	(6.0)	3.4
5.4.89	Hidden (1030)			Hidden (1030)		
6.4.89	Hidden (1230)			Hidden (1230)		
25.4.89	Hidden (1700)			1215	-	8.7
26.4.89	1030	2.6	7.5	1115	-	6.1
27.4.89	1100	-	9.9	1100	-	7.9
28.4.89	1015	5.2	7.6	1000	5.2	9.2
4.5.89}	1130	-	14.4	Hidden (1900)		
4.5.89}				0930	12.2	10.7
5.5.89}	1030	14.4	13.3	Hidden (1030)		
5.5.89}				0830	11.0	11.4
16.5.89	1000	14.8	17.6	0945	13.4	19.5
17.5.89	1015	19.6	12.3	1100	(19.0)	13.0
18.5.89	0930	13.8	11.5	0900	12.6	-
19.5.89	0900	13.8	12.7	0845	13.8	12.6
24.5.89}	0945	23.4	19.3	0800	17.0	-
24.5.89}				0815	17.0	-
25.5.89}	0945	19.2	17.6	1015	17.6	-
25.5.89}				0800	14.6	-
26.5.89}	1030	15.4	15.4	0945	15.8	-
26.5.89}				0945	15.8	14.9
15.6.89	0815	16.0	15.7	1300	15.8	-
16.6.89	0800	14.6	17.2	Hidden (1132)		

Table 4.3: **Comparison of emergence times recorded during the outdoor vivaria experiments for *Natrix natrix* and *Vipera berus*.** Times of emergence are provided with model ambient temperature (T_a °C) and body temperature (T_b °C) immediately prior to emergence. Ambient temperature values in parentheses are shade air temperatures rather than model ambient temperatures. Where snakes were not observed to emerge and remained 'hidden', the time of the last observation is recorded.

Laboratory Experiments

Smooth snakes were studied in the laboratory on 37 days but recording of morning periods was performed on 27 days only. For grass snakes, morning periods were monitored on 33 out of 45 days and for adders, 28 out of 38 days.

When nocturnal activity occurred in the laboratory arena it was difficult to give an exact emergence time. Therefore, when snakes were observed outside their refuges at some point after midnight and before the light switched on, emergence times were not calculated. Smooth snakes were observed outside refuges during nocturnal periods after midnight on 6 out of 27 days (leaving 21 days for which emergence times are provided) and 7 out of 33 days for grass snakes (leaving 24 days). Very little emergence data were available for adders as they were observed outside refuges during nocturnal periods after midnight on 26 out of 28 days (leaving 2 days for which emergence times are provided). Further details of nocturnal activity in adders and the other 2 species are given in Section 4.3.3,'Laboratory Experiments'.

There were some nights when snakes did not fully emerge from their refuges but engaged in varying degrees of 'refuge thigmothermy' or 'refuge stationary' behaviour. In these cases, 'head emergence' times are not provided but 'full emergence' times are given. Such behaviour was observed after midnight during nocturnal periods on 10 days for smooth snakes (out of the 21 days for which emergence times are provided) and 7 days for grass snakes (out of 24 days). This therefore left a total of 11 days for smooth snakes, 19 days for grass snakes and 2 days for adders when the snakes did not emerge (not even partially) after midnight and before the light was on.

Tables 4.4 and 4.5 provide details of the times of emergence in smooth snakes and grass snakes respectively. In the case of smooth snakes, head emergence behaviour was observed on 10 out of 11 days. Out of those 10 days, head emergence occurred on 8 days after the light switched on (and before the heatlamp switched on) and 2 days after the heatlamp was on (when the light was already on as well). However, full emergence, details for which are provided for 16 days, occurred on only 4 days after the light switched on and on 12 days after the heatlamp switched on. Smooth snakes in the refuge nearest to the heatlamp emerged at a median time of 17 mins after the heatlamp switched on (n = 7, range 1 - 110 mins, mean 44.6 mins ± 43.2) whereas those in refuges at the opposite end of the arena tended to emerge later (median 240 mins, n = 5, range 14 - 325 mins, mean 189.8 mins ± 150.3).

			Head emergence		Full emergence	
	Date	Refuge	Time after light on (mins)	Time after heatlamp on (mins)	Time after light on (mins)	Time after heatlamp on (mins)
(i)	18.7.87	1	57	-	102	-
	29.8.87	2	-	344	-	240
	30.8.87	2	-	1	-	14
	2.6.88	1	13	-	-	3
	3.6.88	1	24	-	-	96
	4.6.88	2	48	-	-	46
	8.7.88	1	74	not applicable (0723)	not applicable (0723)	
	16.7.88	1	19	-	-	17
	17.7.88	1	70	-	-	1
	1.8.88	1	-	-	-	13
	31.8.88	2	37	-	not applicable (1200)	
(ii)	27.6.87	2			102	-
	3.7.87	2			12	-
	20.7.87	1			9	-
	6.7.88	1			-	72
	28.8.88	1			-	110
	29.8.88	2			-	325
	30.8.88	2			-	324

Table 4.4: **Head and full emergence times of *Coronella austriaca* in the laboratory arena.** The light came on at 0545 hours and the heatlamp came on at 0725 hours. In group (i) data are provided for snakes that had remained in refuges since midnight. In group (ii), data are provided for snakes that had been observed partially emerged from their refuges for some periods since midnight ('refuge stationary' or 'refuge thigmothermy' behaviour) and so only the full emergence times are provided. Where full emergence was not observed, the term 'not applicable' has been used with the time of the last observation in parentheses. Details of the refuge used prior to emergence are provided. Refuge 1 was near to the heatlamp whereas refuge 2 was at the opposite end of the arena to the heatlamp (see Fig. 2.9).

Note for 8.7.88 the last observation was recorded at 0723 hours just before the heatlamp switched on.

		Head emergence		Full emergence	
Date	Refuge	Time after light on (mins)	Time after heatlamp on (mins)	Time after light on (mins)	Time after heatlamp on (mins)
(i) 23.5.87	2	16	-	-	104
31.5.87	3	-	44	-	212
1.6.87	3	33	-	not applicable (1200)	
3.6.87	3	not applicable		6	-
4.6.87	3	not applicable		36	-
25.3.88	1	-	20	-	52
26.3.88	2	16	-	-	333
27.3.88	1	-	2	-	234
21.5.88	1	-	23	-	162
22.5.88	3	46	-	-	179
24.5.88	3	3	-	33	-
2.7.88	2	-	61	-	136
3.7.88	3	-	44	-	340
4.7.88	3	73	-	-	187
8.9.88	1	23	-	-	43
9.9.88	2	6	-	-	77
18.9.88	3	-	51	-	119
19.9.88	3	16	-	-	105
20.9.88	3	-	1	-	15
(ii) 20.5.88	2			-	559
23.5.88	2			-	542
9.6.88	1			41	-
10.6.88	1			48	-
25.6.88	1			-	110
7.9.88	2			-	122

Table 4.5: **Head and full emergence times of *Natrix natrix* in the laboratory arena.** The light came on at 0545 hours and the heat lamp came on at 0725 hours. In group (i) data are provided for snakes that had remained in refuges since midnight. In group (ii), data are provided for snakes that had been observed partially emerged from their refuges for some periods since midnight ('refuge stationary' or 'refuge thigmothermy' behaviour) and so only the full emergence times are provided. Where full emergence was not observed, the term 'not applicable' has been used with the time of the last observation in parentheses. Details of the refuge used prior to emergence are provided. Refuge 1 was near to the heatlamp whereas refuges 2 and 3 were at the opposite end of the arena to the heatlamp (see Fig. 2.9).

Head emergence behaviour was observed in grass snakes on 17 out of 19 days. Out of those 17 days, head emergence behaviour was observed on 9 days after the light switched on (and before the heatlamp switched on) and 8 days after the heatlamp switched on (when the light was already on). Full emergence, details for which are provided for 24 days, occurred on 5 days after the light switched on and on 19 days after the heatlamp switched on. Grass snakes in the refuge closest to the heatlamp fully emerged at a median time of 110 mins after the heatlamp switched on (n = 5, range 43 - 234 mins, mean 120.2 mins ± 71.3). Grass snakes in the refuges at the opposite end of the arena to the heatlamp, fully emerged at a median time of 157.5 mins after the heatlamp switched on (n = 14, range 15 - 559 mins, mean 216.4 mins ± 161.3).

There were 2 days for which the emergence data of adders could be used. On 9.5.87 an adder showed no head emergence behaviour but fully emerged 42 mins after the light switched on (and before the heatlamp switched on). On 3.10.88, another adder displayed head emergence 10 mins, and fully emerged 14 mins, after the heatlamp switched on (after it had been in the refuge closest to the heatlamp).

The ambient temperatures at the time of emergence did not vary much between days. Full emergence occurred at mean ambient temperatures of 19.5°C ± 1.26 for smooth snakes (n = 16), 18.3°C ± 1.75 for grass snakes (n = 24) and 18.5°C ± 0.5 for adders (n = 2).

4.3.3. Behaviour Time Budgets

Outdoor Vivaria Experiments

'On-the-dot' or 'point' sampling was used in the outdoor vivaria. For the purpose of this analysis, the behaviour of the snakes has been divided into 6 categories ; basking, mosaic basking, moving, hidden from view, drinking, swimming. Table 4.6 and Fig. 4.1 gives the results of the behaviour observed throughout all the experiments performed with the outdoor vivaria. Note that drinking and swimming behaviour was recorded on only 1 occasion each and therefore these behavioural categories were not included in Fig. 4.1.

In all 3 species, snakes were usually hidden from view when behavioural observations were made. This was especially the case with smooth snakes which were hidden during 85.6% of the observations. This compares to 78.1% in the case of grass snakes and 63.7% for adders.

When snakes were recorded as being hidden they might not necessarily have been submerged in a refuge. Sometimes relatively high body temperatures were simultaneously recorded during 'hidden behaviour' which meant that they could have been mosaic basking in well concealed sites. Differences in the frequency of the observed behavioural categories were detected between smooth snakes and grass snakes, smooth snakes and adders, and grass snakes and adders ($G = 152.72$, $G = 276.43$, $G = 298.18$ respectively, $p < 0.001$ with 3 d.f. in all cases).

Environmental conditions were categorised into thermally limiting, thermally unlimiting and 'unlit' (also thermally limiting) following the same criteria as defined in Chapter Three. The results of the behavioural observations are presented in Table 4.6 and, in the case of the former two categories, in Fig. 4.2.

During thermally unlimiting conditions (model temperatures $\geq 37°C$), a significant difference was detected between the frequencies of the four main behavioural categories of adders and grass snakes ($G = 110.63$, $p < 0.001$, 3 d.f.). Because no basking behaviour was observed in smooth snakes during these periods, basking and mosaic basking behaviour frequencies were combined to allow comparison with the other two species. Significant differences were found between smooth snakes and grass snakes ($G = 94.578$, $p < 0.001$, 2 d.f.) and smooth snakes and adders ($G = 86.112$, $p < 0.001$, 2 d.f.).

Similar comparisons were made between observed behaviour frequencies of the 3 different species during thermally limiting conditions (model temperatures $< 34°C$). Significant differences were found in all possible combinations ($G = 56.215$ for smooth snakes and grass snakes, $G = 188.63$ for smooth snakes and adders, $G = 198.93$ for grass snakes and adders, $p < 0.001$ and 3 d.f. for all cases).

During thermally unlimiting conditions, adders and smooth snakes were observed basking (i.e. not under any cover) on proportionately fewer occasions than during thermally limiting conditions. In fact smooth snakes were not observed basking during thermally unlimiting conditions at any time. Even during thermally limiting conditions smooth snakes were only observed basking on 15 occasions (1.9%). Smooth snakes seemed to prefer mosaic basking to basking and during thermally limiting conditions the former method was observed on 114 occasions (14.7%, a ratio of 1 : 7.6 basking to mosaic basking).

		Coronella austriaca		*Natrix natrix*		*Vipera berus*	
1. All periods		n	%	n	%	n	%
	Basking	15	1.1	61	2.3	218	10.5
	Mosaic basking	165	12.0	259	9.6	423	20.4
	Moving	16	1.2	269	10.0	113	5.4
	Hidden	1181	85.6	2098	78.1	1322	63.7
	Drinking	1	0.07	0	0	0	0
	Swimming	0	0	1	0.04	0	0
	Total	**1378**		**2688**		**2076**	
2. Thermally unlimiting conditions		n	%	n	%	n	%
	Basking	0	0	13	2.4	33	4.7
	Mosaic basking	39	10.3	52	9.7	187	26.8
	Moving	4	1.1	103	19.2	35	5.0
	Hidden	334	88.4	368	68.7	442	63.4
	Drinking	1	0.3	0	0	0	0
	Swimming	0	0	0	0	0	0
	Total	**378**		**536**		**697**	
3. Thermally limiting conditions		n	%	n	%	n	%
	Basking	15	1.9	43	2.8	161	18.2
	Mosaic basking	114	14.7	170	11.2	151	17.1
	Moving	12	1.5	126	8.3	61	6.9
	Hidden	635	81.8	1181	77.7	512	57.9
	Drinking	0	0	0	0	0	0
	Swimming	0	0	0	0	0	0
	Total	**776**		**1520**		**885**	
4. 'Unlit' periods		n	%	n	%	n	%
	Basking	0	0	0	0	1	1.0
	Mosaic basking	0	0	0	0	0	0
	Moving	0	0	4	2.4	0	0
	Hidden	54	100	161	97.6	101	99.0
	Drinking	0	0	0	0	0	0
	Swimming	0	0	0	0	0	0
	Total	**54**		**165**		**102**	

Table 4.6: **Frequency and percentage frequency of observations for the main behavioural categories during the outdoor vivaria experiments.**

Smooth snake data from 10 animals over 47 days, grass snake data from 18 animals over 98 days, adder data from 13 animals over 71 days.

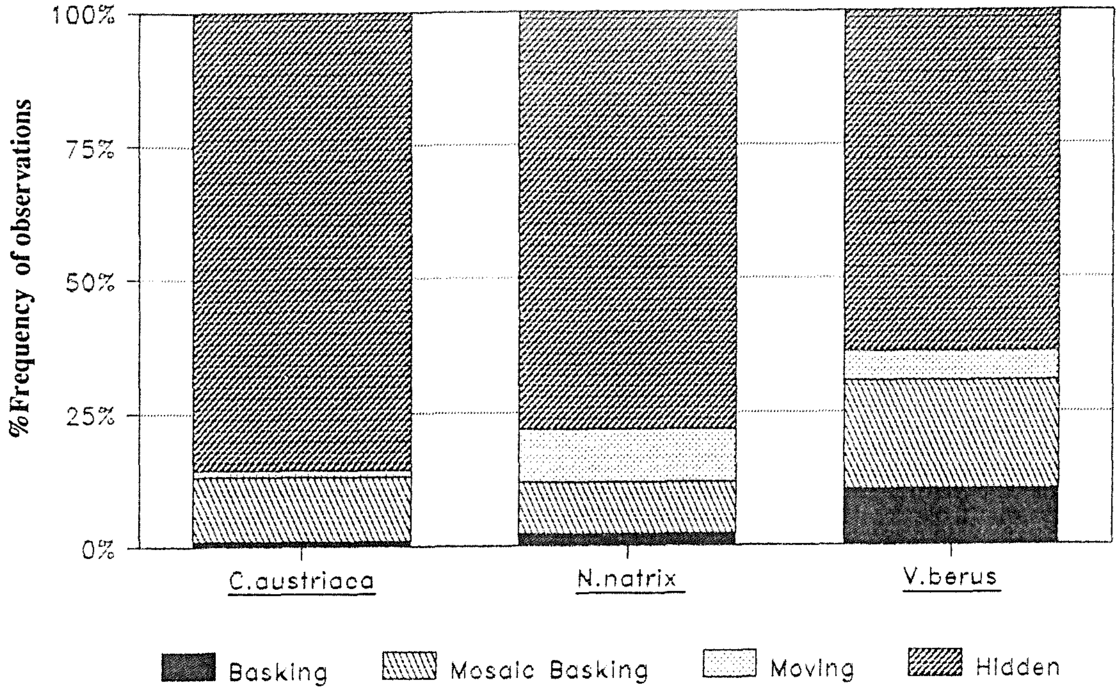
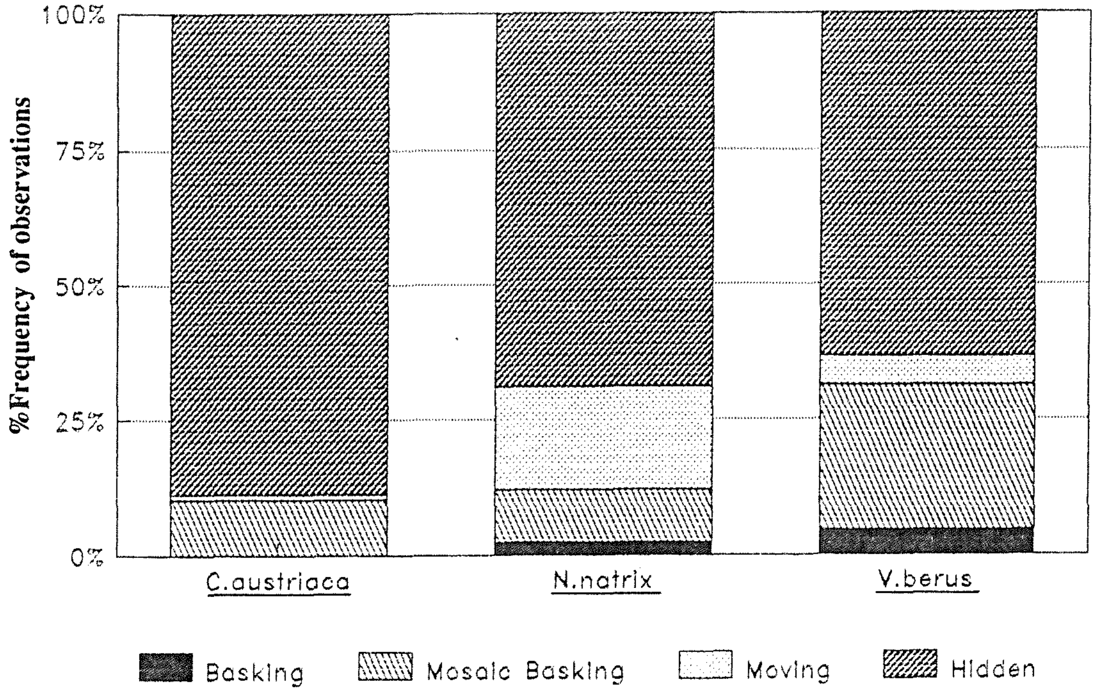


Fig. 4.1: **Percentage number of observations assigned to each of the main behavioural categories during all periods of the outdoor vivaria experiments.** The earliest behavioural observations were made at 0645 hours; the latest at 2000 hours.

1. Thermally unlimiting conditions



2. Thermally limiting conditions

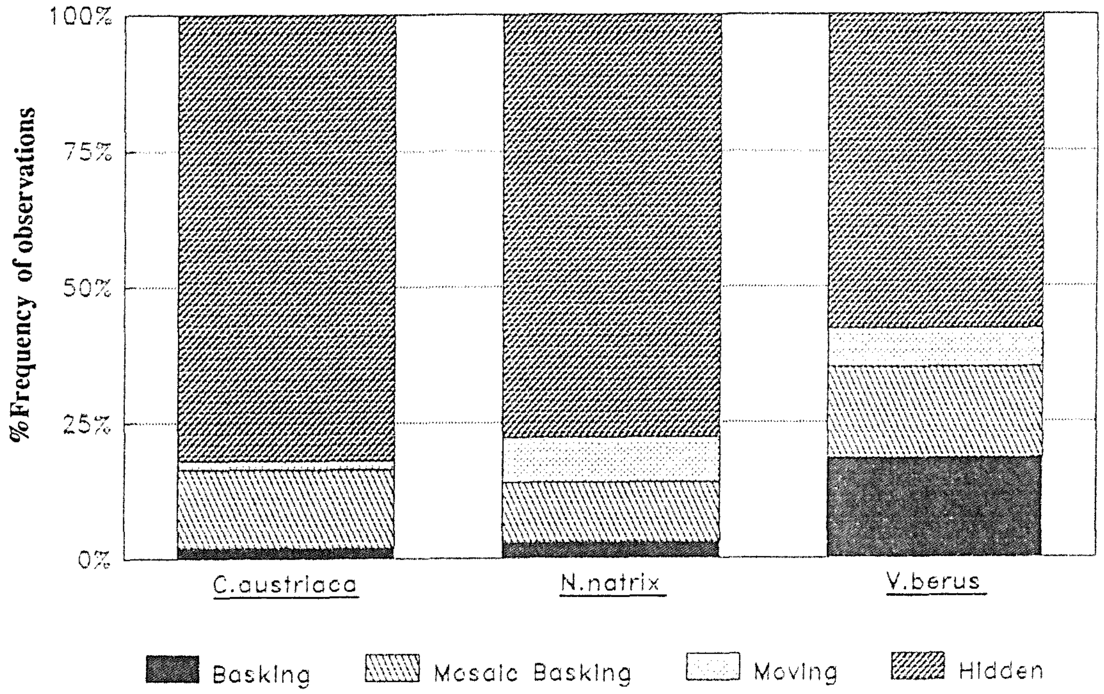


Fig. 4.2: Percentage number of observations assigned to each of the main behavioural categories during thermally unlimiting and limiting conditions for the outdoor vivaria experiments.

Adders were observed basking during 4.7% of the observations and mosaic basking 26.8% when conditions were thermally unlimiting (a ratio of 1 : 5.7). When conditions were thermally limiting, basking was observed on 18.2% occasions and mosaic basking 17.1% (a more equal ratio of 1 : 0.9). The frequencies of the 4 main behavioural categories were significantly different for adders between thermally limiting and unlimiting conditions ($G = 85.712$, $p < 0.001$, 3 d.f.). However, when basking and mosaic basking are combined into one behavioural category, there is no such difference ($G = 5.867$, $p > 0.05$, 2 d.f.). This suggests that although there is a difference in the overall thermoregulatory behaviour during different thermal conditions, the time spent on such behaviour remains about the same.

Grass snakes were observed moving more than the other 2 species, especially when conditions were thermally unlimiting. Mosaic basking was observed more often than basking during both conditions (ratio of 1 : 4 during both conditions). A significant difference between the frequency of the 4 main behavioural categories was found between the 2 conditions ($G = 43.367$, $p < 0.001$, 3 d.f.) and when basking and mosaic basking were combined ($G = 43.366$, $p < 0.001$, 2 d.f.). Similar results were found when the observed behaviour frequency of smooth snakes were compared between thermally limiting and unlimiting conditions, although the differences were not as great ($G = 9.113$, $p < 0.05$, 2 d.f.). When conditions were 'unlit', snakes were only very rarely observed exhibiting any behaviour other than 'hidden'. On 4 occasions grass snakes were observed moving and on 1 occasion an adder was observed 'basking'. On all occasions these were observed immediately after the vivaria had moved into the evening shadow. The adder could not strictly be described as basking as it was in shadow, but it was stationary and would probably have soon moved under cover if it had not been removed from the vivarium for processing purposes.

Laboratory Experiments

Behaviour in the laboratory was continuously recorded and so results are given as time durations rather than frequency of observed behavioural categories (as used in the outdoor vivaria). The laboratory environment was different to that of the outdoor vivaria so that behaviour definition was slightly modified. Basking and refuge basking were only recorded during thermally unlimiting conditions (i.e. when the heatlamp was on) and thigmothermy and refuge thigmothermy only during thermally limiting conditions (i.e. when the heatlamp was off).

Overall behavioural time budgets are provided in Table 4.7 for thermally limiting conditions, thermally unlimiting conditions and both conditions combined. Further details of time durations for the main behavioural categories are provided in Table 4.8 for thermally unlimiting conditions and Table 4.9 for thermally limiting conditions. Drinking and swimming behaviour was observed for relatively little time and so these are not included in the graphical versions of the results (Figs. 4.3 and 4.4).

An examination of the overall time budgets indicates that when conditions were thermally unlimiting, adders were observed basking more than any other behaviour (73.2%). Very little time was spent refuge basking (only 0.9%) and most of the rest of their time was spent engaged in movement activity (21.3%). Smooth snakes spent less time basking and refuge basking (41.5% and 8.6% respectively) than adders spent basking, and more time hidden under the refuges (25.2%). It is interesting to note that smooth snakes were under or partially under the cover of refuges (displayed as 'in refuge', refuge basking or refuge stationary) for a total of 45.3% of the time, grass snakes 55.5% and adders only 5.3%.

During thermally limiting conditions, one of the most striking results was that adders were observed moving during 49.4% of the overall time. This compared with 4.6% for smooth snakes and 4.5% for grass snakes. The latter two species spent the majority of the periods of thermally limiting conditions under refuges. Thigmothermy was observed for a proportionately longer time in adders (16.2%) compared to smooth snakes (5.9%) and grass snakes (6.4%). However, grass snakes displayed refuge thigmothermy for 14.4% of the time period whereas for smooth snakes the value was 3.8% and adders, 0.9%.

4.3.4. Related Samples Time Budgets

There were 23 days when behaviour observations were recorded simultaneously for all 3 species in the outdoor vivaria. The number of observations made on any one day ranged from 5 to 48 simultaneous recordings. In total, 681 recordings were made during these days, recorded from 5 individuals of each species. The number of observations for each of the 4 main behavioural categories (basking, mosaic basking, moving and hidden) was recorded for each day and interspecific comparisons made using Wilcoxon matched-pairs signed-ranks tests. A category was also made for combined basking and mosaic basking and tested in the same way. The results are presented in Table 4.10.

		Coronella austriaca		*Natrix natrix*		*Vipera berus*	
1. All periods		Duration (mins)	% duration	Duration (mins)	% duration	Duration (mins)	% duration
	Basking	8206	20.3	6673	14.0	14749	36.5
	Refuge basking	1693	4.2	3956	8.3	186	0.5
	Moving	2166	5.4	4310	9.1	14283	35.4
	Hidden	19801	49.1	17702	37.2	6085	15.1
	Thigmothermy	1209	3.0	1528	3.2	3261	8.1
	Refuge thigmothermy	785	1.9	3444	7.2	172	0.4
	Stationary	2278	5.6	830	1.7	889	2.2
	Refuge stationary	4226	10.5	9079	19.1	668	1.7
	Drinking	6	0.01	8	0.02	39	0.1
	Swimming	7	0.02	42	0.09	0	0
	Total duration	**40377**		**47572**		**40332**	
2. Thermally unlimiting conditions (heatlamp on)		Duration (mins)	% duration	Duration (mins)	% duration	Duration (mins)	% duration
	Basking	8206	41.5	6673	28.2	14749	73.2
	Refuge basking	1693	8.6	3956	16.7	186	0.9
	Moving	1210	6.1	3244	13.7	4309	21.3
	Hidden	4973	25.2	3867	16.3	840	4.2
	Thigmothermy	--	--	--	--	--	--
	Refuge thigmothermy	--	--	--	--	--	--
	Stationary	1410	7.1	562	2.4	19	0.09
	Refuge stationary	2253	11.5	5327	22.5	33	0.2
	Drinking	4	0.02	4	0.02	16	0.08
	Swimming	5	0.03	35	0.1	0	0
	Total duration	**19754**		**23668**		**20152**	
3. Thermally limiting conditions (heatlamp off)		Duration (mins)	% duration	Duration (mins)	% duration	Duration (mins)	% duration
	Basking	--	--	--	--	--	--
	Refuge basking	--	--	--	--	--	--
	Moving	956	4.6	1066	4.5	9974	49.4
	Hidden	14828	71.9	13835	57.9	5245	26.0
	Thigmothermy	1209	5.9	1528	6.4	3261	16.2
	Refuge thigmothermy	785	3.8	3444	14.4	172	0.9
	Stationary	868	4.2	268	1.1	870	4.3
	Refuge stationary	1973	9.6	3752	15.7	635	3.1
	Drinking	2	0.01	4	0.02	23	0.1
	Swimming	2	0.01	7	0.03	0	0
	Total duration	**20623**		**23904**		**20180**	

Table 4.7: **Overall time duration and percentage time duration of main behavioural categories observed from video recordings of laboratory experiments.**

Smooth snake data from 10 animals over a total of 37 days, grass snake data from 11 animals over 45 days, adder data from 10 animals over 38 days.

Behaviour		n	%n	sum	%sum	Mean	SD	Median	Min	Max	Skewness	Kurtosis
		Time duration (mins)										
Thigmothermy	*Coronella austriaca*	74	19.3	8206	41.5	110.9	131.91	45.5	1	476	1.25	0.61
	Natrix natrix	163	16.4	6673	28.2	40.9	70.49	12.0	1	455	2.92	9.86
	Vipera berus	574	45.4	14749	73.2	25.7	46.35	11.0	1	427	4.33	24.10
Refuge thigmothermy	*Coronella austriaca*	60	15.6	1693	8.6	28.2	48.50	9.0	1	264	3.09	10.64
	Natrix natrix	161	16.2	3956	16.7	24.6	38.75	10.0	1	239	3.12	11.97
	Vipera berus	43	3.4	186	0.9	4.3	3.84	3.0	1	19	2.00	4.44
Moving	*Coronella austriaca*	103	26.9	1210	6.1	11.7	10.84	8.0	1	59	1.86	4.06
	Natrix natrix	330	33.1	3244	13.7	9.8	10.93	6.0	1	65	2.28	6.22
	Vipera berus	561	44.4	4309	21.3	7.7	6.44	6.0	1	55	2.29	8.51
In refuge	*Coronella austriaca*	71	18.5	4973	25.2	70.0	127.03	12.0	1	720	2.94	10.39
	Natrix natrix	162	16.3	3867	16.3	23.9	44.08	6.0	1	291	3.37	13.16
	Vipera berus	60	4.8	840	4.2	14.0	25.38	6.5	1	128	3.22	10.27
Stationary	*Coronella austriaca*	17	4.4	1410	7.1	82.9	83.71	80.0	2	255	0.930	-0.02
	Natrix natrix	16	1.6	562	2.4	35.1	38.49	21.0	1	128	1.15	0.63
	Vipera berus	2	0.2	19	0.09	9.5	0.71	9.5	9	10	-	-
Refuge stationary	*Coronella austriaca*	51	13.3	2253	11.5	44.2	72.04	15.0	1	275	2.11	3.53
	Natrix natrix	149	15.0	5327	22.5	36.0	61.80	9.0	1	332	2.74	8.39
	Vipera berus	12	1.0	33	0.2	2.8	1.86	2.5	1	7	1.14	1.08
Drinking	*Coronella austriaca*	4	1.0	4	0.02	1.0	0	1.0	1	1	-	-
	Natrix natrix	3	0.3	4	0.02	1.3	0.58	1.0	1	2	1.73	2.0
	Vipera berus	11	0.9	16	0.08	1.5	0.52	1.0	1	2	0.21	-2.4
Swimming	*Coronella austriaca*	4	1.0	5	0.03	1.2	0.50	1.0	1	2	2.0	4.0
	Natrix natrix	12	1.2	35	0.1	2.9	1.50	3.0	1	6	0.74	0.26
	Vipera berus	0	0	0	0	-	-	-	-	-	-	-
Total	*Coronella austriaca*	384	100.0	19754	100.0							
	Natrix natrix	996	100.1	23668	100.05							
	Vipera berus	1 263	100.1	20152	99.97							

Table 4.8: Summary statistics of time budgets for the main behavioural categories recorded during thermally unlimiting conditions (i.e. heatlamp on) for the laboratory experiments.

Behaviour		Time duration (mins)										
		n	%n	sum	%sum	Mean	SD	Median	Min	Max	Skewness	Kurtosis
Thigmothermy	*Coronella austriaca*	26	8.9	1209	5.9	46.5	63.51	18.5	3	222	1.87	2.54
	Natrix natrix	20	6.6	1528	6.4	76.4	101.22	41.5	1	445	2.76	9.36
	Vipera berus	145	23.3	3261	16.2	22.5	45.99	7.0	1	424	5.46	41.15
Refuge thigmothermy	*Coronella austriaca*	30	10.2	785	3.8	26.2	29.12	12.5	2	97	1.17	-0.10
	Natrix natrix	39	12.9	3444	14.4	86.9	124.09	29.0	1	445	1.95	2.90
	Vipera berus	15	2.4	172	0.9	11.5	15.40	8.0	2	65	3.39	12.34
Moving	*Coronella austriaca*	45	15.4	956	4.6	21.2	30.30	10.0	1	139	2.41	5.58
	Natrix natrix	74	24.4	1066	4.5	14.4	17.28	8.0	1	90	2.23	5.78
	Vipera berus	260	41.9	9974	49.4	38.3	52.19	20.0	1	378	3.14	12.34
In refuge	*Coronella austriaca*	114	38.9	14828	71.9	130.1	166.55	56.5	1	445	2.42	10.26
	Natrix natrix	98	32.3	13835	57.9	141.2	158.36	46.0	2	445	0.79	-0.94
	Vipera berus	96	15.5	5245	26.0	54.6	95.22	9.5	1	445	2.25	4.52
Stationary	*Coronella austriaca*	11	3.8	868	4.2	78.9	86.63	61.0	2	297	1.78	3.58
	Natrix natrix	10	3.3	268	1.1	26.8	29.92	12.5	3	90	1.54	1.27
	Vipera berus	27	4.3	870	4.3	32.2	61.83	7.0	2	321	4.19	19.72
Refuge stationary	*Coronella austriaca*	64	21.8	1973	9.6	30.8	42.56	15.0	1	259	3.00	12.59
	Natrix natrix	58	19.1	3752	15.7	64.7	96.74	22.0	1	445	2.04	3.83
	Vipera berus	71	11.4	635	3.1	8.9	11.81	4.0	1	69	2.84	9.75
Drinking	*Coronella austriaca*	1	0.3	2	0.01	2.0	-	2.0	2	2	-	-
	Natrix natrix	1	0.3	4	0.02	4.0	-	4.0	4	4	-	-
	Vipera berus	7	1.1	23	0.1	3.3	3.25	2.0	1	10	1.88	3.38
Swimming	*Coronella austriaca*	2	0.7	2	0.01	1.0	0	1.0	1	1	-	-
	Natrix natrix	3	1.0	7	0.03	2.3	0.58	2.0	2	3	1.73	-
	Vipera berus	0	0	0	0	-	-	-	-	-	-	-
Total	*Coronella austriaca*	293	100.0	20623	100.02							
	Natrix natrix	303	99.9	23904	100.05							
	Vipera berus	621	99.9	20180	100.0							

Table 4.9: Summary statistics of time budgets for the main behavioural categories recorded during thermally limiting conditions (i.e. heatlamp off) for the laboratory experiments.

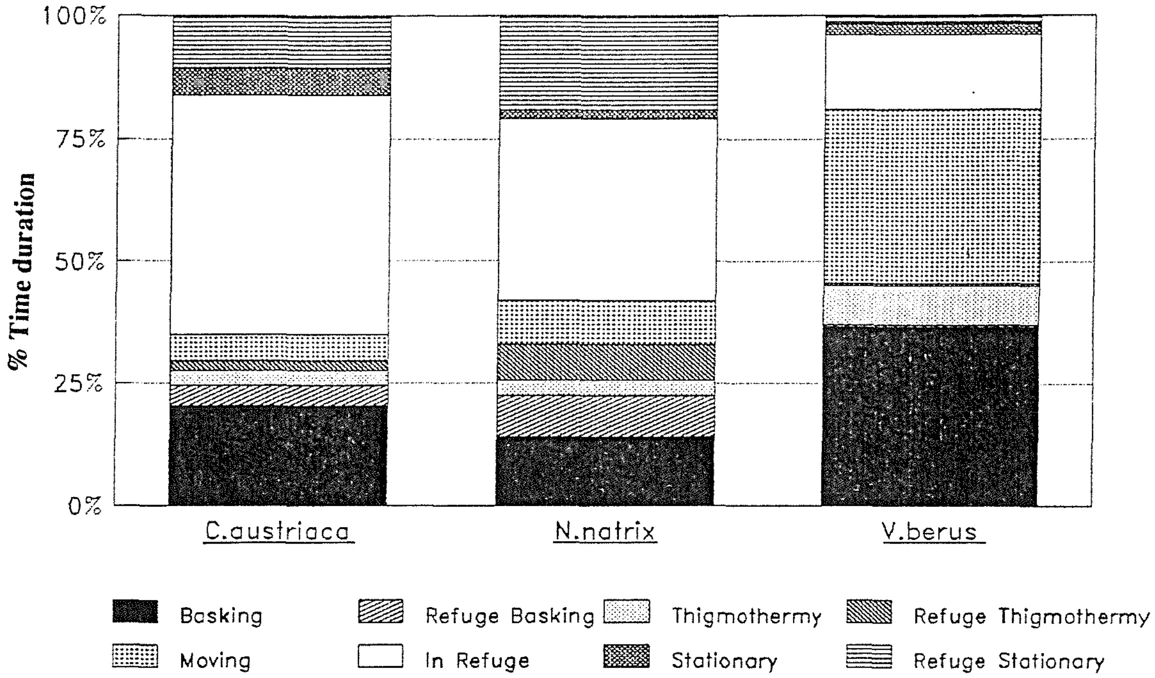
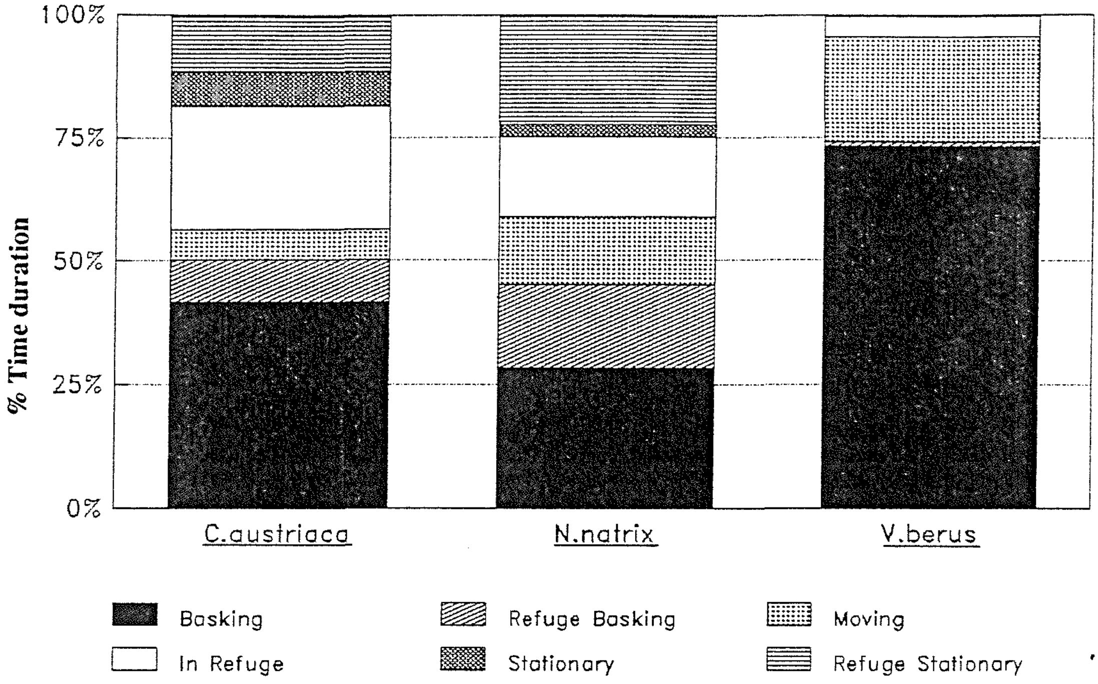


Fig. 4.3: **Percentage time duration assigned to each of the main behavioural categories during all periods of the laboratory experiments (i.e. periods when the heatlamp was on combined with periods when the heatlamp was off).**

1. Thermally unlimiting conditions (heatlamp on)



2. Thermally limiting conditions (heatlamp off)

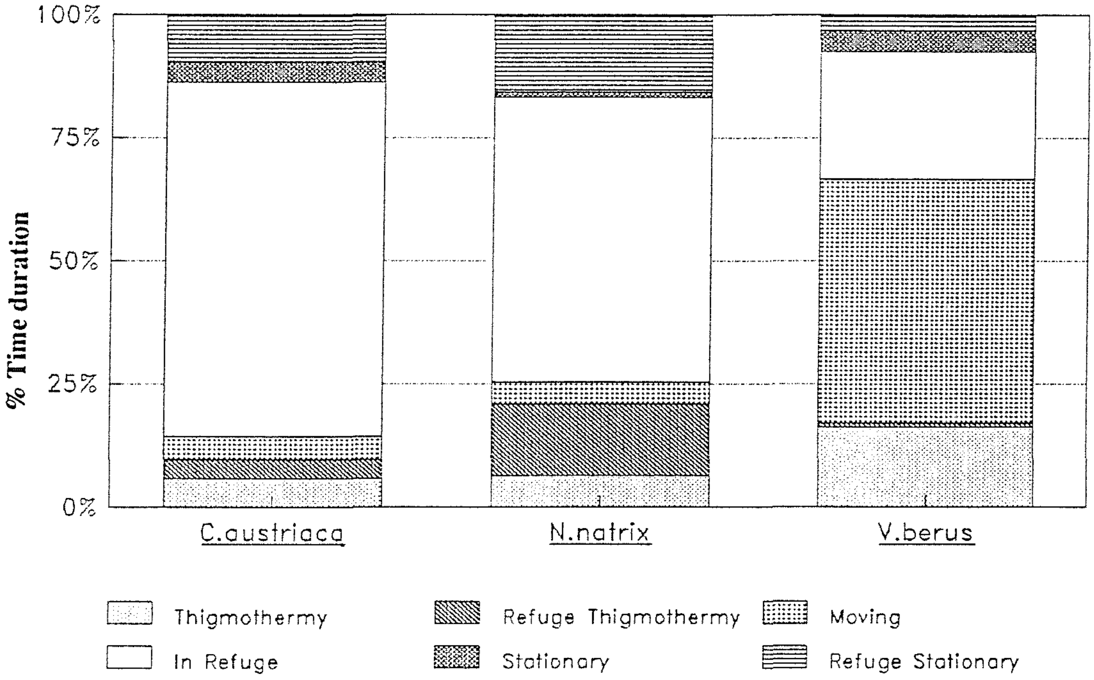


Fig. 4.4: Percentage time duration assigned to each of the main behavioural categories during thermally unlimiting and limiting conditions for the laboratory experiments.

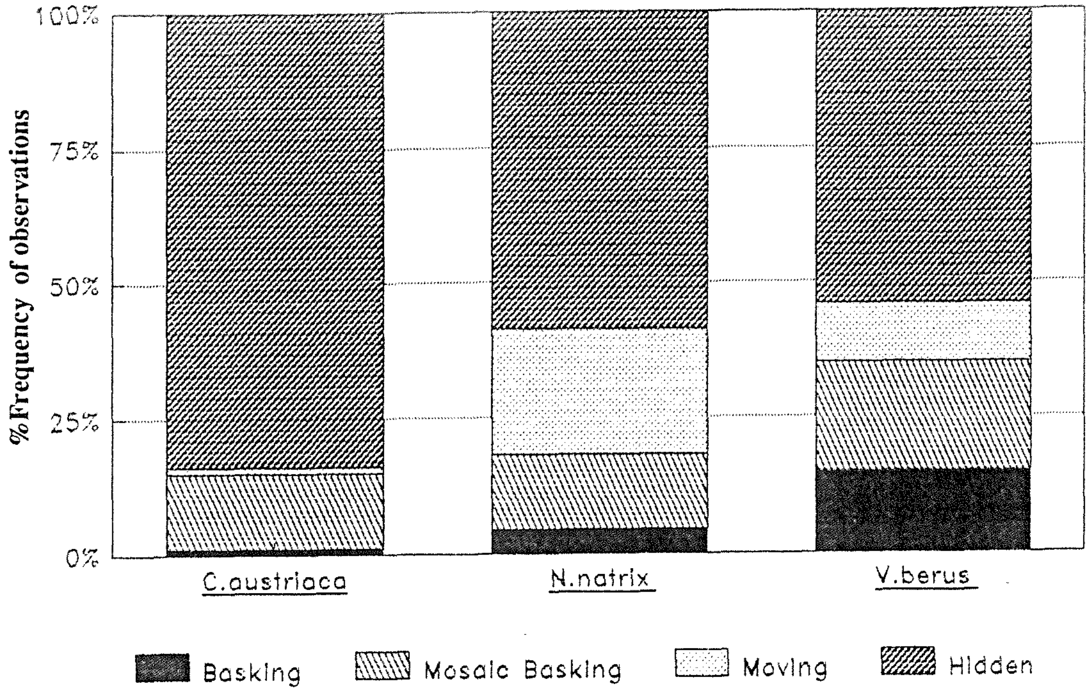


Fig. 4.5: Percentage number of observations assigned to each of the main behavioural categories during simultaneous recording in the outdoor vivaria experiments (related samples record).

	Comparisons					
	Coronella austriaca *Natrix natrix*		*Coronella austriaca* *Vipera berus*		*Natrix natrix* *Vipera berus*	
	z	p	z	p	z	p
Basking	2.045	*	3.598	***	3.266	**
Mosaic basking	0.207	NS	1.087	NS	1.350	NS
Basking + mosaic basking	0.776	NS	3.005	**	2.817	**
Moving	3.598	***	3.264	**	2.837	**
Hidden	3.159	**	3.491	***	0.952	NS

Table 4.10: **Interspecific comparisons of frequencies of observed behavioural categories recorded during simultaneous recording in the outdoor vivaria.** There were 23 days when behaviour observations were simultaneously recorded for all 3 species. Wilcoxon matched-pairs signed-ranks test statistics (z) are presented with significance levels.

NS = $p > 0.05$
* = $p < 0.05$
** = $p < 0.01$
*** = $p < 0.001$

	Coronella austriaca	*Natrix natrix*	*Vipera berus*
Basking	7	31	100
Mosaic basking	95	93	138
Basking + mosaic basking	102	124	238
Moving	9	158	74
Hidden	570	399	369
Total number of observations	681	681	681

Table 4.11: Frequencies of observed behavioural categories recorded during simultaneous recording in the outdoor vivaria.

As the results show, significant differences were detected in the frequency of basking for all 3 species but not in the frequency of mosaic basking. When basking and mosaic basking were combined, no significant difference was found between smooth snakes and grass snakes but there was significant differences between adders and smooth snakes and between adders and grass snakes. Significant differences were apparent in all the other categories except for the frequency of 'hidden' observations between grass snakes and adders.

The overall results of Table 4.11 are also presented in Fig. 4.5. A G-test was performed on the data and significant differences found in the total behaviour frequencies between smooth snakes and grass snakes, smooth snakes and adders and between grass snakes and adders ($G = 208.16$, $G = 206.05$, $G = 79.355$ respectively, $p < 0.001$, 3 d.f. in all cases).

4.3.5. Relationship Between Observed Behaviour and Body Temperature

Outdoor Vivaria Experiments

Body temperatures were recorded simultaneously with a large proportion of the behavioural observations that were made. This meant that it was possible to compare the body temperatures that were maintained by the snakes during different behavioural activities. The summary statistics of all body temperatures measured while snakes were engaged in the 4 main behavioural categories (basking, mosaic basking, moving, hidden) are provided in Table 4.12. The mean body temperatures are presented graphically in Fig. 4.6.

To allow meaningful comparisons of body temperatures and behaviour, data recorded during thermally limiting and thermally unlimiting conditions were used for statistical analysis. The basic summary statistics are provided in Table 4.13 and Fig. 4.7. Note that during thermally unlimiting conditions no body temperature data were available for smooth snakes observed basking.

Two main statistical tests were performed on the data. An interspecific comparison of body temperatures was carried out for the 4 main behavioural categories plus a combined basking/mosaic basking category. A Kruskal-Wallis test was performed on each behavioural category between the 3 species. If a significant result was found, then a series of Wilcoxon/Mann-Whitney tests was performed on each species pairwise combination. The results are displayed in Table 4.14. Note that during thermally limiting conditions, significant

		Body temperatures (°C)					
		n	Mean	SD	Median	Min	Max
Basking	*Coronella austriaca*	9	24.86	3.712	24.60	20.3	29.5
	Natrix natrix	49	22.40	4.503	22.40	10.6	30.8
	Vipera berus	171	27.01	5.501	27.80	9.8	36.1
Mosaic basking	*Coronella austriaca*	160	23.78	4.910	24.60	12.7	32.7
	Natrix natrix	160	23.43	5.633	23.85	9.5	34.5
	Vipera berus	347	27.79	7.303	31.00	9.2	39.9
Basking + mosaic basking	*Coronella austriaca*	169	23.84	4.850	24.60	12.7	32.7
	Natrix natrix	209	23.19	5.397	23.40	9.5	34.5
	Vipera berus	518	27.53	6.766	30.00	9.2	39.9
Moving	*Coronella austriaca*	14	23.94	4.841	23.20	14.3	31.5
	Natrix natrix	207	24.80	4.828	26.00	7.5	32.9
	Vipera berus	93	24.31	6.615	25.50	2.8	35.6
Hidden	*Coronella austriaca*	897	20.63	6.995	18.20	7.7	33.4
	Natrix natrix	642	17.58	7.895	15.05	2.8	35.0
	Vipera berus	852	17.80	8.551	15.20	2.2	36.6

Table 4.12: Summary statistics of all body temperatures recorded for the main behavioural categories in the outdoor vivaria.

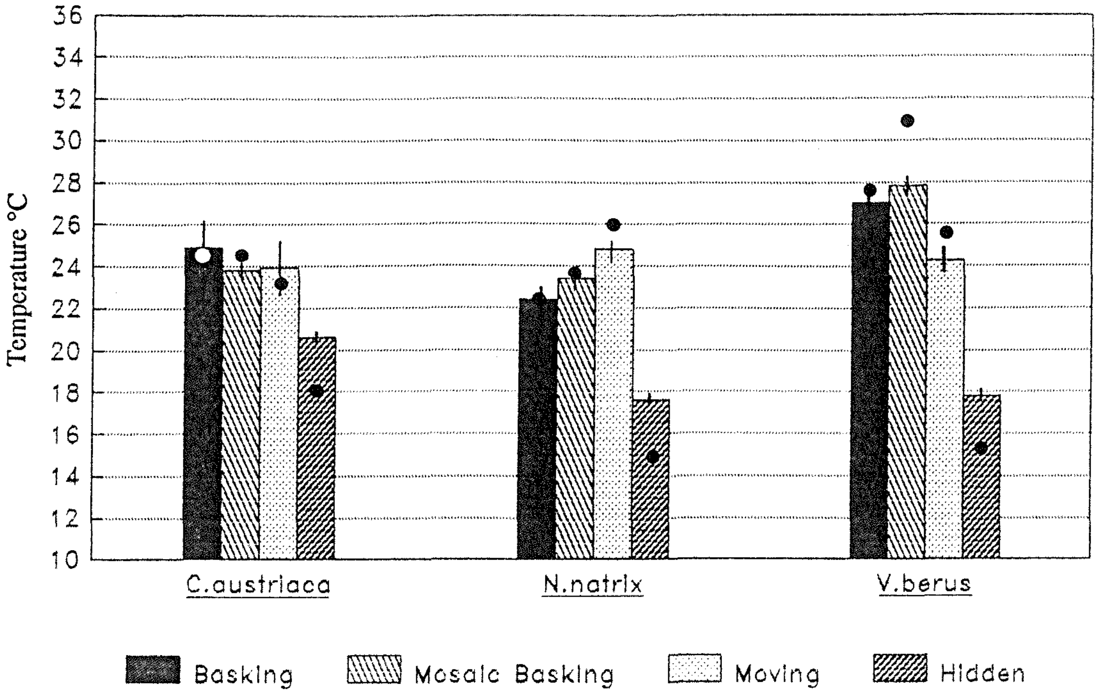


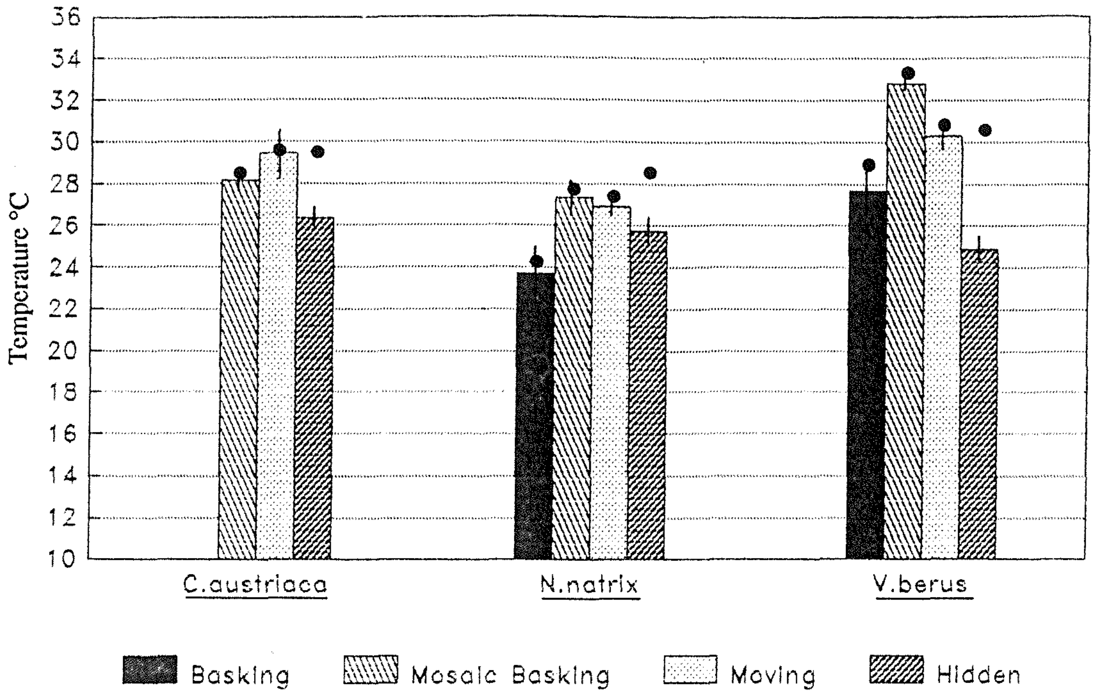
Fig. 4.6: **Mean body temperatures (± 1 s.e.) of snakes recorded for the main behavioural categories in the outdoor vivaria during all periods.** Median body temperature values are marked as •. The earliest recordings were made at 0645 hours; the latest at 2000 hours.

			Body temperatures (°C)				
1. Thermally unlimiting conditions		n	Mean	SD	Median	Min	Max
Basking	*Coronella austriaca*	0	- -	- -	- -	- -	- -
	Natrix natrix	11	23.66	3.703	24.35	16.0	30.2
	Vipera berus	16	27.72	4.493	29.05	17.8	33.7
Mosaic basking	*Coronella austriaca*	39	28.08	3.385	28.60	15.3	32.7
	Natrix natrix	44	27.33	4.732	27.80	14.6	34.5
	Vipera berus	129	32.80	3.127	33.40	21.1	39.9
Basking + mosaic basking	*Coronella austriaca*	39	28.08	3.385	28.60	15.3	32.7
	Natrix natrix	55	26.60	4.751	27.10	14.6	34.5
	Vipera berus	145	32.24	3.654	33.20	17.8	39.9
Moving	*Coronella austriaca*	4	29.35	2.022	29.60	26.7	31.5
	Natrix natrix	89	26.93	3.656	27.40	7.5	32.9
	Vipera berus	25	30.29	2.744	30.90	24.1	35.6
Hidden	*Coronella austriaca*	289	26.29	6.554	29.50	9.1	33.4
	Natrix natrix	181	25.72	6.938	28.70	2.8	35.0
	Vipera berus	215	24.88	9.479	30.50	4.8	36.2

			Body temperatures (°C)				
2. Thermally limiting conditions		n	Mean	SD	Median	Min	Max
Basking	*Coronella austriaca*	9	24.86	3.712	24.60	20.3	29.5
	Natrix natrix	33	22.46	4.793	22.20	10.6	30.8
	Vipera berus	138	26.60	5.505	27.10	9.8	36.1
Mosaic basking	*Coronella austriaca*	110	22.24	4.465	22.55	12.7	32.4
	Natrix natrix	89	21.40	5.140	20.50	9.5	32.3
	Vipera berus	136	23.02	6.859	21.10	9.2	34.5
Basking + mosaic basking	*Coronella austriaca*	119	22.44	4.453	22.60	12.7	32.4
	Natrix natrix	122	21.69	5.050	20.80	9.5	32.3
	Vipera berus	274	24.83	6.456	25.50	9.2	36.1
Moving	*Coronella austriaca*	10	21.78	3.782	21.90	14.3	27.6
	Natrix natrix	95	22.45	4.629	23.50	8.6	30.2
	Vipera berus	53	20.66	5.533	20.10	2.8	33.7
Hidden	*Coronella austriaca*	453	17.67	5.013	16.40	7.7	31.1
	Natrix natrix	303	14.32	5.936	14.00	2.8	33.3
	Vipera berus	386	15.03	6.345	14.50	2.2	36.6

Table 4.13: Summary statistics of body temperatures recorded for the main behavioural categories in the outdoor vivaria during thermally unlimiting and limiting conditions.

1. Thermally unlimiting conditions



2. Thermally limiting conditions

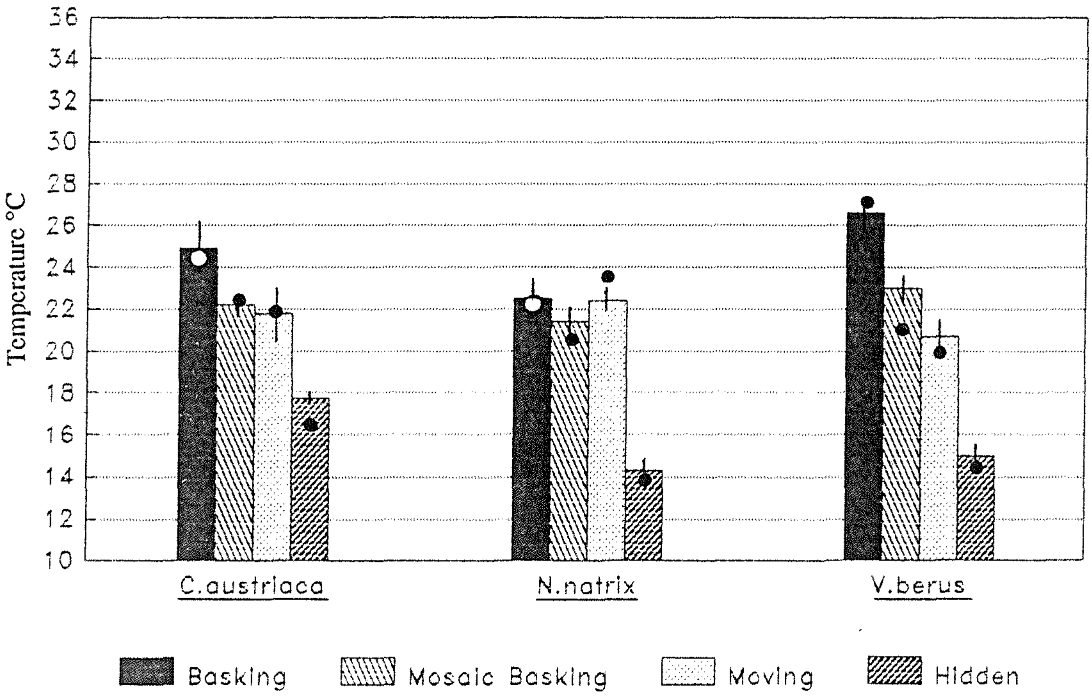


Fig. 4.7: **Mean body temperatures (± 1 s.e.) of snakes recorded for the main behavioural categories in the outdoor vivaria during thermally unlimiting and limiting conditions.** Median body temperature values are marked as •.

	Species combinations for statistical comparison							
	Coronella austriaca *Natrix natrix* *Vipera berus*		*Coronella austriaca* *Natrix natrix*		*Coronella austriaca* *Vipera berus*		*Natrix natrix* *Vipera berus*	
(i) Results from thermally unlimiting conditions	χ^2	p	z	p	z	p	z	p
Basking	NA	NA	NA	NA	NA	NA	2.345	*
Mosaic basking	93.223	***	0.625	NS	7.771	***	7.463	***
Basking plus mosaic basking	89.829	***	1.629	NS	7.049	***	7.821	***
Moving	22.100	***	1.553	NS	0.949	NS	4.551	***
Hidden	6.128	*	1.643	NS	1.777	NS	1.9825	*
(ii) Results from thermally limiting conditions								
Basking	16.297	***	1.472	NS	1.184	NS	3.932	***
Mosaic basking	3.269	NS	- -	- -	- -	- -	- -	- -
Basking plus mosaic basking	30.223	***	1.213	NS	3.919	***	4.818	***
Moving	5.924	NS	- -	- -	- -	- -	- -	- -
Hidden	93.086	***	8.505	***	7.708	***	1.59	NS

Table 4.14: **Interspecific comparison of body temperatures recorded for the main behavioural categories in the outdoor vivaria.**
Comparisons between all 3 species have been made with the Kruskal-Wallis test (statistic = χ^2).
Comparisons between 2 species have been made with the Wilcoxon/Mann-Whitney pairs test (statistic = z).

NS = $p > 0.05$
* = $p < 0.05$
** = $p < 0.01$
*** = $p < 0.001$
NA = not applicable due to small sample size

		Basking	Mosaic Basking	Moving
Natrix natrix	Basking	- -		
	Mosaic basking	2.757 **	- -	
	Moving	3.151 **	1.074 NS	- -
	Hidden	2.124 *	0.618 NS	1.328 NS
Vipera berus	Basking	- -		
	Mosaic basking	4.867 ***	- -	
	Moving	1.764 NS	4.634 ***	- -
	Hidden	0.070 NS	8.066 ***	0.959 NS

Table 4.15: **Intraspecific comparisons of body temperatures recorded for the main behavioural categories in the outdoor vivaria during thermally unlimiting conditions.**
Note that no significant differences were found between the body temperatures of the main behavioural categories in *Coronella austriaca.*

Significance levels are provided with Wilcoxon/Mann-Whitney pairs test statistics (z).

NS = $p > 0.05$
* = $p < 0.05$
** = $p < 0.01$
*** = $p < 0.001$
NA = not applicable due to small sample size

		Basking	Mosaic Basking	Moving
Coronella austriaca	Basking	- -		
	Mosaic basking	1.684 NS	- -	
	Moving	1.675 NS	0.299 NS	- -
	Hidden	3.776 ***	8.541 ***	2.755 **
Natrix natrix	Basking	- -		
	Mosaic basking	1.228 NS	- -	
	Moving	0.087 NS	1.803 NS	- -
	Hidden	6.741 ***	9.250 ***	10.411 ***
Vipera berus	Basking	- -		
	Mosaic basking	4.341 ***	- -	
	Moving	6.031 ***	2.008 *	- -
	Hidden	14.098 ***	11.108 ***	6.825 ***

Table 4.16: **Intraspecific comparisons of body temperatures recorded for the main behavioural categories in the outdoor vivaria during thermally limiting conditions.**
Significance levels are provided with Wilcoxon/Mann-Whitney pairs test statistics (z).

NS = $p > 0.05$
* = $p < 0.05$
** = $p < 0.01$
*** = $p < 0.001$
NA = not applicable due to small sample size

differences were found in the body temperatures of smooth snakes and grass snakes when they were hidden, between smooth snakes and adders when they were hidden and basking/mosaic basking, and between grass snakes and adders when they were observed basking and basking/mosaic basking. During thermally unlimiting conditions, no significant differences were found between the grass snake and smooth snake behavioural categories whereas body temperatures varied significantly for all behavioural categories between grass snakes and adders. Smooth snakes and adders varied significantly in the mosaic basking and basking/mosaic basking categories.

The second main statistical test was an intraspecific comparison of body temperatures between the 4 main behavioural categories for each species. The same procedure was used as that in the interspecific comparison. When conditions were thermally unlimiting, no significant difference was found between the body temperatures of the 4 main behavioural categories of smooth snakes (Kruskal-Wallis chi-squared = 0.712, $n = 341$, $p > 0.05$). Significant differences were found for grass snakes (chi-squared = 8.704, $n = 325$, $p < 0.05$) and adders (chi-squared = 75.631, $n = 385$, $p < 0.001$). When conditions were thermally limiting, significant differences were detected in all 3 species (chi-squared = 88.542, $n = 582$ for smooth snakes, chi-squared = 178.16, $n = 520$ for grass snakes, chi- squared = 280.41, $n = 713$ for adders, $p < 0.001$ in all cases). Where significant differences were found between behavioural categories within species, a series of Wilcoxon/Mann-Whitney comparisons was performed on each behaviour pairwise combination. The results are presented in Tables 4.15 and 4.16.

For grass snakes during thermally unlimiting periods, there were significant differences between the body temperatures of basking behaviour and all other behavioural categories. Mosaic basking adders body temperatures varied significantly from when they were engaged in basking, moving or hidden behaviour.

When conditions were thermally limiting, smooth snakes that were hidden had significantly different body temperatures to when they were observed engaged in the other 3 main behavioural categories. This was also the case for grass snakes and adders. In addition to this, adders also had significantly different body temperatures in all the other 3 possible behaviour combinations.

Activity temperatures were calculated for each species from the combined basking, mosaic basking and moving behavioural categories. During thermally unlimiting conditions, activity temperatures for smooth snakes ranged from 15.3 - 32.2°C (mean 28.10° ± 3.315, median 28.65°C, n = 43). As the minimum and maximum activity temperatures represent extreme values, 5% and 95% percentiles were also calculated (18.4°C and 31.95°C respectively). During thermally limiting conditions, activity temperatures ranged from 12.7 - 32.4°C for smooth snakes (mean 22.39°C ± 4.395, median 22.6°C, 5% percentile 15.3°C, 95% percentile 29.05°C, n = 129).

The activity temperatures of grass snakes during thermally unlimiting conditions ranged from 7.5 - 34.5°C (mean 26.80°C ± 4.096, median 27.4°C, 5% percentile 18.45°C, 95% percentile 32.3°C, n = 144). During thermally limiting conditions, activity temperatures ranged from 8.6 - 32.3°C (mean 22.02°C ± 4.874, median 22.2°C, 5% percentile 14.29°C, 95% percentile 29.53°C, n = 217).

During thermally unlimiting conditions, the activity temperatures recorded for adders ranged from 17.8 - 39.9°C (mean 31.95°C ± 3.595, median 32.9°C, 5% percentile 23.4°C, 95% percentile 35.88°C, n = 170). For measurements from thermally limiting conditions, activity temperatures ranged from 2.8 - 36.1°C (mean 24.15°C ± 6.493, median 24.4°C, n = 327).

Laboratory Experiments

The data recorded during the laboratory experiments were treated in the same way as the data recorded during the outdoor vivaria experiments. Records from thermally unlimiting conditions (heatlamp on) and thermally limiting conditions (heatlamp off) have been analysed separately. The summary statistics of the body temperatures of the behavioural data are given in Table 4.17 for thermally unlimiting conditions and Table 4.18 for thermally limiting conditions. The graphs of Fig. 4.8 illustrate the results for the respective categories.

Interspecific comparisons were once again examined with the aid of Kruskal-Wallis and Wilcoxon/Mann-Whitney tests. The results are given in Table 4.19. During thermally unlimiting conditions, there was significant variation between species for all behavioural categories except refuge basking in the case of smooth snakes and grass snakes and between adders and grass snakes, and stationary behaviour between smooth snakes and grass snakes. There were insufficient data to make a comparison between adders and the other 2 species for the stationary and refuge stationary behavioural categories.

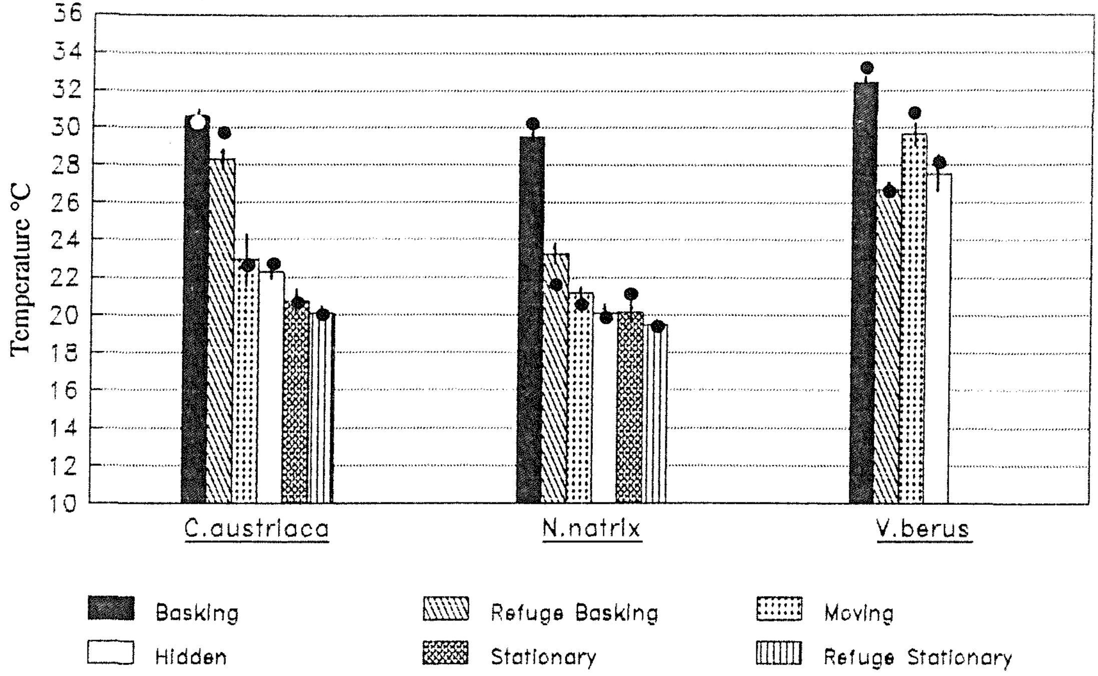
		Body temperatures (°C)					
		n	Mean	SD	Median	Min	Max
Basking	*Coronella austriaca*	234	30.63	1.468	30.55	25.1	35.3
	Natrix natrix	266	29.53	3.838	30.20	17.0	37.1
	Vipera berus	141	32.42	3.028	33.10	19.8	37.2
Refuge basking	*Coronella austriaca*	53	28.32	3.151	29.80	21.4	32.6
	Natrix natrix	141	23.31	4.285	21.70	17.8	35.1
	Vipera berus	8	26.84	5.506	26.90	20.0	34.3
Basking + refuge basking	*Coronella austriaca*	287	30.21	2.091	30.50	21.4	35.3
	Natrix natrix	407	27.37	4.971	28.90	17.0	37.1
	Vipera berus	149	32.12	3.420	33.00	19.8	37.2
Moving	*Coronella austriaca*	12	22.98	3.587	22.50	19.2	32.5
	Natrix natrix	173	21.17	2.817	21.10	16.5	33.4
	Vipera berus	60	29.73	3.567	30.70	18.4	36.3
Hidden	*Coronella austriaca*	49	22.26	1.369	22.70	19.6	24.0
	Natrix natrix	116	20.11	2.629	19.90	16.8	31.5
	Vipera berus	18	27.61	4.274	28.10	18.5	35.0
Thigmothermy	*Coronella austriaca*	}					
	Natrix natrix	}	Not applicable				
	Vipera berus	}					
Refuge thigmothermy	*Coronella austriaca*	}					
	Natrix natrix	}	Not applicable				
	Vipera berus	}					
Stationary	*Coronella austriaca*	18	20.77	1.787	20.75	18.7	23.5
	Natrix natrix	23	20.20	2.240	21.10	16.9	22.7
	Vipera berus	0	- -	- -	- -	- -	- -
Refuge stationary	*Coronella austriaca*	50	20.13	1.788	20.10	18.0	26.0
	Natrix natrix	256	19.49	1.755	19.40	16.7	28.5
	Vipera berus	0	- -	- -	- -	- -	- -

Table 4.17: Summary statistics of body temperatures recorded for the main behavioural categories in the laboratory during thermally unlimiting conditions (heatlamp on).

			Body temperatures (°C)				
		n	Mean	SD	Median	Min	Max
Basking	*Coronella austriaca*	]					
	Natrix natrix	]		Not applicable			
	Vipera berus	]					
Refuge basking	*Coronella austriaca*	]					
	Natrix natrix	]		Not applicable			
	Vipera berus	]					
Basking + refuge basking	*Coronella austriaca*	]					
	Natrix natrix	]		Not applicable			
	Vipera berus	]					
Moving	*Coronella austriaca*	15	21.01	1.468	20.50	19.0	23.6
	Natrix natrix	45	20.70	2.433	20.00	17.2	27.4
	Vipera berus	82	20.55	3.059	21.10	13.6	29.3
Hidden	*Coronella austriaca*	194	21.49	1.273	21.30	18.4	27.4
	Natrix natrix	410	19.47	1.762	19.40	16.5	29.3
	Vipera berus	38	19.30	1.599	18.40	17.1	23.7
Thigmothermy	*Coronella austriaca*	19	27.08	2.896	26.80	20.3	31.4
	Natrix natrix	9	23.07	3.881	20.60	20.4	29.3
	Vipera berus	25	23.91	3.219	23.70	17.8	31.9
Refuge thigmothermy	*Coronella austriaca*	23	22.68	2.525	22.30	19.7	29.5
	Natrix natrix	70	20.63	2.593	19.80	16.9	29.4
	Vipera berus	2	21.40	2.121	21.40	19.9	22.9
Stationary	*Coronella austriaca*	13	19.10	1.365	18.60	17.7	21.7
	Natrix natrix	3	20.60	0.624	20.40	20.1	21.3
	Vipera berus	2	22.70	2.121	22.70	21.2	24.2
Refuge stationary	*Coronella austriaca*	23	20.47	1.225	20.40	18.3	23.7
	Natrix natrix	112	19.24	1.658	18.70	17.1	23.1
	Vipera berus	7	20.76	1.757	21.50	17.8	22.2

Table 4.18: Summary statistics of body temperatures recorded for the main behavioural categories in the laboratory during thermally limiting conditions (heatlamp off).

1. Thermally unlimiting conditions (heatlamp on)



2. Thermally limiting conditions (heatlamp off)

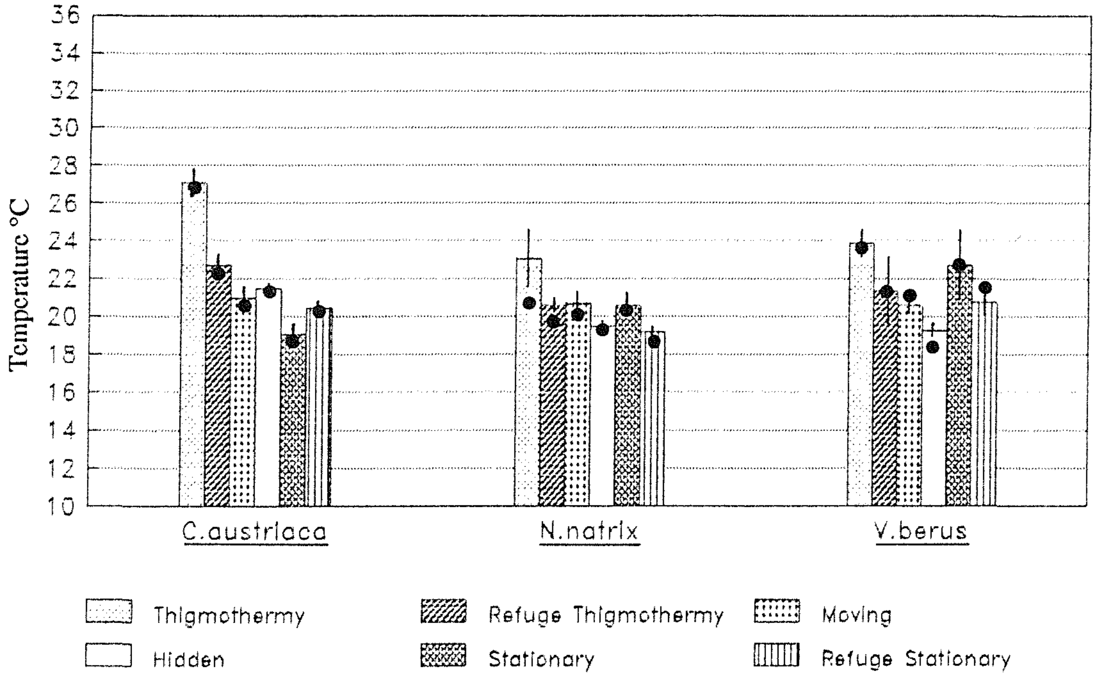


Fig. 4.8: **Mean body temperatures (± 1 s.e.) of snakes recorded for the main behavioural categories in the laboratory during thermally unlimiting and limiting conditions.** Median body temperature values are marked as •.

	Species combinations for statistical comparison							
	Coronella austriaca *Natrix natrix* *Vipera berus*		*Coronella austriaca* *Natrix natrix*		*Coronella austriaca* *Vipera berus*		*Natrix natrix* *Vipera berus*	
(i) Results from thermally unlimiting conditions (heatlamp on)	χ^2	p	z	p	z	p	z	p
Basking	92.591	***	2.527	*	8.715	***	8.399	***
Refuge basking	49.352	***	6.983	***	0.588	NS	1.836	NS
Basking plus refuge basking	154.096	***	6.960	***	8.944	***	10.792	***
Moving	108.356	***	1.993	*	4.156	***	10.280	***
In refuge	74.969	***	7.125	***	4.466	***	5.815	***
Stationary	NA	NA	0.434	NS	NA	NA	NA	NA
Refuge stationary	NA	NA	2.551	*	NA	NA	NA	NA
(ii) Results from thermally limiting conditions (heatlamp off)								
Thigmothermy	12.708	**	2.117	*	3.413	***	1.524	NS
Refuge thigmothermy	15.999	***	3.964	***	0.802	NS	0.772	NS
Moving	1.447	NS	- -	- -	- -	- -	- -	- -
In refuge	219.659	***	14.705	***	6.681	***	0.751	NS
Stationary	5.420	NS	- -	- -	- -	- -	- -	- -
Refuge stationary	13.764	**	3.282	**	1.277	NS	2.017	*

Table 4.19: **Interspecific comparison of body temperatures recorded for the main behavioural categories in the laboratory.**
Comparisons between all 3 species have been made with the Kruskal-Wallis test (statistic = χ^2).
Comparisons between 2 species have been made with the Wilcoxon/Mann-Whitney pairs test (statistic = z).

NS = $p > 0.05$
* = $p < 0.05$
** = $p < 0.01$
*** = $p < 0.001$
NA = not applicable due to small sample size

		Basking	Refuge basking	Moving	In refuge	Stationary
Coronella austriaca	Basking	- -				
	Refuge basking	4.601 ***	- -			
	Moving	4.946 ***	3.898 ***	- -		
	In refuge	11.009 ***	7.959 ***	0.172 NS	- -	
	Stationary	7.070 ***	6.075 ***	1.907 NS	3.044 **	- -
	Refuge stationary	11.095 ***	8.488 ***	3.202 **	5.168 ***	1.656 NS
Natrix natrix	Basking	- -				
	Refuge basking	11.194 ***	- -			
	Moving	15.509 ***	4.294 ***	- -		
	In refuge	14.070 ***	7.018 ***	3.822 ***	- -	
	Stationary	7.345 ***	2.809 **	0.986 NS	0.936 NS	- -
	Refuge stationary	18.591 ***	10.622 ***	6.742 ***	1.922 NS	1.698 NS
Vipera berus	Basking	- -				
	Refuge basking	2.986 **	- -			
	Moving	5.710 ***	1.380 NS	- -		
	In refuge	4.668 ***	0.333 NS	2.070 *	- -	
	Stationary	NA	NA	NA	NA	- -
	Refuge stationary	NA	NA	NA	NA	NA

Table 4.20: **Intraspecific comparisons of body temperatures recorded for the main behavioural categories in the laboratory during thermally unlimiting conditions (heatlamp on).** Significance levels are provided with Wilcoxon/Mann-Whitney pairs test statistics (z).

NS = $p > 0.05$
* = $p < 0.05$
** = $p < 0.01$
*** = $p < 0.001$
NA = not applicable due to small sample size

		Thigmothermy	Refuge Thigmothermy	Moving	In refuge	Stationary
Coronella austriaca	Thigmothermy	- -				
	Refuge thigmothermy	4.095 ***	- -			
	Moving	4.510 ***	2.017 *	- -		
	In refuge	6.388 ***	1.838 NS	1.694 NS	- -	
	Stationary	4.627 ***	4.103 ***	3.066 **	4.524 ***	- -
	Refuge stationary	5.183 ***	3.112 **	0.732 NS	3.862 ***	2.374 *
Natrix natrix	Thigmothermy	- -				
	Refuge thigmothermy	2.764 **	- -			
	Moving	2.113 *	0.568 NS	- -		
	In refuge	3.740 ***	3.368 ***	3.600 ***	- -	
	Stationary	1.129 NS	1.098 NS	0.746 NS	1.806 NS	- -
	Refuge stationary	3.306 ***	4.199 ***	3.841 ***	1.638 NS	1.457 NS
Vipera berus	Thigmothermy	- -				
	Refuge thigmothermy	1.297 NS	- -			
	Moving	4.416 ***	0.367 NS	- -		
	In refuge	5.618 ***	1.556 NS	2.986 **	- -	
	Stationary	0.463 NS	0.775 NS	1.116 NS	1.929 NS	- -
	Refuge stationary	2.852 **	0.596 NS	0.419 NS	2.103 *	0.596 NS

Table 4.21: **Intraspecific comparisons of body temperatures recorded for the main behavioural categories in the laboratory during thermally limiting conditions (heatlamp off).**
Significance levels are provided with Wilcoxon/Mann-Whitney pairs test statistics (z).

NS = p > 0.05
* = p < 0.05
** = p < 0.01
*** = p < 0.001
NA = not applicable due to small sample size

Significant variation in body temperatures was found for thigmothermy, refuge thigmothermy, 'in refuge' and refuge stationary behaviour between smooth snakes and grass snakes when conditions were thermally limiting. Similar results occurred between smooth snakes and adders for thigmothermy and 'in refuge' behaviour and between grass snakes and adders for refuge stationary behaviour.

Intraspecific comparisons of body temperatures during thermally unlimiting conditions were carried out on the main behavioural categories. Kruskal-Wallis tests revealed significant intraspecific differences in behavioural body temperatures for all 3 species in thermally unlimiting periods (chi-squared = 268.94, n = 416 for smooth snakes, chi-squared = 522.23, n = 975 for grass snakes, chi-squared = 51.74, n = 227 for adders, $p < 0.001$ for all cases) and thermally limiting conditions (chi-squared = 76.356, n = 287 for smooth snakes, chi-squared = 43.067, n = 649 for grass snakes, chi-squared = 38.595, n = 156 for adders, $p < 0.001$ in all cases). These comparisons were therefore investigated further using a series of Wilcoxon/Mann-Whitney tests between all behavioural combinations within each species. The results are given in Tables 4.20 and 4.21.

Intraspecific comparisons of data from thermally unlimiting conditions revealed significant differences between the body temperature of most behavioural combinations in each species. The same result was true for smooth snakes when conditions were categorised as thermally limiting. There were less significant differences for the data of grass snakes and adders from the thermally limiting conditions, especially between the stationary category and other behavioural categories, mainly as a result of the very small sample sizes involved.

4.4. Discussion

4.4.1. Daily Emergence

The measurements of daily emergence obtained from the outdoor vivaria showed that snakes emerged over a wide range of times and at varying ambient and body temperatures. However, there were certain patterns to daily emergence that could be identified, and a certain degree of interspecific variation. The role of endogenous rhythms in emergence (and other aspects of daily activity patterns) has not been investigated in the present study. However, as snakes are ectothermic, external environmental factors are likely to heavily influence their behavioural patterns.

The first major point was that no snake of any species was observed to emerge before the beginning of the 'lit' phase. This was noted for all days, not just those that have been used for the interspecific comparisons (Tables 4.1 - 4.3). The beginning of the 'lit' phase (as described in Section 3.3.1) was the time when the sun was in a position to shine directly on the floor of the vivaria, even when it was obscured by cloud. The earliest time that the 'lit' phase began was 0750 hours during experiments that were undertaken in the summer (experiments 3, 4 and 11). The presence of the vivaria walls unavoidably resulted in the vivaria being shaded for a longer time than would have been the case in certain situations in the field. The sun rises at 0450 hours on mid-summer day and so at that time of the year there would have been a gap of about 3 hours before the sun began to shine on the vivaria floor.

Emergence of snakes occurred after the commencement of the 'lit' phase which suggests that the warming effect of the direct sun on the snakes' overnight refuges could have had a direct stimulatory effect. Earlier emergence might have occurred if the vivaria had been in a position to receive the sun earlier. This view is supported by the fact that Prestt (1971) observed adders basking in the sun at 0630 and 0740 hours (Dorset, southern England) and Brown (pers.comm.) monitored grass snakes basking before 0700 hours on sunny, summer mornings.

The comparison between species seemed to indicate that there was no distinct difference between the daily emergence behaviour of smooth snakes and grass snakes. Grass snakes did tend to emerge before smooth snakes on more occasions and at slightly lower ambient and body temperatures but the difference was not great. Adders were observed to emerge more often than smooth snakes, before smooth snakes on more occasions, at slightly earlier times and at lower body temperatures and lower ambient temperatures. The same pattern was observed between adders and grass snakes, with adders emerging more often, earlier and at cooler temperatures.

Saint Girons (1978) noted that the adders he was studying in an outdoor vivarium tended to emerge earlier than the other 5 European viper species he was comparing. However, he considered that the result of an earlier emergence was slower heating rates due to the reduced radiative intensity of the sun. Even so, adders were observed to attain their selected body temperatures before the other species.

There was a general tendency for all 3 species to emerge at earlier times during the mid-summer periods than at other times, although this aspect has not been fully analysed. The pattern was less distinct for 1988, which had a relatively cool summer. Avery and McArdle

(1973) examined the morning emergence of common lizards, Lacerta vivipara, and found that they tended to emerge later on sunny spring days than on sunny summer days. They suggested that the actual time of emergence was related to the speed at which a lizard could reach its selected temperature. If a lizard emerged too early, then it would have to bask for an excessively long time before attaining its selected body temperature. However, if it emerged too late, it might warm up relatively quickly but would have less time available for feeding.

During the mid-summer periods the maximum operative temperatures available for post-emergent snakes at the beginning of the 'lit' phase was usually higher than during the early or later part of their activity season. Thus snakes tended to delay emergence during the latter periods until operative temperatures had increased. Even so, they still emerged at lower ambient temperatures (and with lower body temperatures) during the early and later period of the activity season. Late April 1989 was a particularly cold time and on 26.4.89 a grass snake emerged at 1030 hours when the ambient temperature was 2.6°C. The emergence body temperature was recorded as 2.8°C but it should be recalled that this was the measurement taken 15 mins before the first siting (i.e. 1015 hours, when the snake was still 'hidden'). The snake was actually 7.5°C when it was seen at 1030 hours. There was no cloud cover, there had been a frost during the night and the ambient temperature was low. However, the sun was also shining and maximum model temperatures were >40°C by 1000 hours. Therefore relating emergence times to ambient temperatures alone can be misleading as they may be low even when maximum operative temperatures are very high. In this example, as in other cases, the grass snake (which was thought to have been under the cover of the dead vegetation in the northwest corner) was probably stimulated to emerge by the effect of the sun shining directly on the area in which it was hidden.

The results of the interspecific comparisons and the overall impression of observations made during the outdoor vivaria experiments suggested that adders tended to emerge earlier and at slightly lower body and ambient temperatures. Snakes basking during the early morning are likely to be at particular risk as they are in the open and at relatively low body temperatures. Locomotory abilities of snakes are affected by body temperatures (Heckrotte 1962, Hailey and Davies 1986) and they are likely to be less able to evade potential predators at low body temperatures. If adders emerge at earlier times they might be expected to heat up at slower rates, which is what Saint Girons (1978) observed (see above). This would therefore imply that the adders are more likely to risk potential predation than smooth snakes and grass snakes by basking earlier and at lower temperatures, but also benefit by attaining selected body temperatures earlier. Other factors will also be involved in determining heating rates, such as behavioural mechanisms (e.g.the dorso-ventral flattening posture displayed by adders), body size and integument reflectance.

It was noticeable that adders were often observed basking in the northwest corner only a few minutes after the first direct sun shone on the floor of the vivaria. This was also observed in grass snakes and smooth snakes but to a lesser extent. It suggests that on those occasions the snakes had been submerged under the heap of decomposing vegetation in the northwest corner and were therefore best able to detect the first direct sunlight in the vivaria. There is a possibility that such sites could have been selected to permit early morning basking behaviour. However, suitable refuges available for submergence were limited in the vivaria and the pile of decomposing vegetation may have been frequently selected as it simply provided good cover.

Details on daily submergence have not been investigated in detail but it was observed that snakes were very rarely observed once the 'lit' phase had ended. Only 4 observations of moving grass snakes and 1 observation of a 'basking' adder were made at the start of the 'unlit' period. The adder had been basking in the last direct rays of the sun and would probably have shortly moved under cover had it not been removed. Snakes were sometimes seen basking at the very end of the 'lit' phase (especially adders) but hid away once the vivaria moved into shadow.

In the laboratory the relatively high ambient, nocturnal temperatures may have resulted in the extensive activity observed in adders. This is discussed further in Section 4.4.3. Grass snakes and smooth snakes were also observed outside refuges after midnight during the nocturnal period but on relatively few days. Head emergence was observed on most days for both grass snakes and smooth snakes. This behaviour has also been observed by Hammerson (1979) and de Bont et al. (1986). The latter authors noted head emergence in smooth snakes prior to full emergence. The former author noted head emergence in the striped racer, Masticophis lateralis, and suggested that the warming of the head in the morning sun may have triggered emergence when a certain precise level of head temperature was reached. Alternatively, it may have functioned to alert the snake to environmental conditions outside the burrow. It would be important for snakes to check for the presence of potential predators as they would be particularly vulnerable after full emergence due to the reasons discussed above.

In the present study, smooth snakes often displayed head emergence after the light turned on but did not fully emerge until the heatlamp was on as well. Grass snakes also did not tend to fully emerge until after the heatlamp was on. Those snakes that were in refuge 1 closest to the heatlamp tended to fully emerge earlier than those in refuges that the opposite end of the arena. A snake that was engaged in head emergence at refuge 1 would have been warmed once the heatlamp turned on and this could have resulted in earlier full emergence. Snakes may have frequently engaged in head emergence prior to full emergence during the outdoor vivaria experiments but it was only seen in grass snakes on a couple of occasions. However, it would have been easy to miss such behaviour due to the dense vegetation in some areas of the vivaria.

4.4.2. Outdoor Vivaria Experiments

The results of all behavioural observations recorded from snakes in the outdoor vivaria were included in Section 4.3.3. Significant differences in the frequencies of the main behavioural categories (basking, mosaic basking, moving, hidden) were observed between species. However, the behaviour of reptiles has been shown to vary with regard to environmental conditions (Heath 1965, Hailey and Davies 1987, Losos 1987) and there is the danger that any interspecific differences that might be shown through comparison of the data could be due to recording from periods of differing operative temperatures. The behavioural recording of smooth snakes, for example, might have occurred during proportionately longer periods of thermally limiting conditions than was the case for adders. The same problem was found in the comparison of body temperatures (discussed in Section 3.4.1). To allow more direct comparisons, conditions were described as thermally limiting or thermally unlimiting and the behavioural data divided according to the type of conditions the snakes were subjected to at the time of each observation.

When conditions were thermally unlimiting it was theoretically possible for snakes to attain selected body temperatures, subject to them being in the right areas of the vivaria. When conditions were described as thermally limiting, maximum model temperatures in the vivaria were <34°C. Although it was more difficult for snakes to maintain selected body temperatures during the latter conditions, the maximum model temperatures (which estimated the operative temperatures) could still vary to some extent below the 34°C level and therefore the body temperatures that could be attained could vary likewise. Therefore caution should be taken when making interspecific comparisons between behavioural data during thermally limiting conditions (as has previously been discussed in Section 3.4.1 with regards to comparison of body temperature data). The frequencies of observations for the different behavioural categories were still significantly different between the 3 species when conditions were thermally limiting or thermally unlimiting.

Another problem was that it was not always possible to tell what form of behaviour a snake was engaged in when it was 'hidden' from view. For this reason a further analysis could be undertaken on behavioural time budget data but with 'hidden' observations excluded. Alternatively, in some cases an examination of body temperature records could provide an indication of a snake's behaviour when hidden and this information could be incorporated into an analysis. However, this is a matter for future consideration.

The proportion of times that smooth snakes were hidden from the observer was particularly high when conditions were thermally unlimiting (88.4% of observations). Heliothermic behaviour was observed in the form of mosaic basking but basking (i.e. not in the shade of cover) was never seen during such conditions. Relatively high body temperatures were recorded during 'hidden' behaviour (mean 26.29°C ± 3.656, median 29.5°C) which were not significantly different from those recorded during moving or mosaic basking behaviour. The maximum body temperature recorded during 'hidden' behaviour was 33.4°C which illustrates that smooth snakes were able to attain relatively high body temperatures even when they were not exposed. On some sunny days during recording, the body temperatures of smooth snakes showed a distinct heating phase and then a precisely maintained plateau phase but it proved impossible to spot the snakes. Binoculars were used and the vivaria were observed from different viewpoints. However, the bask sites of the snakes were well hidden and the animals could not be seen.

During thermally limiting conditions, the proportion of 'hidden' snake observations was slightly less for smooth snakes (81.8%). Basking was seen in this instance (1.9%) but mosaic basking was still the most frequently observed form of the 2 heliothermic categories (14.7%). Mosaic basking and basking were observed more often than during thermally unlimiting conditions. There was a significant difference in the frequencies of behavioural categories between thermally limiting and unlimiting conditions. The lowest body temperatures were recorded for 'hidden' snakes and significant differences were found between this category and the other 3 behavioural categories. No significant differences in body temperatures existed between basking, mosaic basking and moving behaviour.

Grass snakes were less often hidden than smooth snakes when conditions were thermally unlimiting (68.7%). The second most common behaviour was movement (19.2%). A relatively small proportion of basking was observed (2.4%) and mosaic basking was seen on 9.7% of the recordings. The body temperatures of the basking observations were lower and significantly different to those of the other behavioural categories (the body temperatures of the other 3 categories were not significantly different from each other). This fits in with the general observation that during hot days, the grass snakes tended to use basking behaviour soon after emergence but once higher body temperatures were attained, the snakes engaged in one of the other behavioural categories (including mosaic basking). Thus the body temperatures of basking grass snakes were relatively low as they represented the heating phase temperatures. Relatively high body temperatures were again maintained during 'hidden' behaviour.

The frequencies of the observed grass snake behavioural categories during thermally limiting conditions were significantly different to those of thermally unlimiting conditions. The grass snakes were more likely to be hidden during the cooler conditions (77.7%) and the proportion of movement observations, although still higher than the other 2 species during thermally limiting or unlimiting conditions, was lower (8.3%). The proportions of mosaic basking (11.2%) and basking (2.8%) both increased slightly. The body temperatures of grass snakes observed 'hidden' were lowest and were significantly different from those of the other observed behavioural categories. There were no significant differences between the body temperatures of the other behavioural groups.

Adders were the least 'hidden' of the 3 species when conditions were thermally unlimiting (63.4% of observations). More time was spent engaged in the heliothermic behavioural categories than the other 2 species with 26.8% of observations recorded for mosaic basking and 4.7% of observations recorded for basking. The highest body temperatures were measured in adders engaged in mosaic basking behaviour (mean 32.80° ± 3.127, median 33.4°C) and were significantly different from those of the other behavioural categories. There was no significant difference between the body temperatures of the other behavioural categories. Basking behaviour was displayed during the heating phases of adders and, when conditions were thermally unlimiting, they commenced mosaic basking once selected body temperatures had been attained. Thus body temperatures of mosaic basking adders were higher than basking adders in such conditions.

When basking and mosaic basking were combined into one heliothermic behavioural category for adders, it is interesting to note that there was no significant difference in the frequencies of behavioural observations between thermally limiting and thermally unlimiting conditions. The proportions for the combined heliothermic category were 31.5% for thermally unlimiting conditions and 35.3% for thermally limiting conditions. However, when the frequencies of basking and mosaic basking were separated, then a significant difference in the overall behavioural frequencies between the 2 conditions could be identified. This was because the proportion of basking observations was much greater during thermally limiting conditions (18.2% of observations were for basking and 17.1% for mosaic basking). The body temperatures of basking adders were higher and significantly different to the those of the other behavioural categories (mean 26.60° ± 5.505, median 27.1°C). Mosaic basking, moving and 'hidden' behaviour showed successively lower body temperatures and were all significantly different from one another.

Overall, the body temperatures of adders were higher and significantly different to those of all the behavioural categories of grass snakes during thermally unlimiting conditions. They were also higher and significant different to those of the smooth snakes in the mosaic basking and combined basking/mosaic basking categories (although there were no data for smooth snakes when basking). No significant differences existed between smooth snake and grass snake body temperatures.

The results of the related samples behavioural frequency comparisons (Section 4.3.4) appeared to confirm many of the patterns of behavioural budgeting that was observed in the 3 species in the above paragraphs. Observations were made during varying environmental conditions but as recordings for the 3 species were made simultaneously, direct comparisons could be made. Smooth snakes, which were most frequently hidden from the observer, also had significantly different 'hidden' observation frequencies from the other 2 species. There was no significant difference between the 'hidden' observation frequencies of adders and grass snakes. All species differed significantly in the frequencies of movement behaviour displayed. Grass snakes were observed moving for the greatest proportion of observations (23.2% overall), then adders (10.9%) and smooth snakes (1.3%) in decreasing order.

There was no significant difference in the proportions of mosaic basking displayed by the 3 species during the related samples investigations. Although mosaic basking was used more often than basking by all 3 species, it appeared to be proportionately more important as a means of heliothermic behaviour for smooth snakes (ratio of 1 : 13.6 basking to mosaic basking observations for smooth snakes, 1 : 3 for grass snakes and 1 : 1.4 for adders). In contrast to mosaic basking, there were significant differences in basking frequency observations between all 3 species (1% of observations for smooth snakes, 4.6% for grass snakes, 14.7% for adders). When the heliothermic behavioural categories were combined together (basking plus mosaic basking) there was no significant differences in the frequencies of heliothermic behaviour between grass snakes and smooth snakes. Significant differences did exist between adders and smooth snakes and adders and grass snakes for combined basking/mosaic basking.

The activity temperatures calculated for the snakes were calculated from thermally limiting conditions and thermally unlimiting conditions. Adders had the highest mean and median activity temperatures during both situations which again indicates the thermophilic nature of the species. However, during thermally limiting conditions, the lowest activity temperature measured for an adder was 2.8°C. This was recorded on 7.4.89 at 0845 hours after a cold night when model temperatures had dropped below zero. The snake was seen moving very slowly out of the heap of dead vegetation, which was in the sun by that time. After 15 minutes of basking, its body temperature had increased to 10°C.

Thus adders are capable of activity (although maybe only limited) at very low temperatures which may be a result of acclimitisation, genetic adaptation of metabolism or a combination of both (Davies et al. 1981). They were also observed active during thermally unlimiting conditions with the highest body temperatures. Such thermal generalism may play a factor in their more northerly distribution. In fact, all 3 species were observed active over a wide range of temperatures during both categories of thermal conditions. This would be advantageous in a cool temperate climate where operative temperatures may vary a great deal and imposed eurythermy may often occur.

Utilisation of Cover.

The observation that smooth snakes spend much of their time hidden from view or partly under cover (i.e. mosaic basking) has been noted by other workers. Gent (1988) used biotelemetric equipment to locate smooth snakes in the field and observed that on 62.8% of observations they were below cover (not seen or >95% concealed, n = 1313). 'Basking' (a combination of basking and mosaic basking) was observed for 30.7% and movement for 6.5% of the recordings. The use of radio equipment to precisely locate the animals might account for the smaller percentage of 'hidden' observations that Gent noted compared to the present study. Relatively high and precisely maintained body temperatures that were recorded for 'hidden' smooth snakes suggests that basking or mosaic basking animals were sometimes overlooked in the outdoor vivaria. Gent also commented that partial shading of basking smooth snakes by varying degrees of vegetation (described as mosaic basking in the present study) was observed during his project. Personal observations carried out during the present study also confirmed that smooth snakes were often seen to mosaic bask in the field.

Spellerberg and Phelps (1977) noted that much of the daily activity behaviour of smooth snakes was spent deep amongst vegetation. They suggested this was orientated towards seeking out the nests of small mammals. Behaviour characterised by the head exposed to sunlight and the body in the shade of vegetation was described as ‘partial basking’. De Bont et al. (1986) carried out a biotelemetric study of smooth snakes in the field which utilised temperature-sensitive transmitters. They made similar observations to the present study in that snakes that were not visible to them still showed marked rises in temperature on some occasions. The smooth snakes were classed as ‘in-active’ as they could not be seen but the body temperature pattern suggested that they were mosaic basking at the base of vegetation.

The use of vegetative cover seems to be more prevalent in smooth snakes than grass snakes or adders. Even so, ‘hidden’ behaviour was still the most frequently exhibited category for both the latter species. Mosaic basking was also observed in all 3 species more often than fully exposed basking during thermally unlimiting conditions, and for smooth snakes and grass snakes during thermally limiting conditions. Mosaic basking was more frequently seen in adders during thermally unlimiting conditions (26.8%) and thermally limiting conditions (17.1%) than in the other 2 species, but for smooth snakes mosaic basking was the more important and proportionately the more frequently observed heliothermic behaviour (i.e. mosaic basking seen considerably more often than basking).

Madsen (1987) used biotelemetric equipment on a study of grass snakes in Sweden and noted that male grass snakes were hidden on 64.2% of observations during May, June and July and 57.6% of observations during August and September. Females were hidden 34.2% and 52.5% of observations respectively. The difference in female observations between the 2 periods was attributed to gravid animals basking for longer periods than post-gravid specimens. No details of mosaic basking was recorded in the study nor was the behaviour related to thermal conditions. Prestt (1971) noted that adders were sometimes partially or almost completely hidden in vegetation during ‘lying-out’ (i.e. basking/mosaic basking) behaviour. Hailey and Davies (1987) observed that basking Natrix maura exposed most of their bodies during cool periods but retreated into cover when the weather was hot. Sometimes the snakes were completely shaded but still appeared to be thermoregulating.

Snakes that were 'hidden' in the outdoor vivaria could have been engaged in different forms of behaviour. They may have been totally submerged (possibly below ground) and inactive below cover. One particular adder specimen (specimen Vb9) was monitored during 4 hot days in May 1989 but was always hidden from view. Body temperature measurements remained relatively low throughout the period and indicated that the adder was probably below ground. The behaviour could have been partly accounted for by the fact that it was in a pre-slough condition. During this period of the sloughing cycle the eyes appear 'clouded' due to the secretion of fluid between the epidermis and the stratus corneum. This could have reduced the snake's ability to detect predators and so submergence below cover would have made it less vulnerable. Madsen (1984) and Gent (1988) noted reduced movements of grass snakes and smooth snakes respectively when the snakes were in pre-slough condition. Their results suggested a reduction of snake activity occurred during periods when the vulnerability to predation increased.

Other periods of submergence below cover occurred during the evenings and following mornings (observations were not made at night). If the thermal conditions were sufficient then emergence from the overnight cover was followed by a period of basking. If the thermal conditions were particularly cold (maximum model temperatures in the region of <20°C) then the snakes very often remained hidden and, presumably, submerged below cover.

Alternatively, as stated above, the snakes may have been engaged in some form of thermoregulatory activity when hidden from the observer. The body temperatures of hidden snakes when conditions were thermally unlimiting were relatively high. This could be partly due to the fact that ambient temperatures were also likely to have been high and so a snake thermoconforming under the cover of vegetation would have raised body temperatures. However, it was clear that snakes were very often maintaining high body temperatures at precise levels when hidden, particularly in the case of smooth snakes. During thermally limiting conditions the body temperatures of 'hidden' smooth snakes were higher and significantly different to those of the other 2 species which could reflect higher overall ambient temperatures when smooth snake data were recorded or thermoregulatory behaviour that was not seen by the observer.

The use of cover when basking (i.e. mosaic basking) could be attributable to several factors. It was noticeable in the case of smooth snakes that basking without any cover was never observed when conditions were described as thermally unlimiting whereas mosaic basking was. However, basking was seen in this species when conditions were cooler and thermally limiting (although still only 1.9% of observations). The same pattern was seen in adders with a relatively larger proportion of mosaic basking observations to basking observations when conditions were thermally unlimiting (ratio of 1 : 5.7 basking to mosaic basking) than when thermally limiting (1 : 0.9 basking to mosaic basking). No such pattern was discernible in grass snakes, with little difference in basking frequencies and only a slight increase in mosaic basking frequencies during thermally limiting conditions.

When conditions were described as thermally unlimiting, maximum model temperatures were equal or greater than 37°C. In fact, they were very often higher than the maximum temperatures that could be recorded by the automatic loggers (40°C). A snake remaining in sunny areas of the vivaria would rapidly heat up and attain body temperatures greater than selected body temperatures. On particularly hot days, body temperatures would approach maximum critical or even lethal levels. Therefore it was not unexpected to find that snakes were observed basking in the open for relatively short periods (or not at all in the case of smooth snakes). When they did, it tended to be during their heating phases only and so the body temperatures for basking behaviour were comparatively low. The use of cover through mosaic basking in the partial shade of vegetation prevented body temperatures from approaching potentially dangerous levels. Body temperatures were maintained at relatively high levels when mosaic basking (mean 28.08°C ± 3.385 for smooth snakes, 27.33°C ± 4.732 for grass snakes, 32.80°C ± 3.127 for adders).

During thermally limiting conditions, maximum model temperatures were less than 34°C and all 3 species were observed basking in the open more often. This was especially true for adders. All 3 species were also observed basking/mosaic basking proportionately more often during thermally limiting conditions although by relatively small amounts. To reach selected body temperatures during thermally limiting conditions would have been more difficult for the snakes to achieve but this could have accounted for the slight increase in observed basking/mosaic basking behaviour. The adders were observed to respond most effectively by basking in the open to a large extent thus exposing themselves to maximum available direct solar radiation. The body temperatures the adders achieved when basking were higher than when they were mosaic basking whereas the reverse had been true during thermally unlimiting conditions. They were also higher than the body temperatures of smooth snakes and grass snakes engaged in basking during thermally limiting conditions.

Avery (1982) pointed out that snakes did not always seem to attempt to expose the whole of their bodies simultaneously (mosaic basking or shading by body coils) and that it was difficult to explain such thermal strategies. Mosaic basking during thermally unlimiting conditions could be explained as a means of avoiding potentially harmful conditions. However, why was mosaic basking so prevalent when conditions were thermally limiting ? If a snake needed to attain selected body temperatures (or increase body temperatures to some extent) then theoretically one might expect to see basking behaviour more frequently. Adders did display basking behaviour far more often during thermally limiting conditions but they still displayed an approximately equal degree of mosaic basking behaviour. There are several possible explanations. On some occasions the maximum operative temperatures described as thermally limiting were particularly low (e.g. cold, overcast, windy days) and it might not have been thermally advantageous for mosaic basking snakes to move into the open. There were also occasions on days of 'changeable' weather conditions when brief spells of thermally limiting conditions were interspersed by periods of thermally unlimiting conditions. Snakes may have selected high body temperature levels during the latter periods when mosaic basking, and maintained them during the brief thermally limiting periods (e.g. through tight body coiling etc.) and thus there was no need to move into the open and bask. Note that the maximum body temperatures of mosaic basking snakes during thermally limiting conditions were above mean selected body temperature values.

Another possibility is that snakes that basked fully exposed in the open were more at risk from predation (particularly avian predation) than those under the partial cover of vegetation. Madsen (1987) believed that mature female grass snakes had relatively high mortality rates due to their high basking activity. Crows (Corvus corone), magpies (Pica pica) and jays (Garrulus glandarius) were known to feed on grass snakes in his study area and the possibility of predation on a basking animal may have been greater than on one that was hidden. Buzzards (Buteo buteo) have been known to feed on grass snakes (Frazer 1983) and adders (Dare 1961 in Prestt 1971) in Britain and Prestt (1971) observed kestrels (Falco tinnunculus) feeding on unidentified small snakes in Dorset. Shine (1980) suggested that basking lizards may also be particularly vulnerable to avian predation.

By mosaic basking under the partial cover of vegetation the risk of predation, especially from birds, could be reduced. As Gent (1988) pointed out, smooth snakes rely to a large extent on crypsis as an anti-predator mechanism. In the present study, mosaic basking was far more frequently observed than basking and this would seem to support the importance of crypsis in smooth snakes. Grass snakes also used mosaic basking to a greater degree than basking but they were also observed moving more than smooth snakes. Grass snakes have 2 main methods of defence; the expulsion of a foul-smelling secretion from the anal glands and shamming death. Thus crypsis is likely to be important to grass snakes when they are engaged in basking/mosaic basking behaviour but it is not their only anti-predator behaviour. Adders are probably the most capable of defending themselves as they are venomous. They were most often seen totally exposed and basking.

'Cryptic heliothermy' (S.Hardes, pers.comm.) has been used to describe the theoretical situation where benefits of precise thermoregulation are traded-off against the benefits that maybe derived from basking under partial cover. Gent (1988) suggested that smooth snakes forfeited precise body temperature maintenance through mosaic basking but possibly benefited from being more cryptic amongst the vegetative cover. As was stated above for the mosaic basking behaviour observed during the present study, all 3 species of snake managed to attain relatively high body temperatures during thermally unlimiting conditions, and periods of precisely maintained body temperatures were recorded (and for 'hidden' behaviour in the case of smooth snakes). However, the body temperatures recorded during mosaic basking behaviour were slightly lower than the mean field selected body temperatures. This could be the result of low body temperatures from the heating phases lowering the overall mean value for mosaic basking. It might also suggest a minor 'cost' in terms of thermal gain during mosaic basking.

When conditions were thermally limiting, the possible 'cost' of mosaic basking was apparent in adders with body temperatures of basking snakes recorded as being higher and significantly different to those of mosaic basking snakes. It is also possible that the records for adders engaged in mosaic basking were from more limiting thermal conditions resulting in lower body temperatures. For grass snakes and smooth snakes, mean body temperatures were higher during basking but not significantly different. Thus in adders at least, the data indicates a possible thermal advantage in basking over mosaic basking. The adders appear to bask in the potentially more dangerous sites without cover more often than smooth snakes or grass snakes but attain higher body temperatures in the process. Mosaic basking is examined further in Chapter Five.

Movement.

Movement was rarely observed in smooth snakes during the outdoor vivaria experiments. It is possible that some movements may have been missed as they tend to stay in areas of dense cover. In his study of free-ranging smooth snakes, Gent (1988) concluded that they were relatively immobile although long movements were recorded on a small number of occasions. Median movement rates of 0.54 m/hr and 13.3 m/day (maximum of 44.26 m/hr, 166.81 m/day) were recorded and of 1074 recordings that Gent made, 62.6% were less than 1 m/hr. Direct observations of movement were made on 6.5% of occasions which compares with 1.1% during thermally unlimiting conditions and 1.5% during thermally limiting conditions in the present study. More accurate location of individual animals through biotelemetrical means could account for the difference. There is also the possibility that the snakes could have been moving towards cover in response to Gent approaching them, thus producing an artificially high movement count.

Grass snakes, in contrast, are thought to be highly vagile. In a study of free-ranging grass snakes in Sweden, Madsen (1984) found that males moved a mean distance of 54.8 m/day ± 16.8 in the mating season although this decreased to 13.0 m/day ± 8.6 in June and July. Female grass snakes moved most extensively in the days immediately prior and after oviposition with mean distances of 114.4 m/day being recorded. Brown (pers. comm.) observed typical movements of between 50-100 m/day (maximum of 600 m/day) amongst grass snakes studied in Hampshire, southern England. During the present study, grass snakes were observed to move more often than the other 2 species, particularly when conditions were thermally unlimiting.

Prestt (1971) studied several Dorset populations of adders and found that they did not move very far from their winter hibernation sites during the Spring period. The greatest movements occurred during the seasonal migrations to and from the summer areas where feeding occurred. The summer areas were between 500-1200 m from the winter hibernation sites. Movement to the summer areas tended to occur in stages, with pauses at one or more points along the route. Only local movements were observed once they were in their summer areas. Other studies have been carried out on the movement of free-ranging adders but the results have yet to be published (e.g. Claus and Verheyen 1989). Adders were observed moving more than smooth snakes but less than grass snakes in the outdoor vivaria.

When adders were observed moving in the outdoor vivaria, it was very often in order to find a new bask site. If an adder was in a particular sunny area which eventually became shaded by the vivarium walls, then it would respond by moving to another sunny area. During particularly hot conditions an adder would often be observed basking until it reached selected body temperature levels whereupon it would move to a site partially shaded by vegetation. Therefore if an adder was observed moving on a particular occasion, it was very often stationary and engaged in some form of basking/mosaic basking behaviour (or hidden) again by the time the next observation was made 15 minutes later. Body temperatures of moving adders were therefore relatively high during thermally unlimiting conditions (and significantly different to those of moving grass snakes), although not as high as mosaic basking temperatures. The body temperatures of basking and mosaic basking adders during thermally limiting conditions were also higher than those of moving adders.

The foraging modes of reptiles have been categorised into 2 types; 'sit-and-wait' and 'actively' or 'widely foraging' (Pianka 1977, Huey and Pianka 1981). Adders appear to use the former type most of the time and this was reflected in the relatively small amount of movement that was observed in the outdoor vivaria. Prestt (1971) recorded that adders in his Dorset sites fed mainly on small adult mammals (65% of prey animal samples) but also lizards and slow worms plus bird and mammal nestlings. During a study in Poland (Pomianowska-Pilipiuk 1974) adders were also recorded as feeding mainly on small mammals, in addition to frogs, lizards, slow worms and several other species. Huey and Pianka (1981) predicted that prey type alternates between trophic levels, with sit-and-wait predators catching and being caught by widely foraging animals. This appears to be the case with adders as they mainly utilise a sit-and-wait strategy whereas small mammals tend to be widely foraging. However, the inclusion of nestlings in adders' diets implies that they do widely forage on some occasions.

It has been pointed out by Huey (1982) that the time devoted to thermoregulation can sometimes reduce the time available for other important activities, such as foraging for food. In the case of adders, it is possible that they combine thermoregulatory behaviour (in the form of basking/mosaic basking) with foraging behaviour (in the form of sit-and-wait). This may particularly be the case during mosaic basking when the snakes are partially under the cover of vegetation and maybe harder for potential prey animals to detect. There is the additional factor that the success of prey capture is increased if the snake is at a physiologically optimal body temperature. Greenwald (1974) found that the striking success of gopher snakes (Pituophis catenifer affinis) was greatest at the mean field body temperature of 27°C (and this was also considered to be the optimal body temperature for the species). Although the physiological optimum body temperature (specifically that for striking success) of adders is unknown, it is likely to be in the region of the mean field selected body temperature. The body temperatures of mosaic basking adders during thermally unlimiting conditions were close to such temperatures and so adders may have been able to strike prey with relatively high success rates at such times. Also, the main prey species of adders are endothermic and therefore more independent of environmental temperatures. Adders may need to maintain high body temperatures to be able to successfully predate on these species.

Grass snakes appear to display the widely foraging mode of behaviour. This was also the conclusion of Hailey and Davies (1986) during a comparative study of grass snakes with Natrix maura (a sit-and-wait strategist) in Spain. They measured the mean body temperatures of 'active' (i.e. foraging) grass snakes as 26.8°C ± 1.9 ($n = 22$) during March, April, May and October and 27.8°C ± 3.1 ($n = 6$) during June to September. This compares with mean body temperatures for moving grass snakes of 26.93°C ± 3.656 ($n = 89$) during thermally unlimiting conditions and 22.45°C ± 4.629 ($n = 95$) during thermally limiting conditions in the present study. Grass snakes have been recorded as feeding on frogs, toads, fish, newts and bird fledglings (pers. ob., Frazer 1983).

Unlike adders, the body temperatures of moving grass snakes were not significantly different to those that were mosaic basking when it was thermally unlimiting, nor were they significantly different to those that were basking or mosaic basking when it was thermally limiting. Instead of moving for relatively short periods, they were often seen moving during several consecutive 15-minute observations. Movements were not restricted to simply changing bask sites but extensive forays around the vivaria were frequently witnessed, especially when the weather was warm.

A common pattern of behaviour observed during thermally unlimiting conditions was a period of basking and/or mosaic basking during the grass snakes' heating phase followed by extensive movements interspersed with mosaic basking or hidden behaviour. During particularly hot periods they retreated under cover. Body temperatures were not maintained as precisely as adders or smooth snakes during thermally unlimiting conditions (see Chapter Five) and the variation of body temperatures measured during basking, mosaic basking or movement behaviour was greatest in grass snakes.

The large proportion of movement activity witnessed in grass snakes during thermally unlimiting conditions suggests that they forage most extensively when body temperatures can be maintained at relatively high levels. Usually, ambient temperatures would also be high in such circumstances so body temperatures would remain raised during forays in the shade of vegetation even though they might appear to be thermoconforming. The grass snakes were often observed moving in the direct sunlight above cover so their body temperatures could be increased without having to stop and engage in basking or mosaic basking behaviour. In effect the grass snakes displayed a form of 'shuttling heliothermy' with post-emergence basking phase followed by periods of basking/mosaic basking interspersed with movement activity.

Hailey and Davies (1986) found the 'burst speed' of grass snakes to be greatest at 30°C ambient temperature (measured at 5°C intervals from 5-35°C). The results suggested that at those temperature levels, grass snakes would be most successful at catching prey and avoiding predation. Grass snakes were seen moving considerably less when conditions were thermally limiting and this could relate to the fact that they would be less effective at foraging and more vulnerable to predation at such times. Instead they were observed mosaic basking and 'hidden' on proportionately more occasions. Madsen (1987) believed that male grass snakes suffered high mortality from avian predators during the mating season due to their increased mobility. The male grass snakes may have appeared more conspicuous during their movement activities. Therefore if a grass snake needed to move (and therefore risk predation) it would be best to do it when temperatures were sufficient to the allow the best physical response to potential danger.

Smooth snakes have been described as 'opportunist' by Goddard (1981, 1984). He examined the prey regurgitation samples of adult smooth snakes from the New Forest and found that 84% were small mammals and 16% common lizards. Of the former category, 40% were nestlings which suggested that the snakes fed on sedentary and widely foraging prey. Gent (1988) believed that both sit-and-wait and widely foraging behaviour were used by smooth snakes. The sit-and-wait strategy reduces the need for locomotion and therefore reduces their conspicuousness. This would be particularly important for a species that relies on crypsis as their main predator-avoidance behaviour. Even when widely foraging activity was observed by Gent, it tended to be amongst dense vegetation.

In the present study, movement was rarely seen in smooth snakes but it is possible that some movement amongst dense vegetation was missed and therefore classed as 'hidden'. The few movements observed in smooth snakes were not extensive and appeared to be restricted to seeking out more beneficial basking sites.

4.4.3. Laboratory Experiments

The criteria used to define the main behavioural categories in the laboratory were slightly different to those in the outdoor vivaria. In the outdoor vivaria there was no equivalent to 'stationary' or 'refuge stationary' behaviour. This was because in the laboratory the influence of the heatlamp was restricted to a specific area and when a snake was motionless within that area it was defined as 'basking' or (if it was partly in refuge 1 at the entrance closest to the heatlamp) 'refuge basking'. If the snake was motionless and outside the area influenced by the heatlamp it was described as 'stationary' or 'refuge stationary'. In the outdoor vivarium when a snake was observed motionless it was described as basking or mosaic basking. These descriptions were used even when the sky was overcast. However, it was difficult to judge at what point (i.e. degree of cloud cover etc.) a snake was no longer gaining some form of thermal benefit by remaining motionless, therefore all such behaviour was classed as basking/mosaic basking.

When the heatlamp turned off, there was no longer any direct radiation from above but the sand remained warm. When a snake was observed motionless in the area that had been influenced by the heatlamp then it was described as exhibiting 'thigmothermy' or 'refuge thigmothermy'. Even at the end of the thermally limiting phase (i.e. heatlamp off) the sand temperatures underneath the heatlamp were still up to 1.5°C warmer than sand temperatures inside the refuges. A snake would therefore thermally benefit to some extent by being in contact with the warmer sand.

The heatlamp was set to turn on and off at 12 hour intervals. During the period described as thermally limiting (i.e. heatlamp off) there were also periods of darkness. In the 12 hours that the heatlamp was off, the laboratory arena was dark for 9 hrs 20 mins. Thus, unlike the outdoor vivaria experiments, it was also possible to monitor nocturnal periods of activity.

Thermally Unlimiting Conditions (Heatlamp on).

In all 3 species there was a higher proportion of time spent basking and refuge basking during thermally unlimiting conditions than was observed during the outdoor vivaria experiments. Basking behaviour was also observed more than refuge basking behaviour. The equivalent of refuge basking in the outdoor vivaria was mosaic basking and the latter behaviour tended to be observed more often than basking in the open (except for adders during thermally limiting conditions). The other main difference between the laboratory and outdoor vivaria results was in the amount of time that snakes were observed under cover. During thermally unlimiting conditions in the laboratory, snakes were hidden 'in refuge' for less time than snakes were 'hidden' in the outdoor vivaria.

Why did snakes in the laboratory utilise cover to a less extent (in the form of 'in refuge', refuge basking or refuge stationary behaviour) than snakes in the outdoor vivaria (in the form of 'hidden' or mosaic basking behaviour)? One possibility was that snakes that were 'hidden' in the outdoor vivaria were actually engaged in another form of behaviour such as mosaic basking or moving but without being observed. In contrast to this, it was always possible to tell with certainty when a snake was engaged in a particular activity during the laboratory experiments. However, although this may have occurred on some occasions (particularly with the more cryptic smooth snakes) it is unlikely that this was an important factor in the discrepancy.

The heat source in the laboratory was constant and predictable. In the outdoor vivaria, the quantity and quality of solar radiation was not always as reliable. Snakes also had to change bask sites when the walls of the outdoor vivaria eventually shaded them. It may therefore have been less energetically demanding for snakes to thermoregulate in the laboratory set-up as there was only one potential basking site to choose from. In addition to this there was no risk of predation in the laboratory and the snakes were always left undisturbed during the acclimation and recording period. In the field situation, snakes may intermittently detect the presence of birds flying overhead resulting in an increased use of cover. A decrease in the use of cover in the laboratory may have been an indication that predation was not considered to be as much as a danger as would have been the case in the outdoor vivarium.

Smooth snakes were observed hidden under the refuges for the longest overall periods. They also used cover to some extent in the form of 'refuge basking' and 'refuge stationary' behaviour (a total of 45.3% including the time for 'in refuge'). Grass snakes were also observed using cover to a relatively large extent (55.6% of time for 'refuge basking', 'refuge stationary' and 'in refuge' combined). Adders, however, hardly used cover at all. They were only observed totally hidden in their refuges for 4.2% of the time plus an additional 1.1% for time engaged in 'refuge stationary' or 'refuge basking' behaviour. This supports the observation of the outdoor vivaria experiments when adders were more likely to be observed openly basking and engaged in overt thermoregulatory behaviour than the other 2 species. Smooth snakes were also more frequently classed as 'hidden' during the outdoor vivaria experiments.

For all 3 snake species, basking was observed for greater periods than refuge basking. This was not the case during thermally unlimiting conditions in the outdoor vivaria when basking was observed less frequently than mosaic basking (considered to be the equivalent of refuge basking). This may partly be due to the reasons discussed above with regards to the difference in the cover utilisation between the outdoor vivaria and laboratory experiments. However, there is a more important factor which is likely to account for the difference.

During thermally unlimiting periods in the outdoor vivaria, the snakes avoided the hot conditions by moving into the partial shade of cover and mosaic basking. In the laboratory, the thermally unlimiting conditions only existed directly beneath the heatlamp. The snakes could avoid reaching excessively high body temperatures by simply moving away from directly beneath it. There was a gradient of decreasing sand temperatures (and, theoretically, operative temperatures) from the centre of the heatlamp hotspot. Directly under the heatlamp, maximum sand temperatures of over 40°C were recorded. Approximately 35cm away at the entrance to refuge 1, maximum sand temperatures reached 26.5°C. In the outdoor vivaria there was little choice to moving under cover to avoid excessive heat during thermally unlimiting conditions.

The temperatures attained by all 3 species were highest during basking behaviour. They were also significantly different to the body temperatures of all the other behavioural categories (including refuge basking). The mean body temperature of smooth snakes during basking behaviour was 30.63°C ± 1.468 (n = 234), grass snakes 29.53°C ± 3.838 (n = 266) and adders 32.42°C ± 3.028 (n = 141). Not only do adders have higher mean and significantly different overall body temperatures during thermally unlimiting conditions in the laboratory than the other 2 species (see Section 3.3.2), the same can be stated of the body temperatures maintained during overt thermoregulatory behaviour (i.e. basking). Smooth snakes' basking body temperatures were also significantly different to those of grass snakes.

Other distinct interspecific differences were noted from the body temperature and behavioural time budgeting results. Smooth snakes basked for 41.5% of the time which was more than grass snakes (28.2%) and less than adders (73.2%). However, the median time of the smooth snake basking behaviour was 45.5 mins and therefore considerably longer than those of grass snakes or adders (12 mins and 11 mins respectively). The variation in body temperatures during basking behaviour was less than the other 2 species. Also, of 234 measurements, the minimum recorded body temperature was 25.1°C which compares with 17.0°C for grass snakes and 19.8°C for adders. The minimum refuge basking body temperature was 21.4°C.

Basking behaviour in smooth snakes was not observed when body temperatures were comparatively low. Refuge basking was observed at lower temperatures however. This can be explained by the observation that smooth snakes often engaged in refuge basking after emergence from their refuge. Thus the body temperatures of the smooth snakes were raised first before completely moving out of the refuges and basking. The results also suggest that when smooth snakes bask, it tends to be for relatively long periods. This could account for the smaller standard deviation in body temperature during basking. The results also showed that the smooth snakes appeared to move less than the grass snakes or adders which supports the findings of the outdoor vivaria experiments.

The overall mean body temperature of grass snakes recorded during the thermally unlimiting conditions (as discussed in Chapter Three) in the laboratory was 23.19°C ± 5.15 (n = 983). This compares with 27.44°C ± 4.63 (n = 416) for smooth snakes and 31.09°C ± 3.84 (n = 228) for adders. The overall basking time of grass snakes was the lowest of the 3 species (28.2%). Refuge basking, although observed less than basking, was seen most often in grass snakes (16.7%). Refuge basking was a less efficient means of raising body temperatures in the laboratory . Even when basking was used, the median time of duration was only 12 mins. The grass snakes appeared to thermoregulate with the least precision of the 3 species and overt thermoregulatory behaviour was observed less often in this species. Movement was observed in grass snakes proportionately more than in smooth snakes although less than in adders.

Adders maintained the highest overall body temperatures of the 3 species and the highest body temperatures for basking, moving, 'in refuge' and combined basking/refuge basking behaviour. Interspecific significant differences existed for all the preceding categories. The only exception to this pattern was for refuge basking in which smooth snakes recorded the highest temperatures, although there was a very small sample size (n = 8) for adders. They were observed basking for much longer periods than the other 2 species (73.2% of the time). The less thermally beneficial refuge basking behaviour was only observed for 0.9% of the time, refuge stationary for 0.2% and stationary 0.09%.

Movement was the second most used behaviour (21.3%) by adders. Median basking times were calculated as 12 mins, considerably less than smooth snakes. Median movement times were calculated to be 6 mins. Unlike smooth snakes, adders tended to bask straight away without an initial refuge basking period. The results suggest that they maintained body temperatures at relatively high levels throughout the thermally unlimiting phase using 'shuttling' behaviour. Short periods of basking were followed by shorter periods of movement. This is further illustrated by the proportion of number of times that each behaviour was displayed being about the same for moving and basking behaviour (44.4% and 45.4%

respectively). Even though the median basking time duration was short, it was still longer than all the other behavioural categories that the adders displayed. Thus body temperatures never had time to cool down to any great extent before they were 'boosted' again by another period of basking. This is well illustrated in Fig. 4.8.

Grass snakes displayed a similar form of behaviour in the laboratory as they did in the outdoor vivaria. A relatively limited time was spent on basking and refuge basking behaviour and even when it was used, body temperatures were not raised as high as adders or even smooth snakes. Much time was spent in behaviour that was not overtly thermoregulatory. At intervals, body temperatures were raised again by a period of basking. This would appear to be a crude form of shuttling heliothermic behaviour. The shuttling heliothermy that the adders displayed was more sophisticated and body temperatures did not drop very far.

Further details of shuttling heliothermy are provided in Chapter Five. There is also a discussion as to why such behaviour was observed in adders in the laboratory but not in the outdoor vivaria. Other aspects of thermoregulatory behaviour observed in the laboratory are also investigated.

Thermally Limiting Conditions (Heatlamp off)

For smooth snakes and grass snakes, the main behaviour observed during thermally limiting conditions was of the animals under the cover of the refuges (71.9% and 57.9% of the time respectively). Smooth snakes spent an additional 13.4% of the time engaged in behaviour under the partial cover of refuges (refuge stationary and refuge thigmothermy). In grass snakes the figure was an additional 30.1% of the time. For adders however, only 26.0% of the time was spent in the refuges plus 4.0% engaged in refuge stationary and refuge thigmothermy behaviour.

For about 78% of the time that the heatlamp was off, the laboratory arena was in the dark. Although smooth snakes and grass snakes were in or partially under the refuges for most of the thermally limiting period, and most of the nocturnal period (i.e. when the light was off as well) it was interesting to note that this was not the case for adders.

Smooth snakes have been described as diurnal by other workers (Spellerberg and Phelps 1977, Arnold and Burton 1978). De Bont et al. (1986) noted that smooth snakes remained submerged during the night and usually emerged in the morning. Gent (1988) measured the activity of 3 snakes over 9 days (of which 4 days provided a complete nocturnal record) in the field and detected only occasional and small movements in the period between 60-120 mins after sunset until 15-90 mins after sunrise. He also found diurnal behaviour was displayed in smooth snakes studied in a laboratory arena. When they were not below cover during nocturnal periods in the laboratory, they were generally described as 'inactive'

Grass snakes have also been described as a diurnal species (Arnold and Burton 1978, Hailey and Davies 1986). Arnold and Burton (1978) considered adders to be largely diurnal, especially in the north of its distribution. Zuffi (1989) found adders in an Italian alpine population between 0700 hours and 1900 hours although it is unclear whether nocturnal searches were made. Prestt (1971) recorded the Dorset population of adders as displaying diurnal behaviour as no snakes were observed before 0630 hours or after 1930 hours. However, adders were occasionally noted remaining in the open all night during a study of European vipers in an outdoor vivarium by Saint Girons (1978).

Adders were observed moving during 49.4% of the time when conditions were thermally limiting. Much of this was also during the period when the light was off as well. Nocturnal activity by adders in the laboratory may have been the result of the animals being kept in artificial surrounding resulting in atypical behaviour being displayed. There is also the possibility that the red and infra-red lights, which were used to light the arena to permit video recording during the dark phase, may have stimulated activity. Snakes of the subfamily Crotalinae (pit vipers) have paired heat-sensory pits between the eye and nostril. Similar structures can be found in the marginal scales of some boas and pythons (Spellerberg 1982). The pit organs of the crotaline vipers are known to be highly sensitive to infra-red light. It is theoretically possible that some snakes may have some kind of rudimentary skin receptor, not as specialised as a proper pit organ but still with some functional value (A. Bellairs, pers. comm.).

There is an alternative explanation for the relatively high nocturnal activity of adders which relates to the thermal environment available to the snakes. The mean minimum shade air temperature recorded in the laboratory arena was 17.9°C ± 1.74 (n = 31 experiments). Data from the Southampton Weather Centre indicated that during July, the month with the warmest minimum temperatures, the average minimum temperature for the 1971-1980 period was 12.7°C. July, 1989 was a particularly warm month and a mean minimum temperature of

15.0°C was recorded. This illustrates that the ambient temperatures during the dark phases in the laboratory were warmer than most nights outdoors.

In addition to relatively high ambient temperatures, adders also exhibited a certain degree of thigmothermic behaviour by positioning themselves on the sand that had been warmed by the heatlamp (16.2% of the time). Mean body temperatures of 20.55°C ± 3.059 (n = 82) were recorded for moving adders in the laboratory. Relatively high degrees of nocturnal activity could have been the result of higher body temperatures than the adders might have usually attained during such periods in the field in southern England. However, it does suggest that adders might engage in crepuscular or nocturnal activity during particularly warm summer nights. It may also be more frequently displayed in the southern part of its range.

Smooth snakes and grass snakes may have been more active during nocturnal periods if temperatures had been even higher in the laboratory. Spellerberg and Phelps (1977) kept smooth snakes in an activity cage at ambient temperatures of 25°C and 30°C. The nocturnal activity of the smooth snakes was much greater at the latter levels. Hailey and Davies (1986) measured the activity of grass snakes at ambient temperatures of 15°C, 25°C and 35°C. Diurnal behaviour was observed at the 2 former temperature levels but at 35°C, diurnal and nocturnal patterns of behaviour were recorded. They pointed out that there was only one published record of nocturnal behaviour in free-ranging specimens. There has also been an observation of a grass snake seen crossing a road on a late-June night during a warm summer spell in England (J. Buckley, pers.comm.).

Adders were observed engaged in thigmothermic behaviour for a longer overall period of time and on more occasions. However the median time for each period of thigmothermy was short (7 mins) compared to that of grass snakes and smooth snakes (41.5 mins and 18.5 mins respectively). The body temperatures that smooth snakes attained during thigmothermy were higher and significantly different to those of the other 2 species. The smooth snakes were sometimes basking under the heatlamp when it turned off but they tended to stay in the area for a while until eventually moving under a refuge. This also happened with grass snakes and adders. However, on the few occasions that thigmothermy was observed, the relatively long median time noted for this behaviour in grass snakes (41.5 mins) suggested that they remained in the area for longer periods during which time the sand, and therefore their own body temperatures, would cool down to a greater extent. Adders also tended to engage in thigmothermy at intervals throughout the night, and so this would result in a relatively low overall body temperature for this behaviour.

4.5. Summary

Outdoor Vivaria Experiments

(i) The behaviour of the 3 British snake species was observed in outdoor vivaria. The 4 main behavioural categories were; basking, mosaic basking, moving, hidden from view.

(ii) Conditions were classed as thermally unlimiting (maximum model temperature available in the vivaria ≥37°C) or thermally limiting (maximum model temperature available in the outdoor vivaria during 'lit' periods <34°C).

(iii) Morning emergence was considered to be stimulated mainly by the warming influence of the direct sun on the snakes' overnight refuges.

(iv) Adders emerged more often, at slightly earlier times and at lower ambient and body temperatures than the other 2 species.

(v) Smooth snakes were the most hidden of the 3 species. Movement behaviour was observed least of all. The proportion of mosaic basking behaviour to basking behaviour was greatest in smooth snakes.

(vi) Grass snakes were observed moving more than the other species, especially during thermally unlimiting conditions. Overall basking plus mosaic basking frequencies did not vary much from smooth snakes although basking was observed more often.

(vii) Adders engaged in basking and combined basking/mosaic basking far more frequently than the other 2 species. They engaged in mosaic basking more frequently than the other 2 species during thermally unlimiting conditions.

(viii) The frequency of basking and mosaic basking varied little between thermally limiting and unlimiting conditions for grass snakes. For smooth snakes, basking was only observed during thermally limiting conditions. For adders, basking was far more frequently used when conditions were thermally limiting.

(ix) When conditions were thermally unlimiting, the body temperatures of adders and grass snakes engaged in mosaic basking were higher and significantly different to when they were engaged in basking. Snakes only tended to bask in the open during their post-emergence heating phases in such conditions, after which they retreated to the cover of vegetation.

(x) Adders had the highest average body temperatures during mosaic basking behaviour in thermally unlimiting conditions (mean 32.80°C ± 3.385, median 33.4°C), followed by smooth snakes (28.08°C ± 3.385, median 28.6°C) and grass snakes (27.33°C ± 4.732, median 27.8°C). They were all significantly different.

(xi) When conditions were thermally limiting, the body temperatures of adders engaged in basking were higher and significantly different to when they were engaged in mosaic basking. No significant differences existed in smooth snakes or grass snakes.

(xii) Snakes that were hidden could have been submerged and inactive. However, smooth snakes in particular often precisely maintained body temperatures when they were hidden suggesting that they were actually 'mosaic basking'. Crypsis appears to be an important aspect of their behaviour.

(xiii) Mosaic basking is involved in thermoregulation. It may also be involved in anti-predator behaviour (especially smooth snakes) or predatory behaviour (sit-and-wait strategists).

(xiv) Grass snakes made extensive movements, often through sunny areas. Periods of basking/mosaic basking 'boosted' body temperatures in between movements. They have been described as a 'widely foraging' species. Increased movement during thermally unlimiting conditions meant body temperatures were higher permitting faster predatory and predator-avoidance reactions.

(xv) Adders are mainly 'sit-and-wait' strategists. Movements were generally restricted to changing basking sites. Basking/mosaic basking behaviour maybe incorporated with 'sit-and-wait' foraging.

(xvi) Smooth snakes have been described as using both 'sit-and-wait' and 'widely foraging' strategies. The movement observed was generally restricted. It is possible that more movement occurred under cover and therefore the snakes remained hidden.

Laboratory Experiments

Thermally unlimiting conditions (heatlamp on);

(i) The main behavioural categories identified in the laboratory were basking, refuge basking, moving, in refuge, stationary, refuge stationary.

(ii) Smooth snakes and grass snakes often emerged the head region of the body prior to full emergence. This frequently occurred after the light switched on although full emergence was usually observed after the heatlamp had switched on as well.

(iii) Smooth snakes were observed under the refuges for the longest time and moved for the least time.

(iv) Grass snakes moved more than smooth snakes but engaged in basking/refuge basking behaviour for less time. A large proportion of time was spent in or near refuges. Refuge basking, which is less thermally beneficial than basking, was observed in grass snakes for the longest time of the 3 species.

(v) Adders engaged in basking behaviour for far longer than the other 2 species. Very little time was spent in or partly in refuges.

(vi) The individual basking periods of smooth snakes were the longest (median = 45.5 mins). They basked quite frequently and for long periods. Mean body temperatures of 30.63°C ± 1.468 ($n = 234$, median 30.6°C) were attained during basking behaviour.

(vii) Grass snake basking periods were short (median = 12 mins) and not always very frequent. Consequently overall body temperatures during thermally unlimiting conditions were the lowest (see Chapter 3). Body temperatures of 29.53°C ± 3.838 ($n = 266$, median 30.2°C) were attained during basking behaviour, the lowest value of the 3 species and significantly different.

(viii) Adder basking periods were also short (median = 11 mins) but they were very frequent. Basking behaviour was alternated with short periods of movement resulting in high and precisely maintained body temperatures for the thermally unlimiting periods (shuttling behaviour). Body temperatures of 32.42°C ± 3.028 (n = 141, median 33.1°C) were attained during basking behaviour.

Thermally limiting conditions (heatlamp off);

(ix) Thigmothermy and refuge thigmothermy behaviour substituted basking and refuge basking behaviour during thermally limiting conditions. This period also included the dark phase.

(x) Nocturnal activity in smooth snakes and grass snakes was restricted. The behaviour that the 2 species exhibited was mostly 'in refuge' or (to less extent) partially in a refuge.

(xi) Adders were observed moving during a large proportion of the thermally limiting and nocturnal periods. This could partly be due to relatively high ambient temperatures. Nocturnal activity in the wild may occur on particularly warm summer nights in the U.K. and in the more southern areas of its range.

(xii) All species showed a degree of thigmothermic behaviour.

CHAPTER FIVE

BEHAVIOURAL THERMOREGULATION

5.1. Introduction

In the classic paper of Cowles and Bogert (1944), desert reptiles were observed to thermoregulate through the selection of positions in or on the soil or below ground, basking with part or all of the body exposed, and (during extreme conditions) panting. These observations demonstrated that reptiles could regulate body temperatures independently of ambient temperatures through a variety of specific behavioural actions. Since then, behavioural thermoregulatory strategies have been identified in a range of reptiles although research has been heavily biased towards lizards.

Behavioural thermoregulation can be divided into two main categories; heliothermy and thigmothermy. Heliothermy involves the absorption of direct solar radiation (i.e. basking) whereas thigmothermy entails obtaining heat through conduction from the surroundings. These broad categories have already been investigated to an extent in Chapter Four.

Heliothermy can be subdivided further. Reptiles that alter the amount of their body surface area exposed to incoming solar radiation through postural alterations can be described as 'postural heliotherms'. Orientation of the long axis of the body to the horizontal and vertical angles of the sun's incoming radiation is adjusted in some species (Heath 1965, Heatwole and Johnson 1979, Muth 1977, Fish and Cosgrove 1987). Heatwole and Taylor (1987) stated that many of the dragons (genus Amphibolurus) change their orientation so regularly and consistently that they could almost be used as sundials. Some lizards adjust their body area in contact with the ground, sometimes holding the body high with only the palms of the feet touching the substrate during particularly hot temperatures (Losos 1987).

The ability to dorso-ventrally flatten the body has been identified in some lizard species (Heath 1965, Cogger 1974, Avery 1979) and snake species (Appleby 1971, Saint Girons 1978, Heatwole and Johnson 1979). Snakes also coil their bodies and the possible thermoregulatory function of such postural behaviour has been examined by Johnson (1972) and Gent (1988). Coiling may have a heliothermic role and an insulative role, reducing the rate of heat loss during cooling periods (Cogger and Holmes 1960, Johnson 1972).

Probably the most important type of thermoregulatory behaviour for lizards from temperate climates and those species from open, sparsely vegetated habitats is 'shuttling heliothermy' (Avery 1979). It has also been identified in snakes (Heatwole and Johnson 1979). Thermoregulation is achieved through a series of movements between sunny and shaded microhabitats (Heath 1965, Spellerberg 1972). In Chapter 4, 'mosaic basking' was identified as a behaviour sometimes utilised by the snakes. Instead of shuttling between sun and shade, the snakes used the partial and diffuse shading of vegetation. Snakes may adjust the amount of body area exposed to the sun as a form of thermoregulation (Hailey and Davies 1987).

Selection of a suitable site for thigmothermal or heliothermal behaviour is another important element of behavioural thermoregulation. Some reptiles seek out 'perches' on small twigs of bushes on which to bask in the early morning. This tends to be carried out in conjunction with postural changes so that absorption of heat is maximised and conductive loss of heat to the cold ground is avoided (Axtell 1960, Cogger 1974). Reptiles can often be observed basking on slopes that face the direction of the sun, thus altering the angle of the body surface to incoming solar radiation in the same way that a postural adjustment in orientation might achieve (Prestt 1971).

It is important to note that reptiles often use a variety of the above strategies simultaneously and/or in sequence. Heliothermy and thigmothermy may be used simultaneously, for example when a snake basks whilst lying on rocks that have been warmed by the sun.

The 2 previous chapters have been concerned with the body temperatures of the snakes and the general behaviour that they engage in. In this chapter a detailed investigation is made into the thermoregulatory behavioural strategies utilised by the 3 species of snakes and an interspecific comparison undertaken. The first task was to attempt to obtain some indication of the degree of thermoregulation and/or thermoconformity exhibited by the snakes through examination of the body temperature data. However, the largest section is devoted to an examination of behaviour displayed by the snakes and its role in thermoregulation. Once again, the use of models in the outdoor vivaria allowed the thermal conditions (in terms of operative temperatures) to be assessed. The frequency of the various behavioural categories was related to the thermal conditions, and the body temperatures that were recorded during such behavioural categories analysed. Similar comparisons were made for the laboratory experiment data.

5.2. Methods

5.2.1. Regression Analysis of Thermoregulation

Regression analyses were performed on data from both the outdoor vivaria and the laboratory experiments. It has been suggested that the slope of the linear regression of body temperature on ambient temperature can be a measure of thermoregulation (Huey and Slatkin 1976, Huey 1982). A slope near 1 suggests thermoconformity whereas a slope near 0 suggests thermoregulation. Shade air temperature is often used as a convenient estimate of ambient temperature during studies of reptilian thermoregulation and it was used during the laboratory experiments of the present study. Shade air temperature was measured by a temperature probe fixed approximately 10 cm above the floor and at the opposite end of the arena to the heatlamp. The probe was shaded by a piece of white card.

In the outdoor vivaria, an estimate of ambient temperature was recorded by models situated in shaded areas of the vivaria (but uncovered by vegetation). During 1988, model 5 (southwest segment) was used to estimate ambient temperatures for experiments 1-7. In 1989, model 5 was moved to the southeast segment and so ambient temperatures were only recorded up to and including 1030 hours for experiments 9-10 (the temperatures could not be recorded during experiment 8 due to a technical problem with the logging device). After 1030 hours, the model was no longer in the shade and so did not measure ambient temperature. Ambient temperatures were measured later in the day during 1989 by model 4 (northwest segment). Model 4 measurements were used from times including and after 1500 hours for experiments 8 and 9, 1600 hours for experiment 10 and 1700 hours for experiment 11. Model 4 was heated up by the direct sun early in the day and so once it was in the shade, time had to be allowed to ensure it had cooled down to ambient levels. The time that model 4 remained in the sun was longer towards the midsummer period and so the times from which recordings could be used to estimate ambient temperatures became later.

Data from the outdoor vivaria experiments were again divided on the basis of whether they were measured during thermally limiting, thermally unlimiting or 'unlit' (also thermally limiting) conditions. The criteria used to define these conditions are given in Section 3.2.1 and Section 4.2.2. Thermally unlimiting conditions were considered to occur when maximum model temperatures indicated that all 3 snake species could attain selected body temperatures (maximum model temperatures ≥37°C in the outdoor vivaria). Maximum model temperatures <34°C during the 'lit' phase were considered to indicate conditions were thermally limiting for all 3 species. Periods when the outdoor vivaria were 'unlit' were always thermally limiting but are categorised separately from the thermally limiting periods of the 'lit' phase (described as 'unlit' and 'thermally limiting' periods respectively). These categorisations are used in analyses throughout this chapter.

The data from the laboratory experiments were categorised into thermally limiting (heatlamp off) and thermally unlimiting (heatlamp on) conditions as originally described in Sections 3.2.2. and 4.2.2. These categorisations are also used in the analysis of various aspects of thermoregulatory behaviour which follow in this chapter.

In addition to producing regression equations for the body temperature and ambient temperature relationships, statistical tests to determine whether the slopes of the regression lines were significantly different from zero (test of the significance of regression coefficients described in Sokal and Rohlf, 1981) were also performed. However, it should be noted that direct observations were the most important means of assessing whether, and to what extent, thermoregulatory behaviour occurred.

5.2.2. Body Posture: Dorso-Ventral Flattening.

Flattening behaviour was only observed in adders and data were only collected during the outdoor vivaria experiments. For all the other behavioural analyses in this chapter, only behavioural records made at 15 minute intervals were used. In the case of body flattening, this tended to be observed only during the heating phases of the adders and these often lasted less than 30 minutes during hot, sunny conditions. Therefore, to allow a more precise record of flattening behaviour, records taken from more frequent intervals have been used.

Rather than investigating flattening behaviour during thermally limiting and thermally unlimiting conditions, a different categorisation was used. When basking or mosaic basking behaviour was observed in the outdoor vivaria, a record was made of whether the conditions were sunny or 'clouded' (either totally overcast or the sun temporarily obscured by cloud). Of 214 observations of basking/mosaic basking observations for adders during thermally unlimiting conditions, 90.7% were during 'sunny' conditions. However, during thermally limiting conditions (n = 303), there were still 49.2% which were sunny. Therefore sunny periods were often considered to be thermally limiting to the snakes.

There could have been several reasons for this. Model temperatures, as has been stated before, were an average of temperatures for half hour periods. Thus a brief period of sun might raise operative temperatures in the outdoor vivaria above the 'thermally unlimiting conditions' level for a few minutes but the overall averaged model temperatures (which estimated operative temperatures) for the 30 minute period might still be relatively low. In addition, even though conditions were sunny, the sun was often not sufficiently strong to increase model temperatures to thermally unlimiting conditions. This was especially the case early in the morning or late in the afternoon, and during the early and later periods of the snakes' activity season.

Because body flattening was considered to be a heliothermic form of behaviour, the observations were examined on the basis of whether they were observed when conditions were classed as either sunny or clouded rather than thermally limiting or unlimiting. Body flattening behaviour was also related to daily body temperature patterns. Body temperatures that were measured at the commencement and termination of flattening behaviour were measured and estimates were made of the durations of flattening behaviour. Details of these measurements are provided in the results section.

5.2.3. Body Posture: Body Coiling

Records of body coil posture were made when snakes were observed basking or mosaic basking in the outdoor vivaria. The degree of coiling was marked on a scale of 1 to 6, with 6 representing the most tight form of body coil posture (see Fig. 2.7). The results were divided according to whether they were observed during thermally limiting or thermally unlimiting conditions to investigate whether there was a relationship between body coil posture and operative temperatures. In a second investigation, they were divided on the basis of whether they were observed when conditions were 'sunny' or 'clouded'. Interspecific comparisons of observation frequencies were performed using G-tests. G-tests were also used to compare observation frequencies between thermally limiting and unlimiting conditions and between sunny and clouded conditions.

During the laboratory experiments, records of body posture coiling were made when snakes were observed basking but not when refuge basking. It was often possible to see the coiling postures of snakes mosaic basking in the outdoor vivaria as their cover was usually vegetation and it was sufficiently diffuse. The refuges used in the laboratory, however, were solid and if part of the snake's body was hidden then frequently it was not possible to be sure of its coiling posture. Therefore, no records were made of body coiling posture of refuge basking snakes in the laboratory. When the heatlamp turned off (and conditions were described as thermally limiting) the body coiling posture of snakes engaged in thigmothermic behaviour were also recorded.

Overall time budgets were calculated for each of the body coiling postures observed in the laboratory. Only 5 postures were listed as opposed to 6 in the outdoor vivaria. The resolution of the video equipment prevented a distinction being made between postures 5 and 6 and therefore they were classed together as posture 5.

The body temperatures measured for snakes engaged in each body coiling posture were analysed. The same analytical techniques were used for the outdoor vivaria and laboratory data. The statistical analyses were performed in the same way as those described in Section 4.2.4 for general behaviour and body temperature. Interspecific comparisons using Kruskal-Wallis and Wilcoxon/Mann-Whitney tests were performed on the body temperatures of each of the body coil posture categories. Then intraspecific comparisons using Kruskal-Wallis and Wilcoxon/Mann-Whitney tests were carried out on the body temperatures of each of the body coil posture categories within each species. Tests were made on data from thermally limiting and unlimiting conditions and (in the case of the outdoor vivaria experiments) sunny and clouded conditions.

5.2.4. Body Posture: Aspect

Body aspect measurements were only collected during the outdoor vivaria experiments when snakes were engaged in basking or mosaic basking. Fig. 2.8 illustrates the categorisation used for describing body aspect. Note that observations were not recorded between 1030 and 1430 hours when the sun was too high in the sky to categorise the body aspect. The results are presented as frequencies of observations recorded when conditions were sunny or clouded.

5.2.5. Use of Cover in Thermoregulation.

The degree of body area exposed was estimated for snakes mosaic basking in the outdoor vivaria. This was marked on a scale of 1 to 3 (1 = 5-35% exposure, 2 = 36-65% exposure, 3 = 66-95% exposure). Fully exposed snakes (>95% exposure) were described as basking and those results were incorporated into the analysis with the mosaic basking results.

The results from the outdoor vivaria were divided into observations from thermally limiting conditions and observations from thermally unlimiting conditions. Interspecific comparisons of observation frequencies for each exposure category were performed using G-tests. G-tests were also used to compare observed frequencies between thermally limiting and unlimiting conditions for each species.

A slightly different categorisation was used to estimate the degree of body area exposed when snakes were observed refuge basking in the laboratory experiments. An estimation was made as to whether the snake was exposing the head region only (= 1), 25% of the body (= 2), 50% of the body (= 3) or 75% of the body (= 4). When reviewing video recordings of the snake experiments, the tapes could be stopped and the amount of body area exposed measured off the monitor screen. The overall time budgets for each of the exposure categories was calculated together with the time budgets of snakes fully exposed and displaying basking behaviour.

The body temperatures of the different exposure categories were compared using the same methods as Section 4.2.4 and Section 5.2.3 above. Interspecific and intraspecific comparisons were performed using Kruskal-Wallis and Wilcoxon/Mann-Whitney tests. Details on the type of cover utilised by the snakes during mosaic basking behaviour in the outdoor vivaria were also recorded.

5.2.6. Shuttling Heliothermy

Analysis of data for this topic was restricted to measurements collected from the laboratory studies during thermally unlimiting conditions. The overall time budgets of basking and refuge basking behaviour were looked at in relation to other behavioural categories. Median time lengths of basking activities and the body temperatures that each species maintained during thermally unlimiting conditions were compared.

The data for basking and mosaic basking behaviour were combined together into one category and the remaining behavioural categories combined into a second category. Thus there were 2 broad behavioural groups of 'general basking' behaviour and 'non-basking' behaviour. A comparison of overall time budgets and of body temperature data was possible with the 2 categories. However, because each of the 2 behavioural amalgamated categories were formed from the smaller behavioural categories it was not possible to compare median time durations between them without altering the data set. For example, in the data set a movement behaviour of 6 mins could be followed by an 'under refuge' behaviour of 3 mins and then a basking behaviour of 4 mins. In the new categorisation, the non-basking behaviour was 9 mins (6 + 3). Insufficient time precluded the data set from being fully modified to make a full analysis of the data.

5.2.7. Basking Sites

All data in this section were taken from observations recorded during the outdoor vivaria experiments. When snakes were observed basking or mosaic basking, information on the slope (if any), position in the vivaria and substrate of the snakes' basking/mosaic basking sites were collected.

In the case of the slope and position measurements, an investigation was made into whether the snakes selected their basking/mosaic basking site position in relation to the position of the sun in the sky. Such patterns would be exhibited as a change in the daily pattern of basking/mosaic basking site selection. A broad categorisation of times was made to examine if such patterns existed. During the 11 experiments carried out in the outdoor vivaria, the longest 'lit' phases (defined in Section 3.2.1) occurred during the midsummer and lasted from 0750 hours until 1915 hours (a duration of 11 hours 25 mins). The shortest 'lit' phase was observed in September 1988 and lasted from 0840 hours until 1800 hours (a duration of 9 hours 20 mins). On the basis of the latter time, the day was divided into approximate 3 hour segments: the beginning of the lit phase until 1159 hours, 1200 hours until 1500 hours, 1501 hours until the end of the lit phase. This categorisation was used for all the experiments. During the first period the northwest, north, west and central segments were in the sun for the longest periods. During the second period most of the vivaria except the areas along the far southern end were in the sun for some time. During the last period, the central, south, east and southeast segments were in the sun for the longest time.

Patterns of basking/mosaic basking site slope selection were illustrated by adapted 'wind rose' diagrams which are usually used to provide details of wind direction, frequency and strength. Patterns of basking/mosaic basking site selection were illustrated using three dimensional mapped grids of the vivaria with frequency data incorporated into them. Finally, an indication of the range and frequency of substrates used by the snakes during basking/mosaic basking behaviour has been included in the results.

5.3. Results

5.3.1. Regression Analysis of Thermoregulation

Outdoor Vivaria Experiments

The body temperatures of snakes measured in the outdoor vivaria were related to ambient temperatures estimated by the models (to be referred to as 'model ambient' temperature or T_{amb} in the equations which follow). The results from all data collected during 1988 and 1989 were as follows. Body temperature is referred to as T_b;

Smooth Snakes: $T_b = 4.131 + 0.936\ T_{amb}$
(Slope significantly different from zero, $t_s = 42.238$, $p < 0.001$, $n = 1193$)

Grass Snakes: $T_b = 4.217 + 0.948\ T_{amb}$
(Slope significantly different from zero, $t_s = 27.241$, $p < 0.001$, $n = 787$)

Adders: $T_b = -2.178 + 1.433\ T_{amb}$
(Slope significantly different from zero, $t_s = 41.524$, $p < 0.001$, $n = 1468$)

However, a comparison between species would not be very meaningful due to the effects of varying environmental conditions when body temperatures were measured. Therefore records have once again been divided into those measured during thermally unlimiting, thermally limiting and 'unlit' (also thermally limiting) periods.

The plots for data measured when conditions were considered to be thermally unlimiting in the outdoor vivaria (maximum measured model temperature $> 37°C$) are provided in Fig. 5.1. The regression equations were calculated as follows;

Smooth Snakes: $T_b = 6.504 + 0.930\ T_{amb}$
(Slope significantly different from zero, $t_s = 7.032$, $p < 0.001$, $n = 128$)

Grass Snakes: $T_b = 7.657 + 0.977\ T_{amb}$
(Slope significantly different from zero, $t_s = 6.472$, $p < 0.001$, $n = 76$)

Adders: $T_b = 18.022 + 0.655\ T_{amb}$
(Slope significantly different from zero, $t_s = 5.477$, $p < 0.001$, $n = 169$)

A visual inspection of the slopes of the regression line shows that the body temperatures of smooth snakes were about 6 to 8°C above model ambient temperature and grass snakes 8 to 9°C above model ambient temperature. The slope of the regression line for adders was much shallower than for the other 2 species and therefore suggests that body temperatures were maintained with a greater degree of independence from model ambient temperature (i.e. greater degree of thermoregulation). However the slope was still significantly different from zero, even when the data from the one specimen that remained submerged during the study are removed (specimen Vb9);

Adders (without Vb9): $T_b = 20.346 + 0.572\ T_{amb}$
(Slope significantly different from zero, $t_s = 5.320$, $p < 0.001$, $n = 160$).

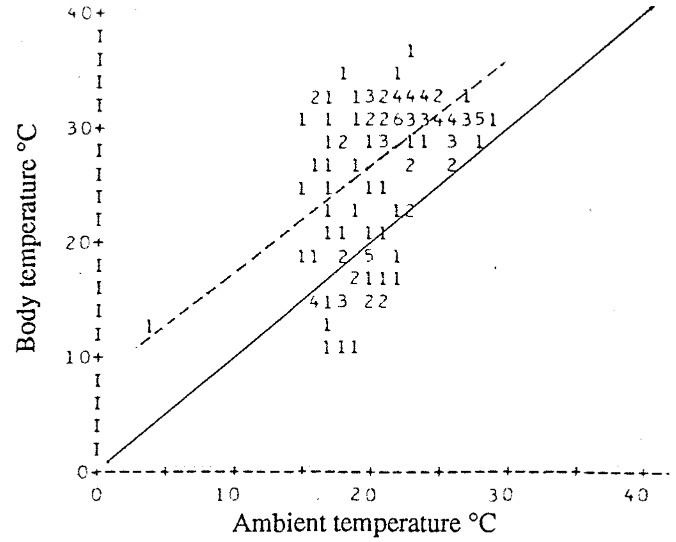
When conditions were thermally limiting, the regression slope of the adder data was much steeper. For smooth snakes and grass snakes there was relatively little difference between the slopes of the regression lines. The regression line for the smooth snake data was closer to the line of equal variable value than that recorded during thermally unlimiting conditions indicating body temperatures were maintained about 3 to 4°C above model ambient temperature. The regression line for grass snakes was actually slightly shallower than that recorded during thermally unlimiting conditions although body temperatures were maintained between only 1 to 3°C above model ambient temperature. The plots for the data are given in Fig. 5.2. The regressions for the same data were;

Smooth Snakes: $T_b = 3.277 + 0.943\ T_{amb}$
(Slope significantly different from zero, $t_s = 17.389$, $p < 0.001$, $n = 342$)

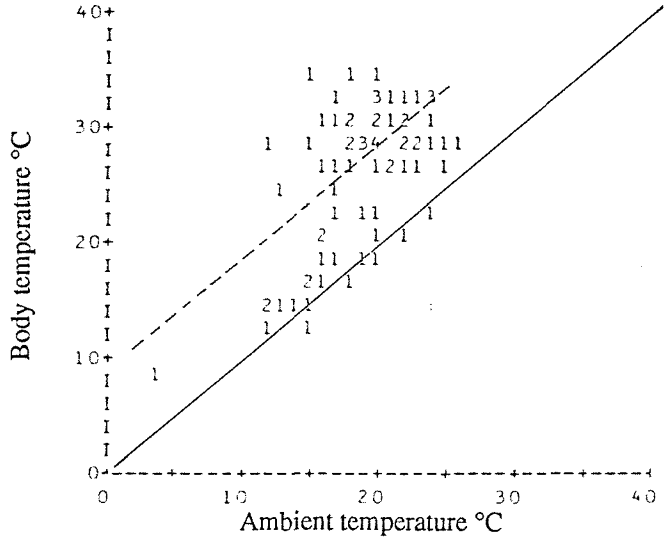
Grass Snakes: $T_b = 3.866 + 0.914\ T_{amb}$
(Slope significantly different from zero, $t_s = 12.614$, $p < 0.001$, $n = 289$)

Adders: $T_b = -0.312 + 1.286\ T_{amb}$
(Slope significantly different from zero, $t_s = 15.696$, $p < 0.001$, $n = 437$)

1. *Coronella austriaca*



2. *Natrix natrix*



3. *Vipera berus*

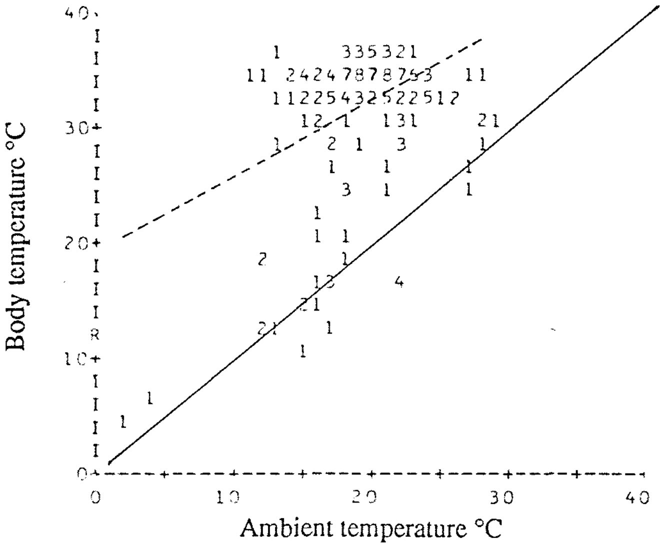
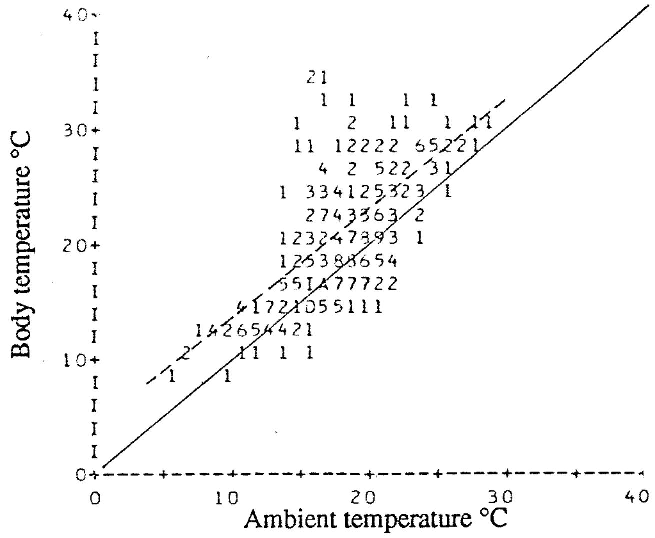


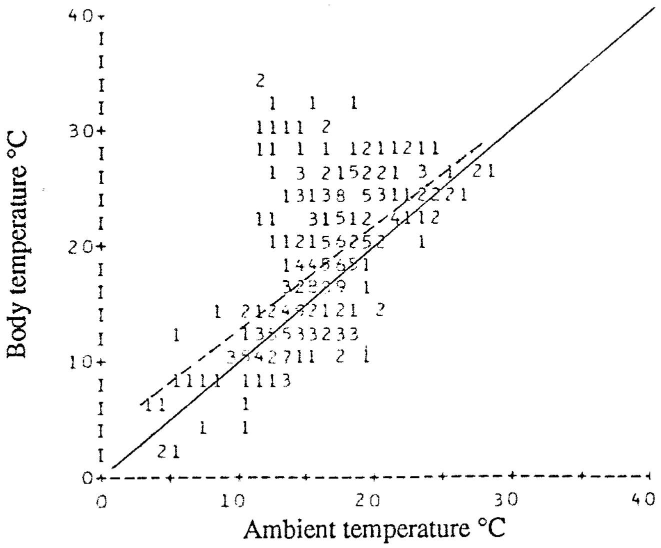
***Fig. 5.1*: Relationship between body temperature and ambient temperature. The regression line is indicated by a dashed line of data recorded during thermally unlimiting conditions for the outdoor vivaria experiments.**

The solid line indicates body temperature equalling ambient temperature. Numbers indicate where more than one recording was made.

1. *Coronella austriaca*



2. *Natrix natrix*



3. *Vipera berus*

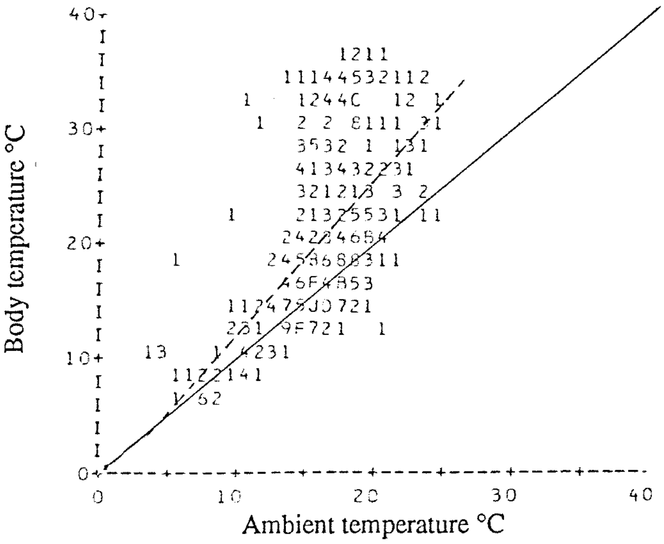


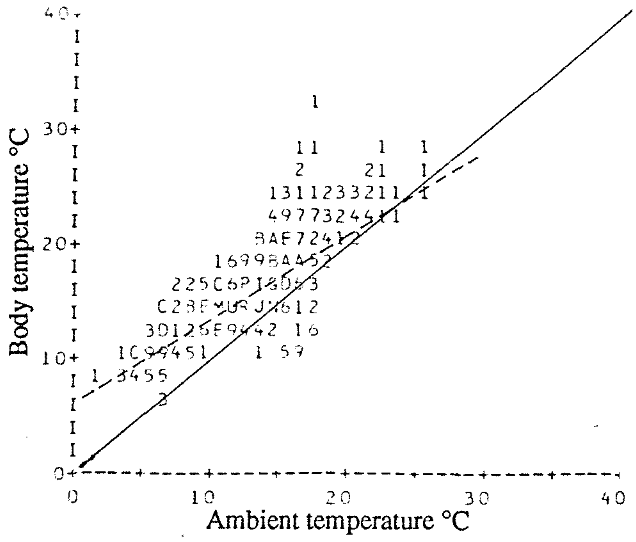
Fig. 5.2: Relationship between body temperature and ambient temperature. The regression line is indicated by a dashed line) of data recorded during thermally limiting conditions for the outdoor vivaria experiments.

The solid line indicates body temperature equalling ambient temperature.

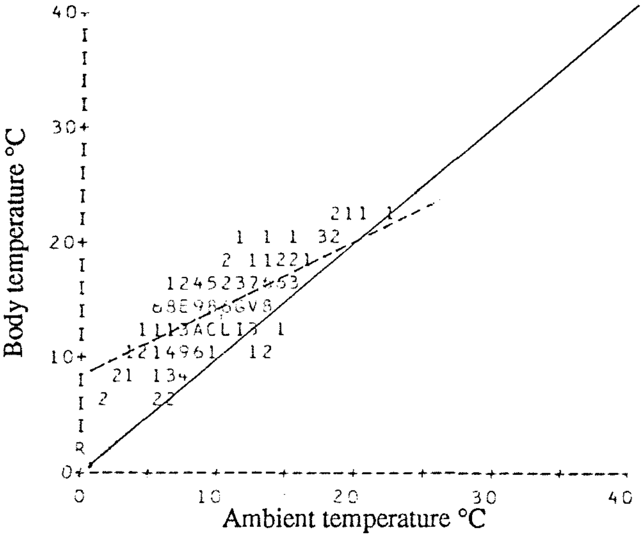
Numbers indicate where more than one recording was made. Lettered symbols represent the following frequencies:

A	10	D	13	G	16	J	19
B	11	E	14	H	17		
C	12	F	15	I	18		

1. *Coronella austriaca*



2. *Natrix natrix*



3. *Vipera berus*

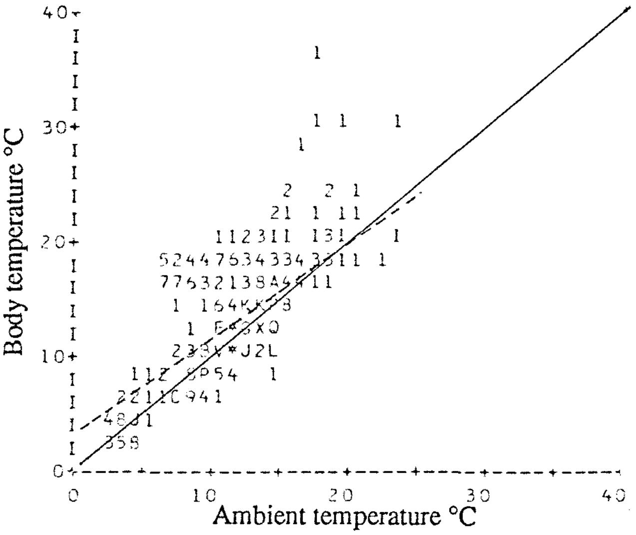


Fig. 5.3: **Relationship between body temperature and ambient temperature. The regression line is indicated by a dashed line of data recorded during 'unlit' periods for the outdoor vivaria experiments.**

The solid line indicates body temperature equalling ambient temperature.

Numbers indicate where more than one recording was made. Lettered symbols represent the following frequencies:

A	10	D	13	G	16	J	19	M	22	P	25	S	28	V	31	Y	34
B	11	E	14	H	17	K	20	N	23	Q	26	T	29	W	32	Z	35
C	12	F	15	I	18	L	21	0	24	R	27	U	30	X	33	*	>35

Finally, data from the 'unlit' times were analysed. Much of this was recorded from nocturnal periods.

Plots of the data are given in Fig. 5.3 and the regression equations were as follows;

Smooth Snakes: $T_b = 6.243 + 0.763\ T_{amb}$
(Slope significantly different from zero, $t_s = 28.663$, $p < 0.001$, $n = 603$)

Grass Snakes: $T_b = 7.538 + 0.600\ T_{amb}$
(Slope significantly different from zero, $t_s = 15.617$, $p < 0.001$, $n = 282$)

Adders: $T_b = 2.311 + 0.891\ T_{amb}$
(Slope significantly different from zero, $t_s = 23.173$, $p < 0.001$, $n = 617$)

Laboratory Experiments

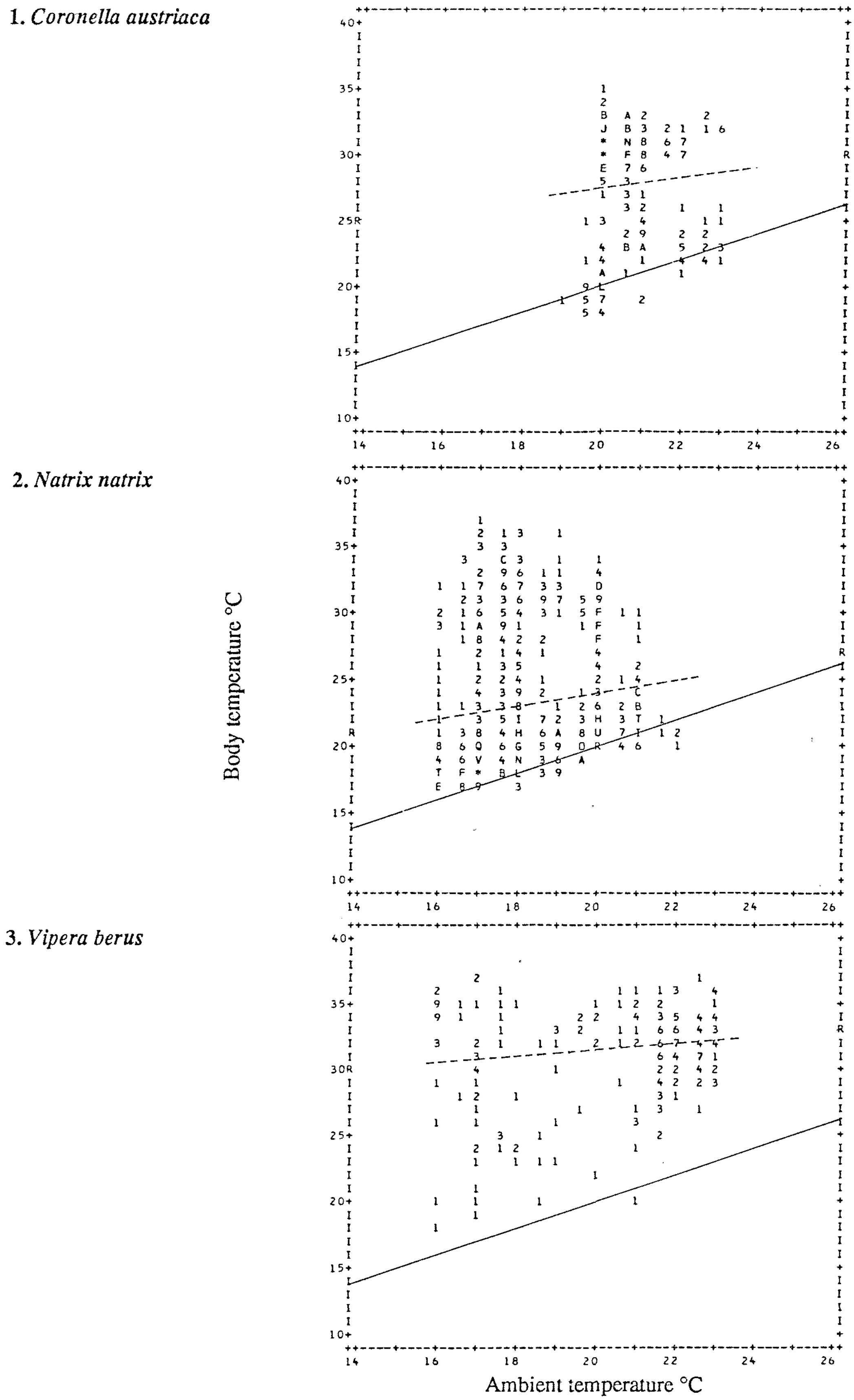
The relationships between body temperatures and ambient temperatures were investigated for thermally unlimiting conditions (heatlamp on) and thermally limiting conditions (heatlamp off). Ambient temperatures were recorded from shade air temperatures measured in the video arena. Plots of the data from thermally unlimiting conditions are given in Fig. 5.4 and regression equations were as follows;

Smooth Snakes: $T_b = 18.716 + 0.427\ T_{amb}$
(Slope not significantly different from zero, $t_s = 1.562$, $p > 0.05$, $n = 414$)

Grass Snakes: $T_b = 14.665 + 0.464\ T_{amb}$
(Slope significantly different from zero, $t_s = 4.315$, $p < 0.001$, $n = 982$)

Adders: $T_b = 26.240 + 0.241\ T_{amb}$
(Slope significantly different from zero, $t_s = 2.326$, $p < 0.05$, $n = 227$)

The regression slope of the adder data was found to be the most shallow among the 3 species, although it was still significantly different from zero. The regression line of the smooth snake data was found to be not significantly different from a slope of zero which suggests that the


1. *Coronella austriaca*

2. *Natrix natrix*

3. *Vipera berus*

Fig. 5.4: **Relationship between body temperature and ambient temperature. The regression line is indicated by a dashed line of data recorded during thermally unlimiting conditions (heatlamp on) for the laboratory experiments.**

The solid line indicates body temperature equalling ambient temperature.

Numbers indicate where more than one recording was made. Lettered symbols represent the following frequencies:

A	10	D	13	G	16	J	19	M	22	P	25	S	28	V	31	Y	34
B	11	E	14	H	17	K	20	N	23	Q	26	T	29	W	32	Z	35
C	12	F	15	I	18	L	21	0	24	R	27	U	30	X	33	*	>35

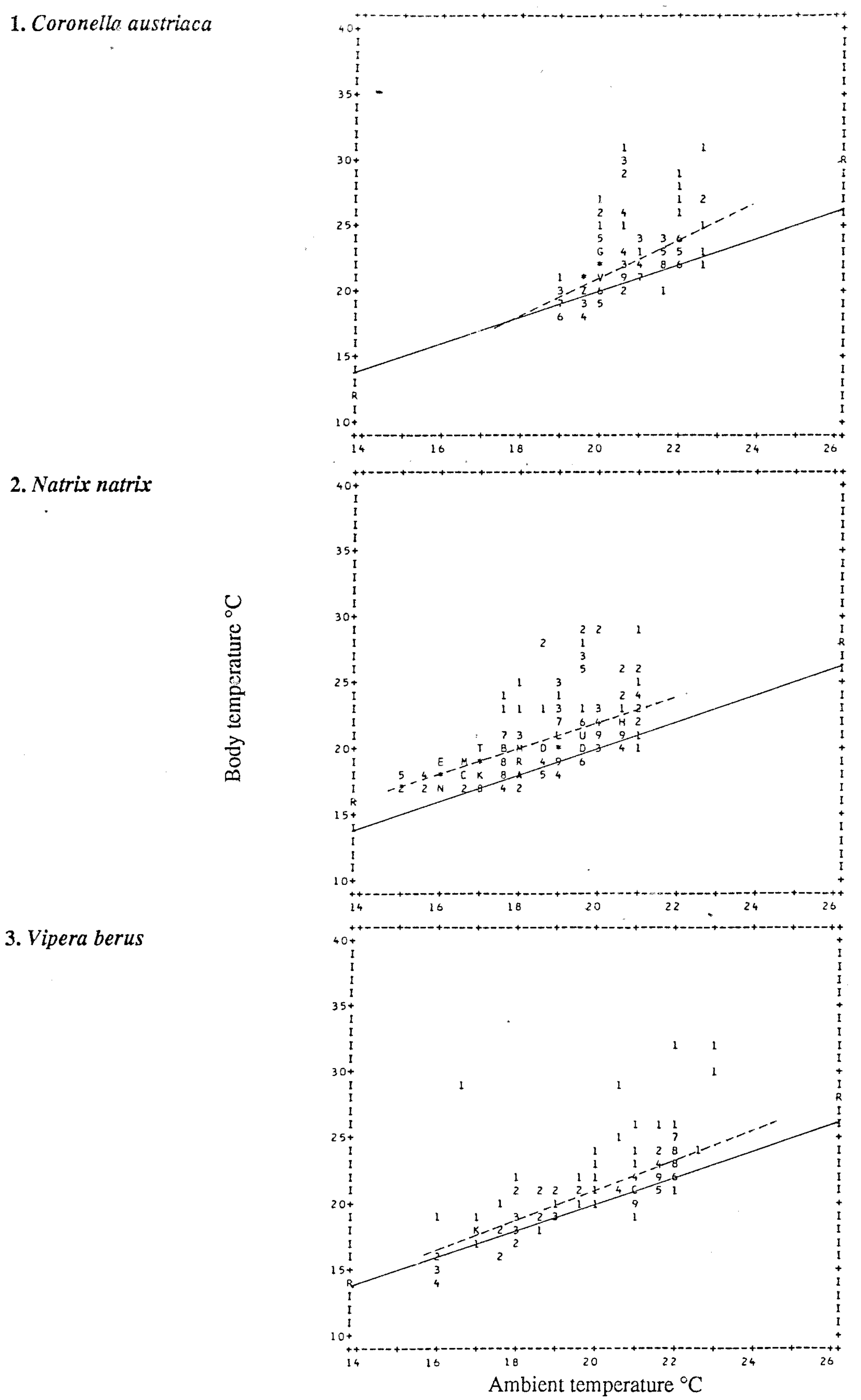


Fig. 5.5: **Relationship between body temperature and ambient temperature. The regression line is indicated by a dashed line of data recorded during thermally limiting conditions (heatlamp off) for the laboratory experiments.**

The solid line indicates body temperature equalling ambient temperature.

Numbers indicate where more than one recording was made. Lettered symbols represent the following frequencies:

A	10	D	13	G	16	J	19	M	22	P	25	S	28	V	31	Y	34
B	11	E	14	H	17	K	20	N	23	Q	26	T	29	W	32	Z	35
C	12	F	15	I	18	L	21	0	24	R	27	U	30	X	33	*	>35

snakes were able to thermoregulate and maintain body temperatures independent from ambient temperatures. The regression slope of the grass snake data was also relatively shallow.

The regression lines of data from thermally limiting conditions were much steeper as shown in Fig. 5.5. Therefore during such conditions in the laboratory the snakes acted more as thermoconformers. The regression equations for the data were;

Smooth Snakes: $T_b = -8.519 + 1.497\ T_{amb}$
(Slope significantly different from zero, $T_s = 11.814$, $p < 0.001$, $n = 289$)

Grass Snakes: $T_b = 2.346 + 0.968\ T_{amb}$
(Slope significantly different from zero, $T_s = 25.340$, $p < 0.001$, $n = 650$)

Adders: $T_b = -1.953 + 1.154\ T_{amb}$
(Slope significantly different from zero, $T_s = 14.881$, $p < 0.001$, $n = 160$)

5.3.2. Body Posture: Dorso-Ventral Flattening

Observations of body flattening were only observed in adders. The limited resolution of the video recordings prevented an investigation of body flattening by adders during the laboratory experiments but observations were made from the outdoor vivaria experiments. In all the behavioural analyses of this chapter and Chapter 3, only observations recorded from 15 minute intervals have been used. However, during the heating phases of the snakes, observations were sometimes taken at more frequent intervals to obtain more detailed information. This additional data will be used in the following investigation of body flattening.

During the 66 snake days that adders were observed, body flattening was observed on 28. Adders were described as being 'flattened', 'semi-flattened' or not flattened. There were 110 occasions when adders were observed to be flattened and 7 occasions when they were observed to be semi-flattened.

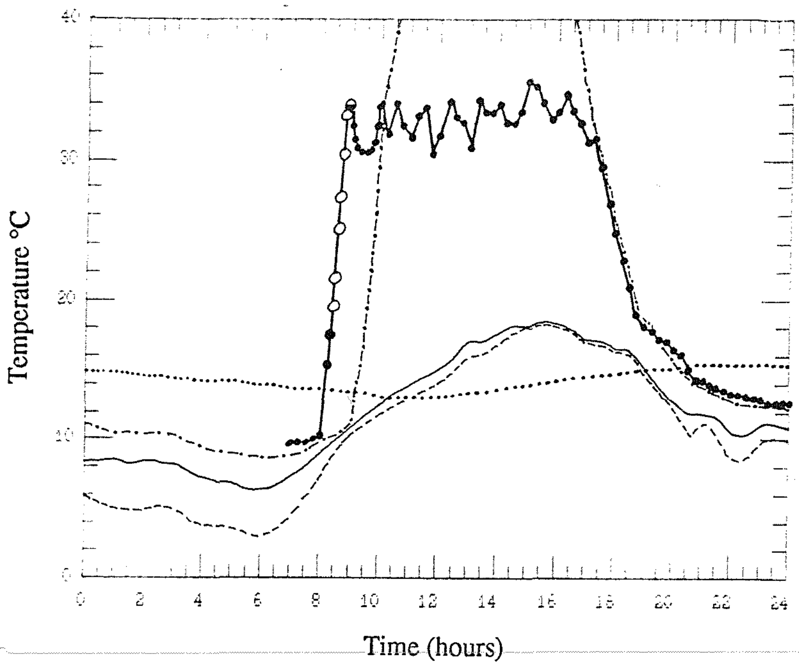
Flattening tended to coincide with the heating phases of the adders. Of the 28 days that flattening was observed, the first flattening observation of the day was recorded before 1200 hours on 26 occasions. For example, Fig. 5.6 illustrates the body temperature pattern of an adder (specimen Vb1) on 11.5.88. At 0800 hours the snake was hidden from view and the body temperature 10.2°C. By the next recording at 0815 hours, the snake had emerged and was mosaic basking (coil posture 4, about 60% exposed from the vegetation) in the west sector of the vivarium and had a body temperature of 15.3°C. It remained in that position for about five minutes before it moved to the northwest sector. At 0827 hours it was mosaic basking (coil posture 4, about 90% exposure, on bare substrate) and the body was flattened (body temperature of 19.5°C). It remained in this site and posture until 0852 hours by which time the body temperature had increased to 33.3°C, with an overall heating rate of 0.55°C/min during the flattening period. By 0855 hours the snake was in the same site and position and was only semi-flattened, with a body temperature of 33.7°C. At 0900 hours it was no longer flattened at all and had moved more into the shade of vegetation (a tighter coil posture of 5, about 50% exposure) and the body temperature had dropped slightly to 32.4°C. Conditions were sunny throughout the whole of the period.

A similar body temperature pattern to that of the above example is also shown in Fig. 5.6 for specimen Vb12 on 26.5.89. The first body temperatures of the day closely followed those of the underground temperature probe suggesting that the adder was submerged below ground. A slight drop in temperature at around 0930 hours probably coincided with emergence above ground where the ambient temperature was cooler. By 0948 hours it was basking on the heap of vegetation in the northwest corner (coil posture 2) and was flattened (body temperature of 17.8°C at 0947 hours). At 0957 hours a body temperature of 25.6°C was recorded, at 0958 hours it was observed in the same position and posture, and at 1000 hours the body temperature was 30.5°C. At 1003 hours the snake no longer appeared to be flattened and 5 minutes later it was mosaic basking (coil posture 5, approximately 90% exposure). The body temperature was 31.2°C at 1007 hours.

The 2 above examples are from days when model temperatures quickly reached relatively high levels indicating conditions were thermally unlimiting for the snakes. During those types of conditions, adders often displayed an initial heating phase and then maintained body temperatures at relatively precise levels (a 'plateau pattern') until eventually cooling down in the evening. Flattening was not observed after the initial heating phase on such days. However, when conditions were more changeable, flattening was observed during 2 distinct periods on 4 days and during 3 distinct periods on 1 day.

Fig. 5.7 illustrates the body temperature pattern on a changeable day. Flattening was observed from 0923 to 0942 hours during the initial heating phase and these observations coincided with

1. 11.5.88, specimen Vb1



2. 26.5.89, specimen Vb12

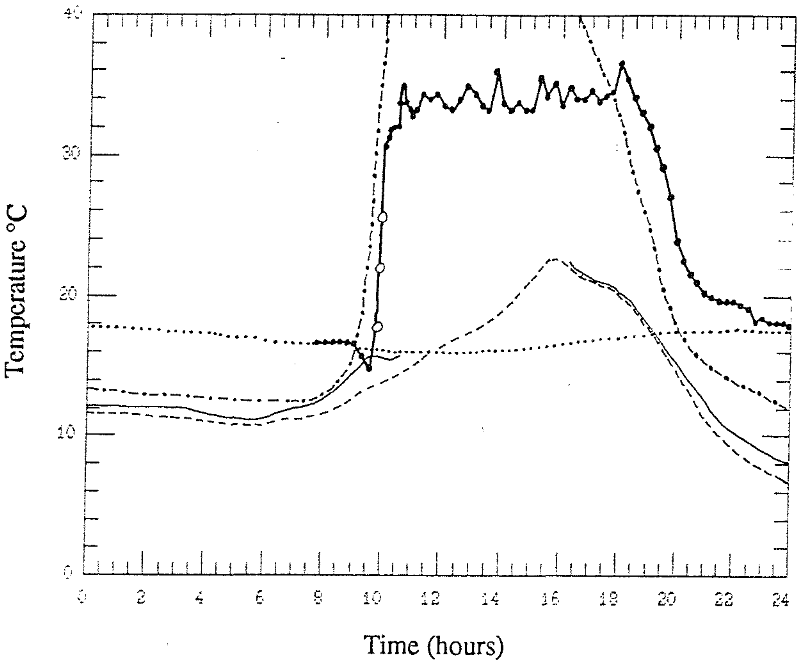


Fig. 5.6: **Body temperature patterns for *Vipera berus* specimens.**
Open circles on the body temperature lines indicate periods when body flattening was observed. Half-filled circles indicate periods when the snakes were observed semi-flattened.

Note that for graph 2 (26.5.89) model ambient temperatures were not recorded during the midday periods.

Key

•—•—•—• body temperature

············ underground refuge temperature

———— model ambient temperature

—·—·—·— maximum model temperature

– – – – minimum model temperature

27.7.88, specimen Vb4

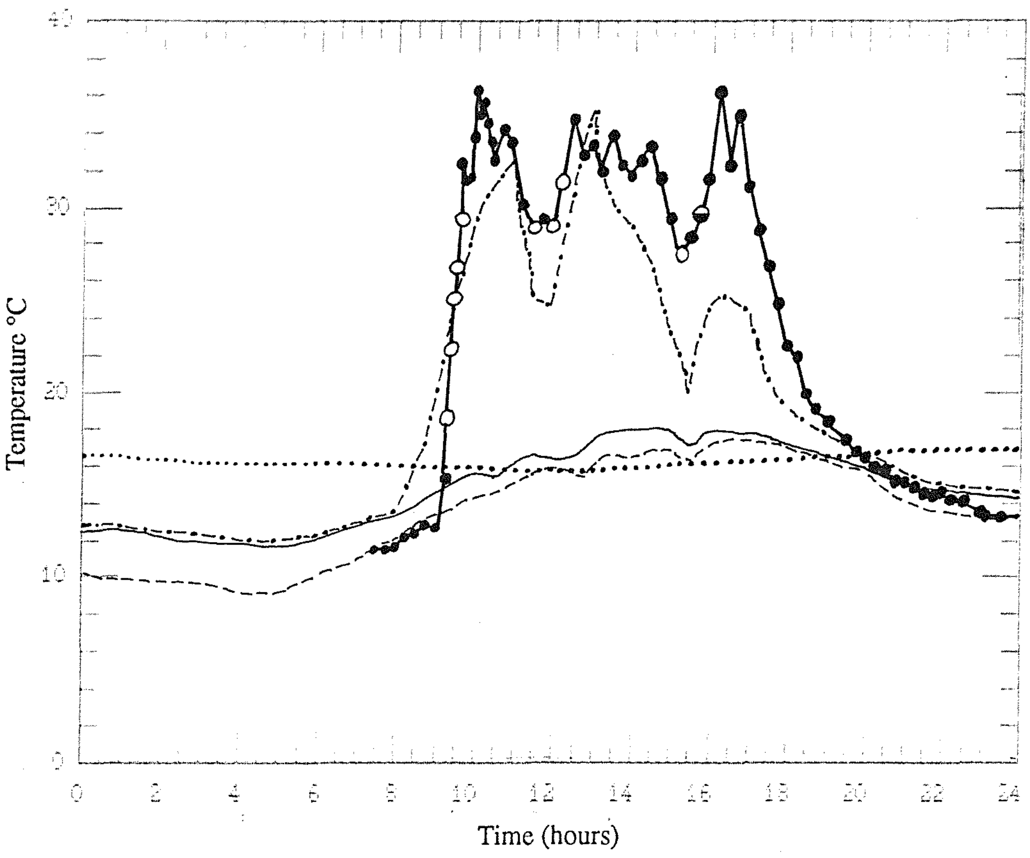


Fig. 5.7: **Body temperature pattern for a *Vipera berus* specimen during a day of changeable conditions.**

Open circles on the body temperature lines indicate periods when body flattening was observed. Half-filled circles indicate periods when the snakes were observed semi-flattened.

Note that the true maximum model temperatures available in the vivarium were not measured during the afternoon period. This was due to models not being situated in the warmest area of the vivarium and accounts for the discrepancy between body temperatures and maximum model temperatures during that period.

Key

●—●—●—● body temperature

············ underground refuge temperature

———— model ambient temperature

—·—·—·— maximum model temperature

– – – – minimum model temperature

sunny conditions. At 0948 hours the sun was obscured by cloud and the adder was no longer flattened. By 1118 hours the sun was still obscured, the snake was basking (not flattened) but the maximum model temperatures and body temperature were decreasing. At 1136 hours the sun came out again and the adder was observed to be flattened. Fifteen minutes later the sun had clouded over again and the snake was not flat, then 12 minutes after that (at 1203 hours) the sun came out and the adder was flattened once again. It increased its body temperature from 28.8°C at 1203 hours to 31.3°C at 1219 hours before hiding from view at 1235 hours (body temperature of 34.6°C). A third phase of flattening was observed after another period of declining model temperatures and cloudy conditions. At 1504 hours the adder was observed mosaic basking but not flattened during cloudy conditions, but by 1523 hours the sun had come out and the adder was flattened. Ten minutes later the sun was obscured once again and the adder was still basking but was no longer flattened.

Thus it appears that flattening is also used after the initial heating phase when body temperatures prematurely decrease (due to decreasing environmental temperatures) and a period of sunny conditions permits the adder to 'boost' its body temperature back to selected levels. This is reflected in the result that of the 110 observations of flattening in adders, 99 occurred when conditions were sunny (90%) and only 11 (10%) when the sun was clouded over.

The durations that adders were observed engaged in flattening behaviour were measured from the initial flattening periods of the days (i.e. not from flattening periods observed after the initial flattening period). This was measured as the time from the first flattening observation to the time of the first semi-flattening or non-flattening observation. These estimates partly depended on the frequency that observations were made. For the 26 days for which the data were calculated, the mean value was calculated as 25.9 mins ± 16.68 (median 25 mins, range 3 - 60 minutes). The durations of the flattening periods were also influenced by environmental conditions as mentioned above. Therefore the data were divided into observations recorded during sunny conditions and observations recorded during changeable/cloudy conditions. The mean duration of flattening periods from sunny conditions was calculated as 22.1 mins ± 14.21 ($n = 17$, median 15 mins, range 3 - 60 mins). The mean duration of flattening periods from changeable/cloudy conditions was 33.0 mins ± 18.58 ($n = 9$, median 29 mins, range 8 - 59 mins).

An indication of the body temperatures that adders were recorded at on commencing flattening was calculated. Body temperatures from adders recorded on the occasion immediately prior to the first flattening observation were used for this investigation ('pre-flattening' body temperature). The mean pre-flattening body temperature was 12.9°C ± 3.30 (n = 20, median 13.5°C, range 7.3 - 17.3°C).

The body temperatures recorded during the last flattening observation of the initial flattening phase were used to estimate the mean body temperature at which flattening ceased. As such observations were unlikely to have been the last exact times that flattening occurred, the result is likely to be an underestimate of the real value. The mean body temperature at which flattening ceased was 26.9°C ± 6.17 (n = 17, median 28.4°C, range 14.3 - 35.5°C). Records from data collected during sunny conditions were divided from those recorded during changeable/overcast conditions. For sunny conditions, the mean body temperature at which flattening ceased was 28.8°C ± 5.43 (n = 12, median 29.2°C, range 14.3 - 35.5°C) and for changeable/overcast conditions 22.4°C ± 5.49 (n = 5, median 24.1°C, range 14.9 - 30.8°C).

5.3.3. Body Posture: Body Coiling

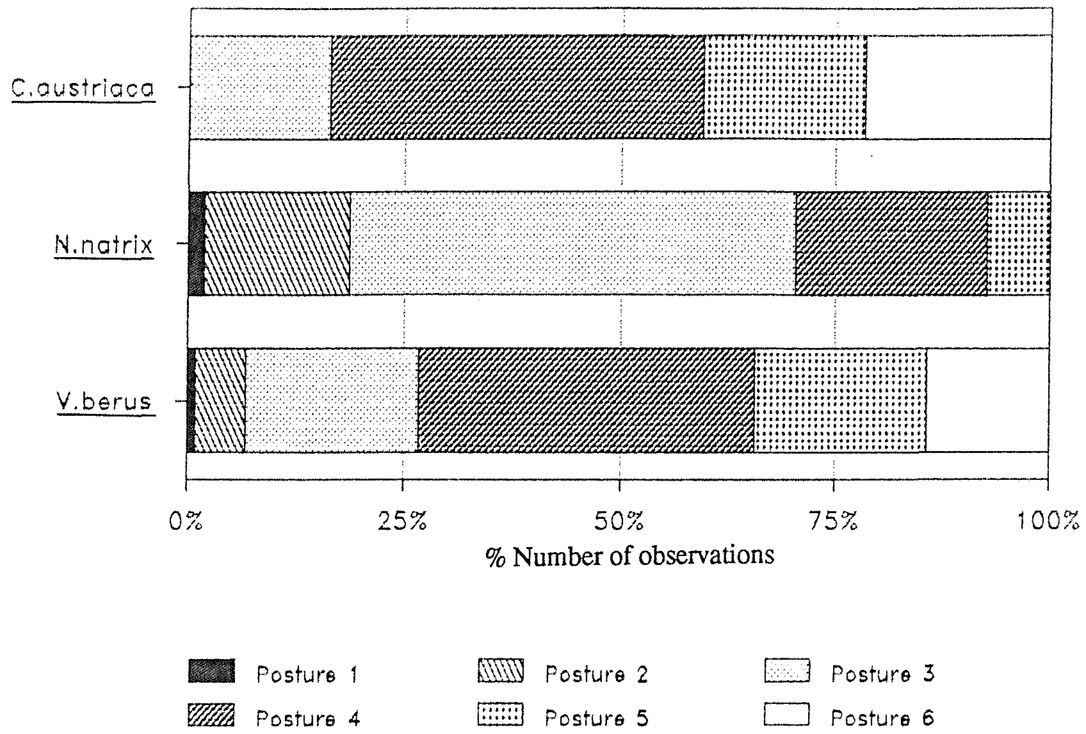
Outdoor Vivaria Experiments

The body coil posture of basking or mosaic basking snakes was recorded using a scale of 1 to 6 (see Fig. 2.7). The frequency and proportion of observations for each of the 6 postures are provided in Table 5.1. Results were separated according to environmental conditions. In the first instance, conditions were divided into thermally unlimiting and thermally limiting periods. In the second case, the frequency of the different body coil postures were measured on the basis of whether they were recorded when conditions were sunny or when the sun was obscured by cloud. Graphical interpretations of the results are provided in Figs. 5.8 and 5.9.

A series of G-tests was carried out on the frequency data. In many cases the number of observations for a particular body coil posture category was less than 5. In these instances the frequencies of adjacent classes were combined until the frequency of observations was greater than or equal to 5. This should be taken into account when examining the results.

The results of the G-tests are given in Table 5.2. Details of the categories that were combined for the purposes of the analysis are provided. Significant differences in the frequencies of body coil postures was found between smooth snakes and grass snakes and between adders

1. Thermally unlimiting conditions



2. Thermally limiting conditions

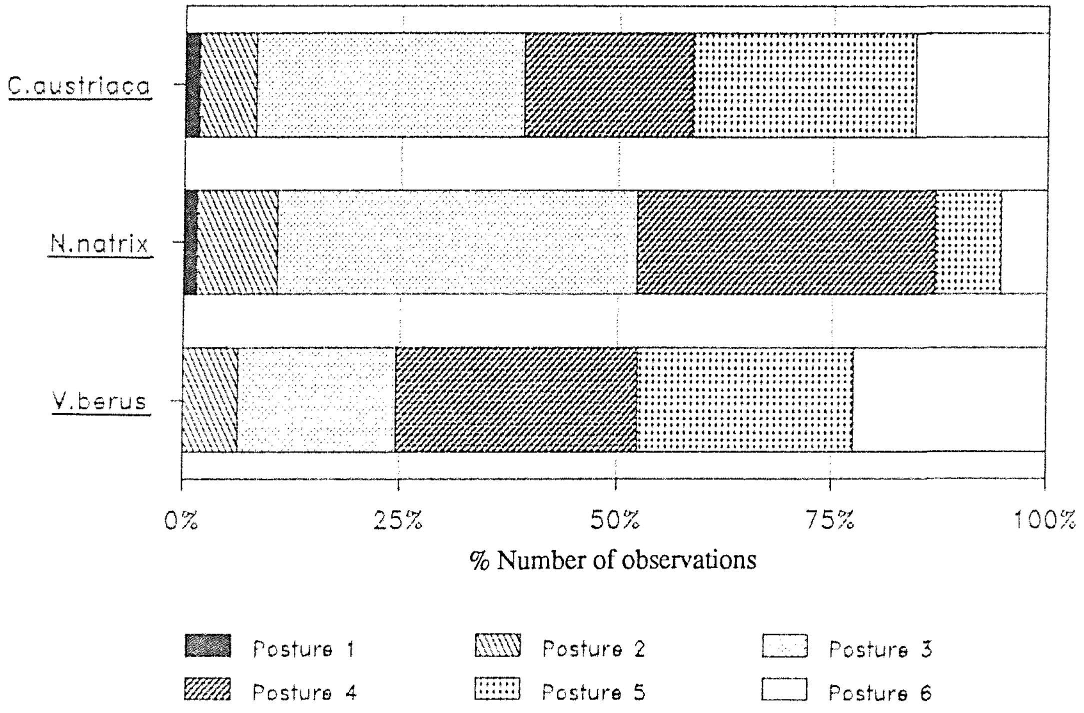
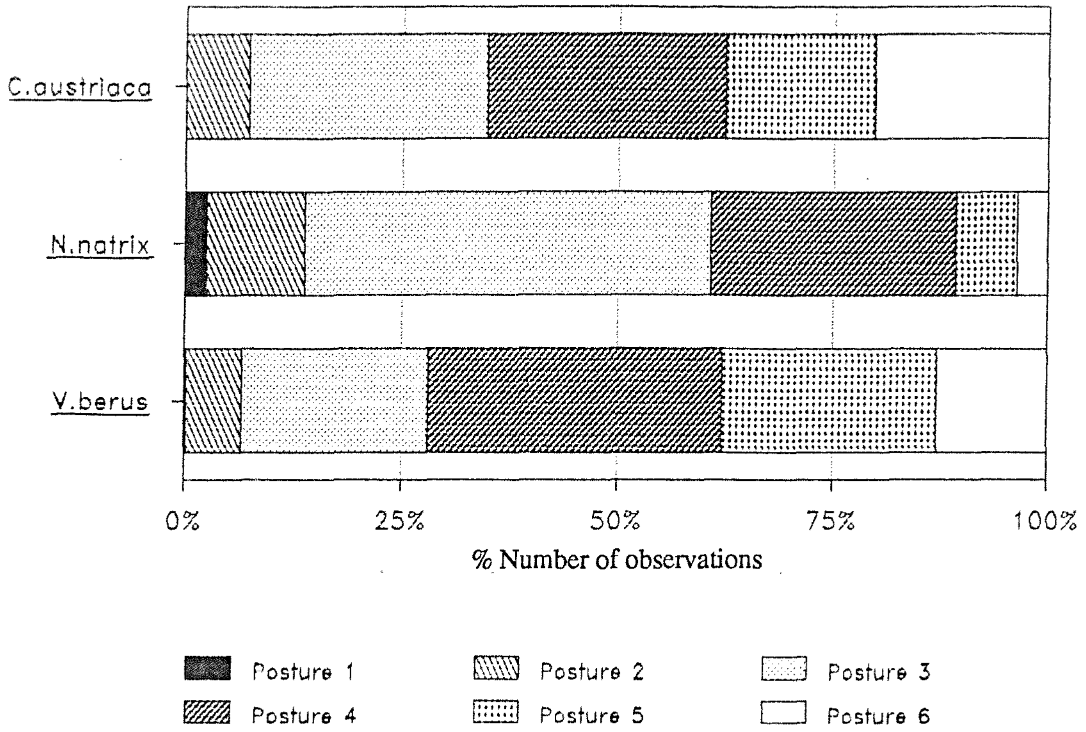


Fig. 5.8: Percentage number of observations assigned to each of the body coiling posture behavioural categories during thermally unlimiting and limiting conditions for the outdoor vivaria experiments.

1. Sunny conditions



2. Clouded conditions

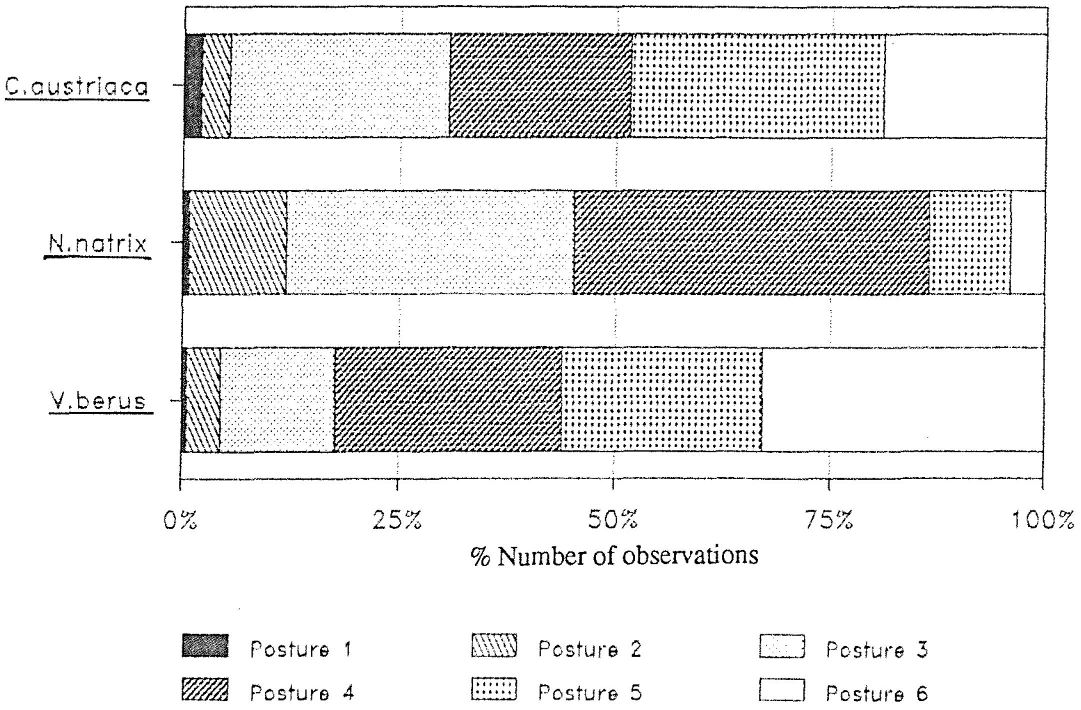


Fig. 5.9: Percentage number of observations assigned to each of the body coiling posture havioural categories during 'sunny' and 'clouded' conditions for the outdoor vivaria experiments.

		Coronella austriaca		*Natrix natrix*		*Vipera berus*	
		n	%	n	%	n	%
1. Thermally unlimiting conditions	Posture 1	0	0	1	1.9	2	1.0
	Posture 2	0	0	9	16.7	11	5.6
	Posture 3	6	16.2	28	51.8	39	20.0
	Posture 4	16	43.3	12	22.2	76	39.0
	Posture 5	7	18.9	4	7.4	39	20.0
	Posture 6	8	21.6	0	0	28	14.4
	Total	**37**		**54**		**195**	
		n	%	n	%	n	%
2. Thermally limiting conditions	Posture 1	2	1.6	3	1.5	0	0
	Posture 2	8	6.5	19	9.3	19	6.3
	Posture 3	38	31.0	85	41.4	55	18.2
	Posture 4	24	19.5	71	34.6	84	27.8
	Posture 5	32	26.0	16	7.8	76	25.2
	Posture 6	19	15.4	11	5.4	68	22.5
	Total	**123**		**205**		**302**	
		n	%	n	%	n	%
3. Sunny conditions	Posture 1	0	0	4	2.4	1	0.3
	Posture 2	5	7.2	19	11.3	25	6.3
	Posture 3	19	27.5	79	47.0	85	21.5
	Posture 4	19	27.5	48	28.6	135	34.1
	Posture 5	12	17.4	12	7.1	99	25.0
	Posture 6	14	20.3	6	3.6	51	12.9
	Total	**69**		**168**		**396**	
		n	%	n	%	n	%
4. Clouded conditions	Posture 1	2	2.1	1	0.8	1	0.5
	Posture 2	3	3.2	14	11.1	7	3.8
	Posture 3	24	25.3	42	33.3	24	13.2
	Posture 4	20	21.1	52	41.3	48	26.4
	Posture 5	28	29.5	12	9.5	42	23.1
	Posture 6	18	18.9	5	4.0	60	33.0
	Total	95		126		182	

Table 5.1: Frequency and percentage frequency of observations for the body coiling posture categories during the outdoor vivaria experiments.

	Groups for comparison	Thermally unlimiting conditions			Thermally limiting conditions		
		Combined behavioural groups	**G**	**p**	**Combined behavioural groups**	**G**	**p**
(i)	*Coronella austriaca, Natrix natrix*	1+2+3/4+5+6	27.623	***	None	34.222	***
	Coronella austriaca, Vipera berus	1+2+3/4/5/6	2.639	NS	None	11.213	*
	Natrix natrix, Vipera berus	1+2/3/4+5+6	34.036	***	None	77.392	***

		Coronella austriaca			*Natrix natrix*		
		Combined behavioural groups	**G**	**p**	**Combined behavioural groups**	**G**	**p**
(ii)	Thermally unlimiting, thermally limiting conditions	1+2+3/4/5/6	12.012	**	1+2/3/4+5+6	6.431	*
	Sunny, clouded conditions	None	3.553	NS	None	7.425	NS

Table 5.2: Continued on next page.

		Sunny conditions			Clouded conditions		
		Combined behavioural groups	G	p	Combined behavioural groups	G	p
(i)	*Coronella austriaca, Natrix natrix*	None	25.623	***	None	34.956	***
	Coronella austriaca, Vipera berus	None	5.379	NS	None	11.463	*
	Natrix natrix, Vipera berus	None	67.115	***	None	69.564	***

		Vipera berus		
		Combined behavioural groups	G	p
(ii)	Thermally unlimiting, thermally limiting conditions	None	10.356	*
	Sunny, clouded conditions	None	32.599	***

Table 5.2: **Comparison of frequencies of body coil postures observed during the outdoor vivaria experiments.** Part (i) presents the results of interspecific comparisons, part (ii) the results of intraspecific comparisons for different environmental conditions. For some comparisons the sample sizes were <5 for particular body coil posture categories. Where this occurred, the frequencies of adjacent categories were combined. For example, 1+2+3/4+5+6 means that the frequencies of body coil postures 1, 2 and 3 were combined into one group, and postures 4, 5 and 6 into a second (see Fig. 2.7 for body coil posture categorisation).

Significance levels are provided with the G-test statistic (G)

NS = p>0.05 * = p<0.05 ** = p<0.01 *** = p<0.001

and grass snakes during thermally limiting conditions, thermally unlimiting conditions, sunny periods and clouded periods. When conditions were thermally unlimiting and when conditions were sunny, there was no significant difference between smooth snake and adder body coil posture frequencies. However, significant differences were found between the latter 2 species during thermally limiting and clouded periods.

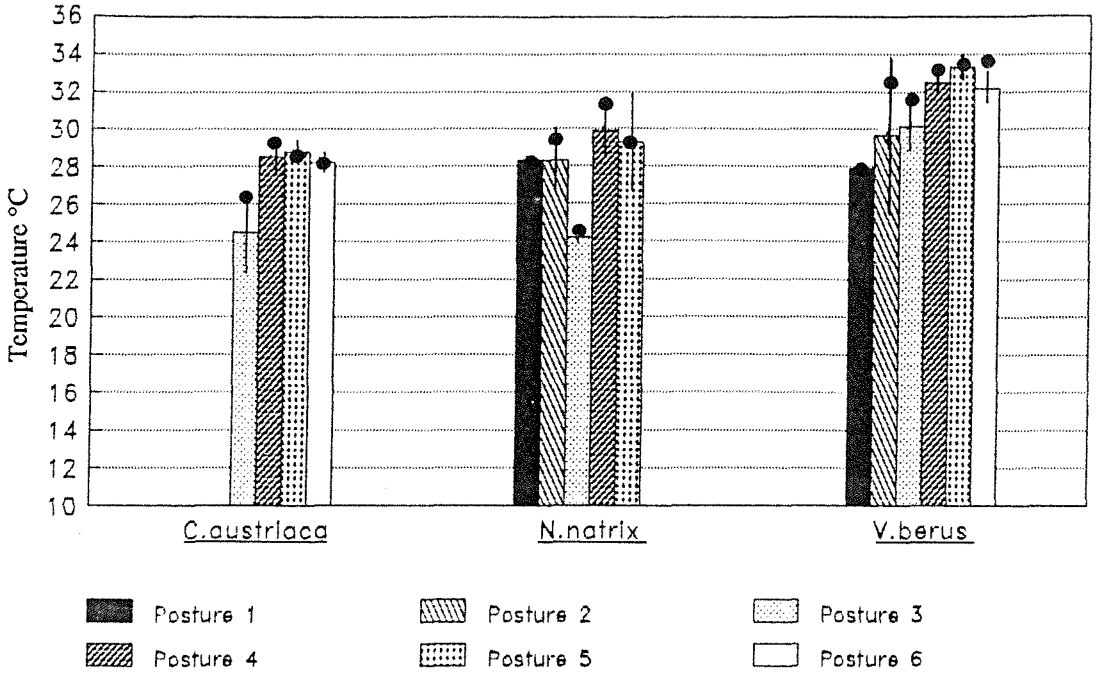
Intra-specific comparisons of body coil posture frequencies indicated that significant differences existed between thermally limiting and thermally unlimiting conditions for each species. This was also the case for adders when comparing data between sunny and overcast conditions. The frequency of the tightest body coil postures were greater for adders during clouded periods than during sunny periods. However, no significant difference was found during the latter conditions for smooth snakes or grass snakes.

Body temperatures were also analysed to investigate whether they varied according to body coil posture. The data were again divided into the categories based on environmental conditions as used in the analysis of frequencies above. Summary statistics of the body temperature data are provided in Tables 5.3 and 5.4 and are also presented in Figs. 5.10 and 5.11.

Results from the thermally limiting and thermally unlimiting conditions will be examined first. An interspecific comparison of body temperatures for each body coil posture was carried out using the same analytical techniques of Section 4.3.5. The results are presented in Table 5.5. Note that for many combinations (and in some of the tests that follow later) small data samples prevented comparisons to be made. In the case of smooth snakes and grass snakes, there did not tend to be significant differences between species for each posture (except posture 3 during thermally limiting conditions). However, significant variation did occur between smooth snakes and adders for postures 3 to 6 (except posture 4 during thermally limiting conditions). Adders had higher mean body temperatures for the body coil postures where significant differences occurred. Significant variation occurred between adders and grass snakes for some of the body coil postures.

An intraspecific comparison of body temperatures for body coil postures within each species was performed on data from thermally limiting and unlimiting data. Neither smooth snakes nor adders showed significant variation between postures when conditions were thermally unlimiting (Kruskal-Wallis chi-squared = 6.788, n = 37 and chi-squared = 5.863, n = 122 respectively, $p > 0.05$ in both cases). Grass snakes, however, did show significant variation

1. Thermally unlimiting conditions



2. Thermally limiting conditions

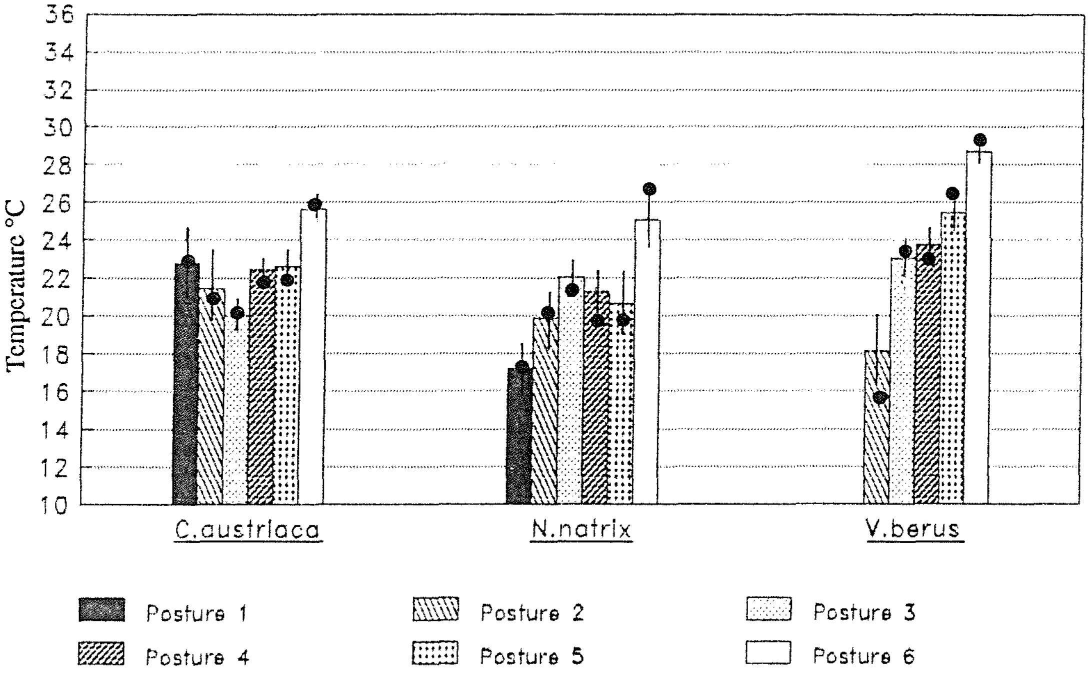
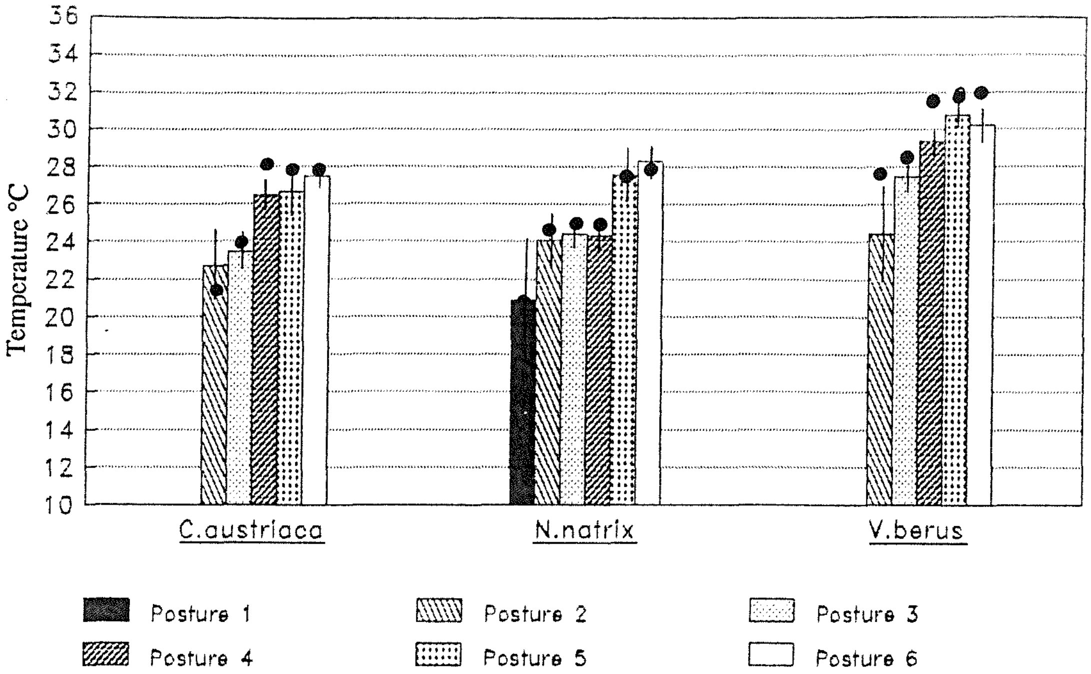


Fig. 5.10: Mean body temperatures (± 1 s.e.) of snakes recorded for the body coiling posture categories in the outdoor vivaria during thermally unlimiting and limiting conditions. Median body temperature values are marked as •.

1. Sunny conditions



2. Clouded conditions

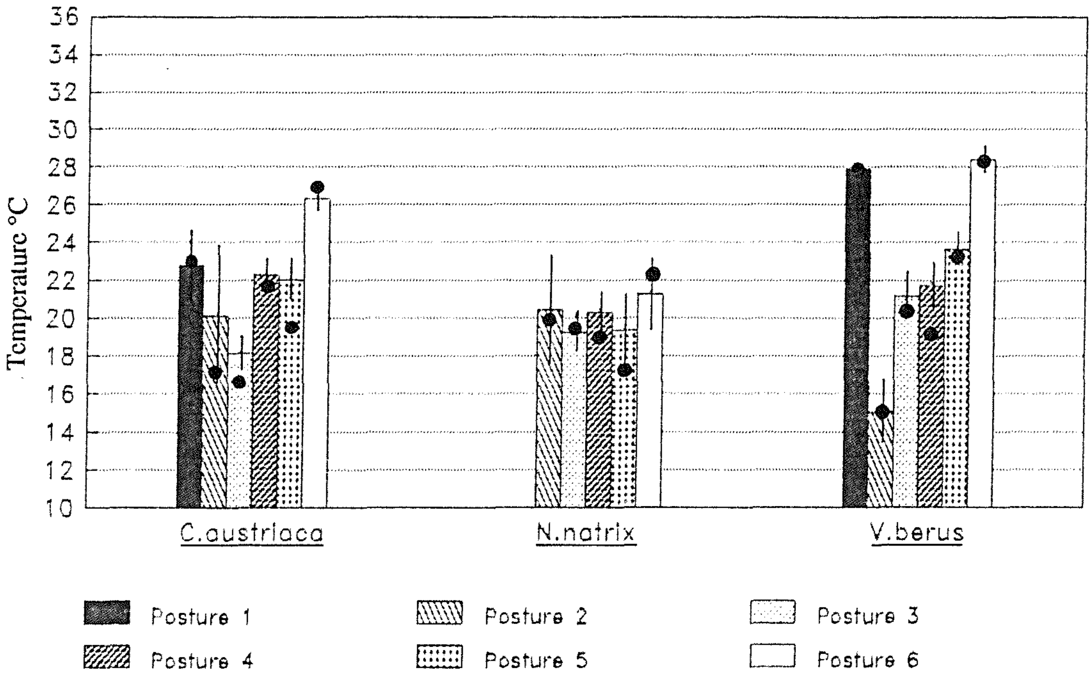


Fig. 5.11: Mean body temperatures (± 1 s.e.) of snakes recorded for the body coiling posture categories in the outdoor vivaria during 'sunny' and 'clouded' conditions. Median body temperature values are marked as •.

			Body temperatures (°C)				
1. Thermally unlimiting conditions		n	Mean	SD	Median	Min	Max
Posture 1	*Coronella austriaca*	0	- -	- -	- -	- -	- -
	Natrix natrix	1	28.30	- -	28.30	28.3	28.3
	Vipera berus	1	27.90	- -	27.90	27.9	27.9
Posture 2	*Coronella austriaca*	0	- -	- -	- -	- -	- -
	Natrix natrix	7	28.31	3.845	29.40	22.5	32.4
	Vipera berus	4	29.68	3.065	32.60	17.8	35.7
Posture 3	*Coronella austriaca*	6	24.52	5.339	26.40	15.3	29.1
	Natrix natrix	27	24.27	5.105	24.60	14.6	33.1
	Vipera berus	17	30.15	4.939	31.70	21.3	37.0
Posture 4	*Coronella austriaca*	16	28.55	3.290	29.10	17.4	32.1
	Natrix natrix	8	29.88	3.938	31.35	22.5	34.5
	Vipera berus	48	32.52	2.872	33.15	21.1	38.5
Posture 5	*Coronella austriaca*	7	28.83	1.564	28.70	26.8	31.3
	Natrix natrix	2	29.25	3.323	29.25	26.9	31.6
	Vipera berus	27	33.33	2.709	33.40	28.7	39.9
Posture 6	*Coronella austriaca*	8	28.25	0.791	28.30	27.2	29.8
	Natrix natrix	0	- -	- -	- -	- -	- -
	Vipera berus	25	32.11	4.216	33.50	22.7	36.1

			Body temperatures (°C)				
2. Thermally limiting conditions		n	Mean	SD	Median	Min	Max
Posture 1	*Coronella austriaca*	2	22.80	2.546	22.80	21.0	24.6
	Natrix natrix	2	17.20	1.838	17.20	15.9	18.5
	Vipera berus	0	- -	- -	- -	- -	- -
Posture 2	*Coronella austriaca*	6	21.42	4.759	21.00	16.2	27.7
	Natrix natrix	10	19.89	5.044	20.05	9.5	25.8
	Vipera berus	16	18.20	7.665	15.55	9.2	34.5
Posture 3	*Coronella austriaca*	38	20.00	4.194	20.15	12.7	26.9
	Natrix natrix	50	22.06	4.850	21.25	10.6	32.3
	Vipera berus	44	23.12	6.269	23.35	9.8	33.8
Posture 4	*Coronella austriaca*	24	22.50	3.518	21.90	17.2	29.5
	Natrix natrix	35	21.28	5.023	19.80	12.8	30.6
	Vipera berus	80	23.79	6.756	22.95	11.2	35.5
Posture 5	*Coronella austriaca*	26	22.61	4.498	21.95	17.3	30.0
	Natrix natrix	9	20.63	4.742	19.90	15.9	28.6
	Vipera berus	67	25.47	5.704	26.40	14.3	34.2
Posture 6	*Coronella austriaca*	18	25.69	2.165	25.90	21.3	28.5
	Natrix natrix	11	25.12	4.683	26.70	14.2	32.1
	Vipera berus	58	28.74	3.825	29.25	18.2	36.1

Table 5.3: Summary statistics of body temperatures recorded for the 6 body coiling postures in the outdoor vivaria during thermally unlimiting and limiting conditions.

			Body temperatures (°C)				
1. Sunny conditions		n	Mean	SD	Median	Min	Max
Posture 1	*Coronella austriaca*	0	- -	- -	- -	- -	- -
	Natrix natrix	4	20.92	5.339	19.75	15.9	28.3
	Vipera berus	0	- -	- -	- -	- -	- -
Posture 2	*Coronella austriaca*	3	22.70	2.951	21.20	20.8	26.1
	Natrix natrix	15	24.07	5.489	24.50	14.7	32.4
	Vipera berus	16	24.50	9.100	27.55	10.0	35.7
Posture 3	*Coronella austriaca*	18	23.42	4.215	23.95	12.7	29.1
	Natrix natrix	66	24.42	4.627	24.90	14.6	33.1
	Vipera berus	52	27.49	6.456	28.45	9.8	37.0
Posture 4	*Coronella austriaca*	19	26.53	4.133	28.20	17.2	31.3
	Natrix natrix	30	24.35	5.672	24.85	14.5	34.5
	Vipera berus	105	29.38	5.905	31.70	12.5	38.5
Posture 5	*Coronella austriaca*	12	26.66	3.746	27.95	19.7	31.3
	Natrix natrix	5	27.52	3.212	27.20	23.0	31.9
	Vipera berus	84	30.78	4.714	31.80	14.3	39.9
Posture 6	*Coronella austriaca*	14	27.49	1.883	27.85	23.3	30.2
	Natrix natrix	6	28.30	1.936	27.80	26.7	32.1
	Vipera berus	49	30.26	4.864	32.00	18.2	36.1

			Body temperatures (°C)				
2. Clouded conditions		n	Mean	SD	Median	Min	Max
Posture 1	*Coronella austriaca*	2	22.80	2.546	22.80	21.0	24.6
	Natrix natrix	0	- -	- -	- -	- -	- -
	Vipera berus	1	27.90	- -	27.90	27.9	27.9
Posture 2	*Coronella austriaca*	3	20.13	6.555	16.50	16.2	27.7
	Natrix natrix	7	20.50	6.443	19.90	9.5	30.2
	Vipera berus	6	15.07	3.767	15.10	9.2	20.5
Posture 3	*Coronella austriaca*	24	18.18	3.468	16.35	14.8	25.4
	Natrix natrix	19	19.24	4.208	19.50	10.6	28.0
	Vipera berus	20	21.21	5.340	20.25	10.9	30.7
Posture 4	*Coronella austriaca*	20	22.30	4.167	21.75	16.8	32.1
	Natrix natrix	24	20.30	4.625	18.90	12.8	30.4
	Vipera berus	44	21.71	7.426	19.30	11.2	34.4
Posture 5	*Coronella austriaca*	23	22.04	4.609	19.60	17.3	30.0
	Natrix natrix	8	19.39	5.235	17.20	15.9	31.6
	Vipera berus	36	23.68	5.361	23.35	16.8	32.9
Posture 6	*Coronella austriaca*	17	26.28	2.372	26.90	21.3	29.8
	Natrix natrix	5	21.30	4.090	22.20	14.2	24.6
	Vipera berus	49	28.39	3.551	28.20	22.3	36.1

Table 5.4: Summary statistics of body temperatures recorded for the 6 body coiling postures in the outdoor vivaria during sunny and clouded conditions.

	Species combinations for statistical comparison							
	Coronella austriaca *Natrix natrix* *Vipera berus*		*Coronella austriaca* *Natrix natrix*		*Coronella austriaca* *Vipera berus*		*Natrix natrix* *Vipera berus*	
(i) Results from thermally unlimiting conditions	χ^2	p	U	p	U	p	U	p
Posture 1	NA	NA	NA	NA	NA	NA	NA	NA
Posture 2	NA	NA	NA	NA	NA	NA	9.0	NS
Posture 3	10.512	**	74.5	NS	22.0	*	100.5	**
Posture 4	23.816	***	38.0	NS	84.5	***	98.0	*
Posture 5	14.549	***	6.0	NS	10.5	***	7.0	NS
Posture 6	NA	NA	NA	NA	32.0	**	NA	NA
(ii) Results from thermally limiting conditions								
Posture 1	NA	NA	NA	NA	NA	NA	NA	NA
Posture 2	3.130	NS	- -	- -	- -	- -	- -	- -
Posture 3	7.275	*	708.5	*	567.5	*	974.5	NS
Posture 4	4.150	NS	- -	- -	- -	- -	- -	- -
Posture 5	10.497	**	83.0	NS	580.5	*	151.5	*
Posture 6	14.969	***	97.0	NS	247.0	***	164.5	*
(iii) Results from sunny conditions								
Posture 1	NA	NA	NA	NA	NA	NA	NA	NA
Posture 2	0.399	NS	- -	- -	- -	- -	- -	- -
Posture 3	12.394	**	531.0	NS	270.5	**	1140.5	**
Posture 4	22.712	***	226.5	NS	575.0	**	782.5	***
Posture 5	15.725	***	30.0	NS	183.0	***	95.0	*
Posture 6	8.926	**	41.5	NS	175.5	**	89.5	NS
(iv) Results from clouded conditions								
Posture 1	NA	NA	NA	NA	NA	NA	NA	NA
Posture 2	3.542	NS	- -	- -	- -	- -	- -	- -
Posture 3	4.843	NS	- -	- -	- -	- -	- -	- -
Posture 4	2.107	NS	- -	- -	- -	- -	- -	- -
Posture 5	6.633	*	52.0	NS	316.0	NS	72.0	*
Posture 6	14.606	***	8.0	**	274.5	*	11.5	***

Table 5.5: **Interspecific comparison of body temperatures recorded for the body coiling posture categories in the outdoor vivaria.**

Comparisons between all 3 species have been made with the Kruskal-Wallis test (statistic = χ^2). Comparisons between 2 species have been made with the Wilcoxon/Mann-Whitney pairs test (statistic = U).

NS = $p > 0.05$
* = $p < 0.05$
** = $p < 0.01$
*** = $p < 0.001$
NA = not applicable due to small sample size

		Body coil posture				
Natrix natrix		1	2	3	4	5
	1	- -				
Body coil posture	2	3.0 NS	- -			
	3	6.0 NS	52.5 NS	- -		
	4	2.0 NS	22.5 NS	43.5 *	- -	
	5	NA	7.0 NS	10.0 NS	6.5 NS	
	6	NA	NA	NA	NA	NA

Table 5.6: **Intraspecific comparisons of body temperatures recorded for the body coiling posture categories in the outdoor vivaria during thermally unlimiting conditions.**
Note that no significant differences were found between the body temperatures of the coiling posture categories in *Coronella austriaca* or *Vipera berus*.
Significance levels are provided with Wilcoxon/Mann-Whitney pairs test statistics (U).

NS = $p > 0.05$
* = $p < 0.05$
** = $p < 0.01$
*** = $p < 0.001$
NA = not applicable due to small sample size

		Body coil posture				
		1	2	3	4	5
Coronella austriaca	1	- -				
Body coil posture	2	5.0 NS	- -			
	3	22.5 NS	88.0 NS	- -		
	4	22.5 NS	60.0 NS	309.5 *	- -	
	5	23.0 NS	63.5 NS	317.5 *	303.5 NS	- -
	6	4.5 NS	24.5 *	86.0 ***	94.0 **	25.5 NS
Vipera berus	1	- -				
Body coil posture	2	NA	- -			
	3	NA	202.0 *	- -		
	4	NA	330.5 **	1692.0 NS	- -	
	5	NA	213.5 ***	1176.5 NS	2288.0 NS	- -
	6	NA	136.5 ***	603.0 ***	1334.0 ***	1332.0 **

Table 5.7: **Intraspecific comparisons of body temperature recorded for the body coiling posture categories in the outdoor vivaria during thermally limiting conditions.**
Note that no significant differences were found between the body temperatures of the coiling posture categories in *Natrix natrix.*

Significance levels are provided with Wilcoxon/Mann-Whitney pairs test statistics (U).

NS = $p > 0.05$
* = $p < 0.05$
** = $p < 0.01$
*** = $p < 0.001$
NA = not applicable due to small sample size

		Body coil posture				
		1	2	3	4	5
Coronella austriaca	1	- -				
Body coil posture	2	NA	- -			
	3	NA	20.0 *	- -		
	4	NA	12.5 NS	94.5 *	- -	
	5	NA	8.0 NS	55.5 *	106.5 NS	- -
	6	NA	3.0 *	45.0 **	130.0 NS	83.0 NS

		1	2	3	4	5
Vipera berus	1	- -				
Body coil posture	2	NA	- -			
	3	NA	345.0 NS	- -		
	4	NA	571.0 *	2242.0 NS	- -	
	5	NA	423.0 *	1571.5 **	4080.5 NS	- -
	6	NA	253.5 *	957.5 *	2407.5 NS	2025.5 NS

Table 5.8: **Intraspecific comparisons of body temperature recorded for the body coiling posture categories in the outdoor vivaria during sunny conditions.**
Note that no significant differences were found between the body temperatures of the coiling posture categories in *Natrix natrix.*
Significance levels are provided with Wilcoxon/Mann-Whitney pairs test statistics (U).

NS = $p > 0.05$
* = $p < 0.05$
** = $p < 0.01$
*** = $p < 0.001$
NA = not applicable due to small sample size

		Body coil posture				
		1	2	3	4	5
Coronella austriaca	1	- -				
Body coil posture	2	2.0 NS	- -			
	3	6.0 NS	24.0 NS	- -		
	4	17.0 NS	17.0 NS	103.5 **	- -	
	5	18.0 NS	20.0 NS	120.0 ***	213.0 NS	- -
	6	3.0 NS	12.0 NS	16.5 ***	68.5 **	95.5 **
Vipera berus	1	- -				
Body coil posture	2	0.0 NS	- -			
	3	3.0 NS	21.5 *	- -		
	4	12.0 NS	65.0 *	434.0 NS	- -	
	5	11.0 NS	17.5 **	287.5 NS	645.0 NS	- -
	6	23.0 NS	0.0 ***	140.0 ***	523.0 ***	451.5 ***

Table 5.9: **Intraspecific comparisons of body temperatures recorded for the body coiling posture categories in the outdoor vivaria during clouded conditions.**

Note that no significant differences were found between the body temperatures of the coiling posture categories in *Natrix natrix.*

Significance levels are provided with Wilcoxon/Mann-Whitney pairs test statistics (U).

NS = $p > 0.05$
* = $p < 0.05$
** = $p < 0.01$
*** = $p < 0.001$
NA = not applicable due to small sample size

(chi-squared = 9.578, n = 45, $p < 0.05$) and so a series of Mann-Whitney tests were performed on all the possible combinations of body coil postures (Table 5.6). The only significant difference was identified between posture 3 and posture 4.

The reverse situation occurred when conditions were thermally limiting. Grass snakes showed no significant variation between body postures (chi-squared = 9.348, n = 117, $p > 0.05$) whereas smooth snakes and adders did (chi- squared = 22.835, n = 114, and chi-squared = 38.496, n = 265 respectively, $p < 0.001$ in both cases). The results of a series of Mann-Whitney comparisons between all posture combinations within the latter 2 species are shown in Fig. 5.7.

The same analytical procedures used on body temperature data for coil postures during thermally unlimiting and limiting conditions were also used for the coil posture data from sunny and clouded conditions. The results of interspecific comparisons for sunny and clouded conditions are also provided in Table 5.5. They were relatively similar to those from thermally limiting and thermally unlimiting conditions.

Grass snakes were found to have no intraspecific differences between the body temperatures of coil postures for when conditions were sunny or clouded (chi-squared = 8.705, n = 126 and chi-squared = 2.418, n = 63 respectively, $p > 0.05$ in both cases). Intraspecific variation was present in smooth snakes during both conditions (chi-squared = 12.546, n = 66, $p < 0.05$ when sunny, chi-squared = 32.546, n = 89, $p < 0.001$ when clouded) and in adders (chi-squared = 11.938, n = 306, $p < 0.05$ when sunny, chi-squared = 40.687, n = 156, $p < 0.001$ when clouded). The comparison between postures for the latter 2 species was therefore investigated further and the results of this are provided in Tables 5.8 and 5.9. It is interesting to note that during sunny conditions, significant intraspecific differences in body coil posture body temperatures tended to occur between the extreme postures but not so often between the more similar postures. This pattern was not quite as evident for data from clouded conditions.

Laboratory Experiments

During the laboratory experiments, body coil posture 5 was the equivalent to body coil postures 5 and 6 in the outdoor vivaria. Otherwise, the same criteria were used to describe body coil posture in the laboratory arena as in the outdoor vivaria. The use of video allowed a continuous record of snake behaviour to be made and therefore time budget results are presented as total time duration that snakes were observed in each body coil posture.

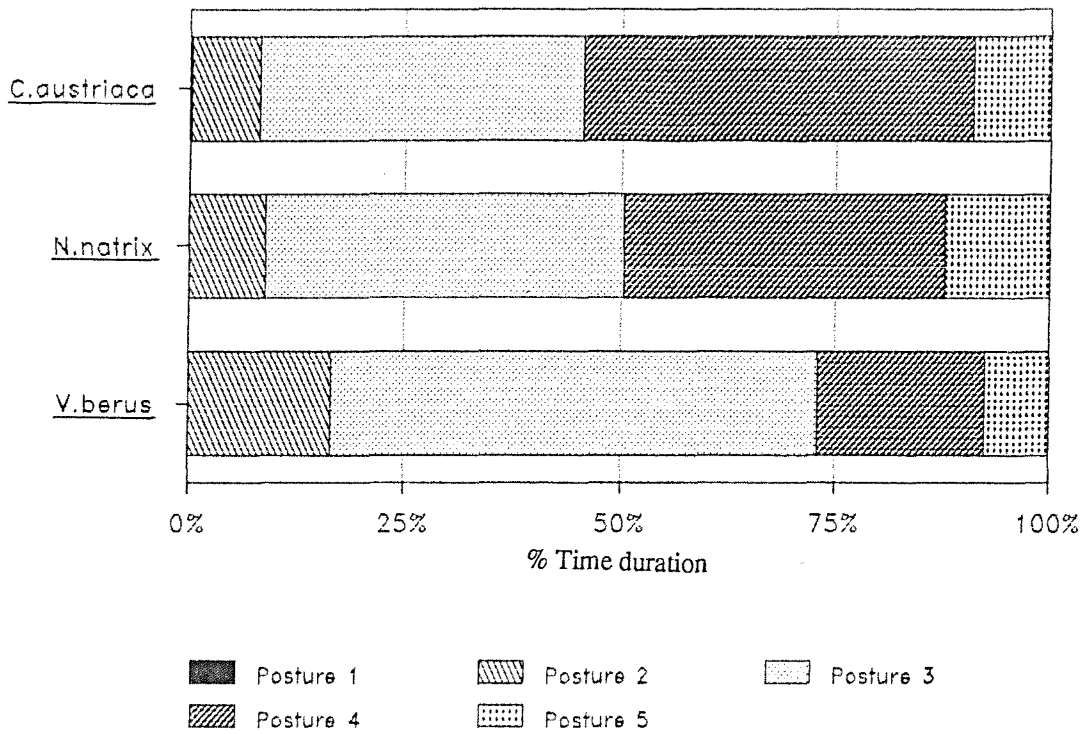
Table 5.10 presents the time budget data for the body coil postures of the 3 species. When conditions were thermally unlimiting (i.e. when the heatlamp was on) data are provided for the body coil postures observed when the snakes were observed basking under the heatlamp. Fig. 5.12 provides a graphical version of the results. For all 3 species, body postures 1,2 and 5 were observed for a relatively small proportion of their basking time. Postures 3 and 4 were most commonly observed during basking activity (mainly posture 3 in the case of the adders with 56.6% of the overall basking time budget).

The body postures of snakes engaged in thigmothermy during thermally limiting conditions (i.e. when the heatlamp was off) is also presented in Table 5.10 and in Fig. 5.12. Body posture 5 was used for the longest periods in the case of smooth snakes (64.7% of time involved in thigmothermy) whereas posture 3 was displayed by grass snakes and adders for the longest duration (60.9% and 54.0% respectively).

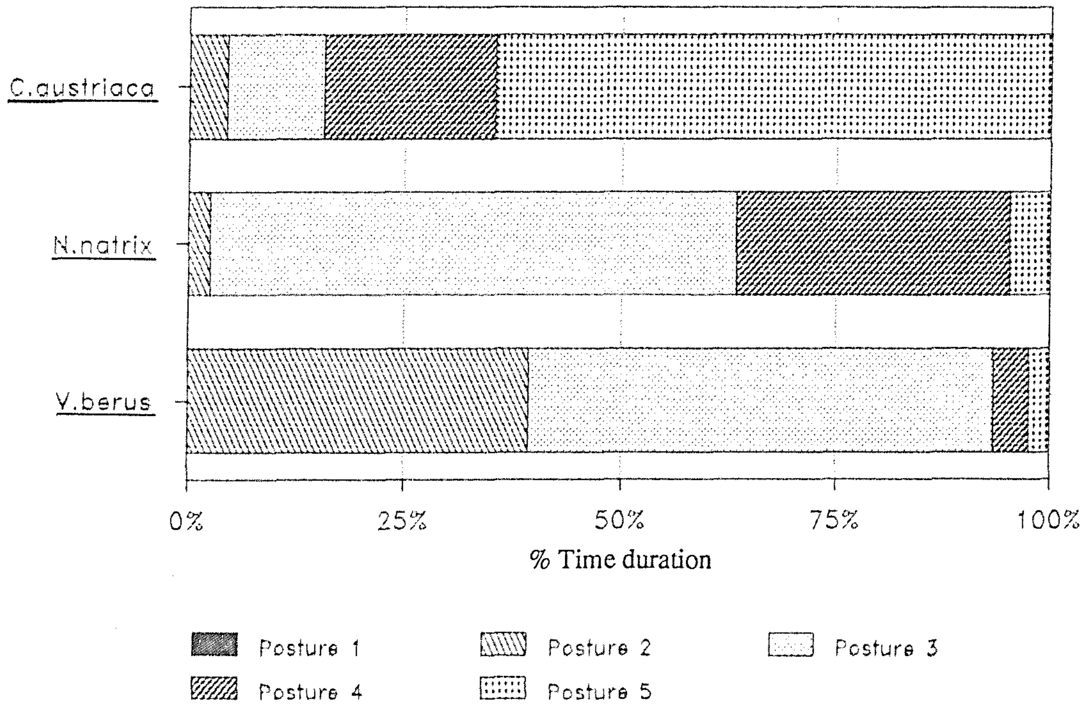
The body temperatures of snakes during the 5 different body coil postures are given in Table 5.11 and Fig. 5.13 for thermally unlimiting (basking behaviour) and thermally limiting (thigmothermy behaviour) conditions. An interspecific comparison of body temperatures for each body coil posture was performed and the results are given in Table 5.12. When conditions were thermally unlimiting, significant interspecific differences existed between the body temperatures for all postures (except between smooth snakes and grass snakes for posture 5) although small sample sizes prevented comparisons being made for posture 1. Mean and median body temperatures were highest in adders for all body coil postures. Smooth snake body temperatures were higher than grass snake body temperatures for postures 2, 3 and 4 but not 5.

Small sample sizes also prevented interspecific comparisons to be made for postures 1 and 5 when conditions were thermally limiting. However, comparisons were possible for posture 3 for which significant interspecific body temperature variation existed, and postures 2 and 3 where no significant differences were found.

Intraspecific comparisons of body temperatures for each of the 3 species was also carried out. In the case of adders during thermally unlimiting conditions, no significant difference was found between the body temperatures of the 5 body coil postures observed in the basking



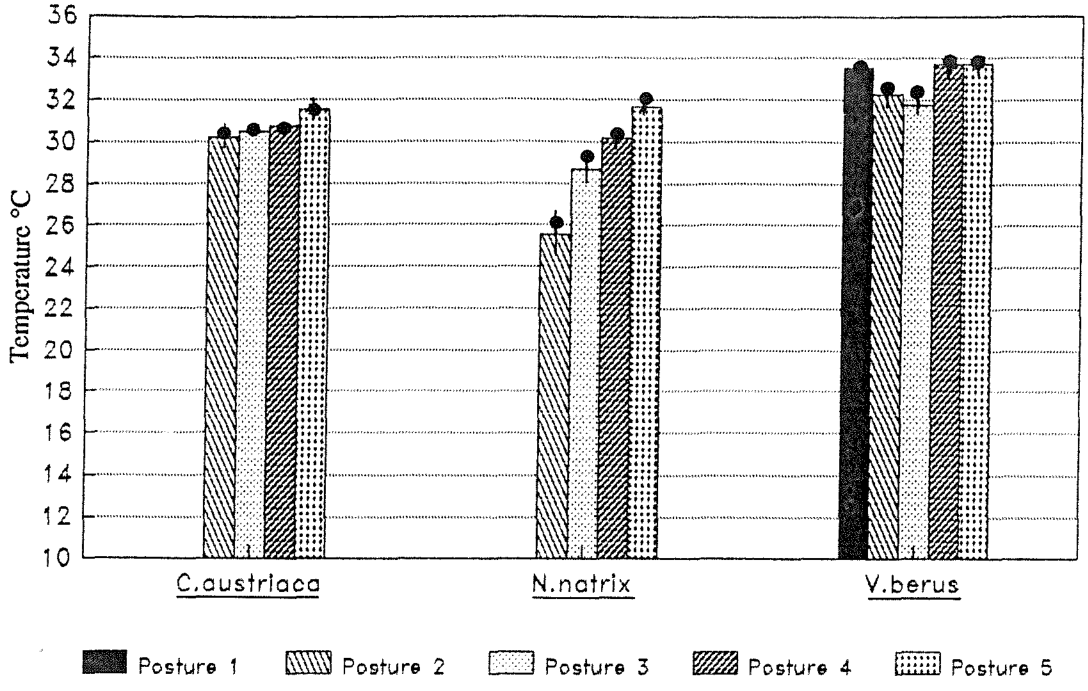
1. Thermally unlimiting conditions (heatlamp on)



2. Thermally limiting conditions (heatlamp off)

Fig. 5.12: Percentage time duration assigned to each of the body coiling posture behavioural categories categories during thermally unlimiting and limiting conditions for the laboratory experiments.

1. Thermally unlimiting conditions (heatlamp on)



2. Thermally limiting conditions (heatlamp off)

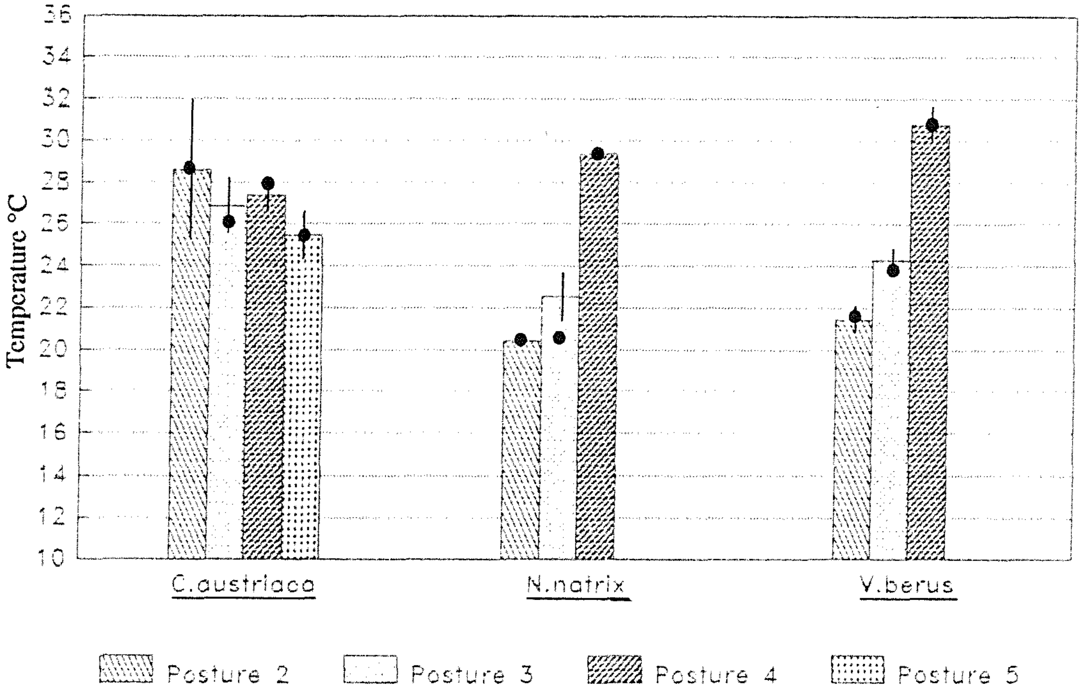


Fig. 5.13: **Mean body temperatures (± 1 s.e.) of snakes recorded for the body coiling posture categories in the laboratory during thermally unlimiting and limiting conditions.** Median body temperature values are marked as •.

	Coronella austriaca		*Natrix natrix*		*Vipera berus*	
1. Thermally unlimiting conditions (heatlamp on)	Duration (mins)	% Duration	Duration (mins)	% Duration	Duration (mins)	% Duration
Posture 1	15	0.2	2	0.03	0	0
Posture 2	571	7.9	585	8.8	2316	16.4
Posture 3	2711	37.4	2769	41.5	7965	56.6
Posture 4	3295	45.4	2493	37.4	2752	19.5
Posture 5	657	9.1	824	12.3	1061	7.5
Total duration	**7249**		**6673**		**14094**	
1. Thermally limiting conditions (heatlamp off)						
Posture 1	0	0	0	0	0	0
Posture 2	52	4.3	38	2.5	1254	39.4
Posture 3	135	11.2	931	60.9	1719	54.0
Posture 4	238	19.8	486	31.8	134	4.2
Posture 5	779	64.7	73	4.8	77	2.4
Total duration	**1204**		**1528**		**3184**	

Table 5.10: Overall time duration and percentage time duration of body coiling posture categories during the laboratory experiments.

			Body temperatures (°C)				
1. Thermally unlimiting conditions		n	Mean	SD	Median	Min	Max
Posture 1	*Coronella austriaca*	0	- -	- -	- -	- -	- -
	Natrix natrix	0	- -	- -	- -	- -	- -
	Vipera berus	1	33.50	- -	33.50	33.5	33.5
Posture 2	*Coronella austriaca*	8	30.20	1.900	30.25	27.2	34.0
	Natrix natrix	20	25.53	5.782	26.10	17.6	34.4
	Vipera berus	25	32.25	3.117	32.70	22.8	36.3
Posture 3	*Coronella austriaca*	113	30.50	1.423	30.60	25.1	33.1
	Natrix natrix	95	28.66	4.498	29.40	17.0	37.1
	Vipera berus	80	31.79	3.259	32.45	19.8	36.7
Posture 4	*Coronella austriaca*	105	30.74	1.495	30.50	25.1	35.3
	Natrix natrix	105	30.13	2.334	30.40	21.6	35.6
	Vipera berus	19	33.72	1.948	33.90	29.0	36.8
Posture 5	*Coronella austriaca*	8	31.56	0.950	31.50	30.3	33.4
	Natrix natrix	46	31.66	1.885	32.05	28.0	35.9
	Vipera berus	6	33.72	0.975	33.75	32.0	34.7

			Body temperatures (°C)				
2. Thermally limiting conditions		n	Mean	SD	Median	Min	Max
Posture 1	*Coronella austriaca*	0	- -	- -	- -	- -	- -
	Natrix natrix	0	- -	- -	- -	- -	- -
	Vipera berus	0	- -	- -	- -	- -	- -
Posture 2	*Coronella austriaca*	2	28.60	3.677	28.60	26.0	31.2
	Natrix natrix	1	20.40	- -	20.40	20.4	20.4
	Vipera berus	8	21.44	1.925	21.50	17.8	24.4
Posture 3	*Coronella austriaca*	7	26.84	3.777	26.00	20.3	31.4
	Natrix natrix	7	22.56	3.482	20.60	20.4	27.8
	Vipera berus	15	24.31	2.318	23.90	21.8	31.9
Posture 4	*Coronella austriaca*	8	27.32	2.312	27.75	23.0	30.0
	Natrix natrix	1	29.30	- -	29.30	29.3	29.3
	Vipera berus	2	30.80	1.131	30.80	30.0	31.6
Posture 5	*Coronella austriaca*	2	25.45	1.909	25.45	24.1	26.8
	Natrix natrix	0	- -	- -	- -	- -	- -
	Vipera berus	0	- -	- -	- -	- -	- -

Table 5.11: Summary statistics of body temperatures recorded for the 5 body coiling postures in the laboratory during thermally unlimiting conditions (heatlamp on) and thermally limiting conditions (heatlamp off).

	Species combinations for statistical comparison							
	Coronella austriaca *Natrix natrix* *Vipera berus*		*Coronella austriaca* *Natrix natrix*		*Coronella austriaca* *Vipera berus*		*Natrix natrix* *Vipera berus*	
(i) Results from thermally unlimiting conditions (heatlamp on) for basking behaviour	χ^2	p	U	p	U	p	U	p
Posture 1	NA	NA	NA	NA	NA	NA	NA	NA
Posture 2	17.756	***	39.5	*	48.5	*	79.0	***
Posture 3	38.396	***	3971.5	**	2580.0	***	2118.5	***
Posture 4	34.937	***	4632.5	*	220.5	***	221.0	***
Posture 5	8.735	*	162.0	NS	2.0	**	42.5	**
(ii) Results from thermally limiting conditions (heatlamp off) for thigmothermic behaviour								
Posture 1	NA	NA	NA	NA	NA	NA	NA	NA
Posture 2	5.420	NS	- -	- -	- -	- -	- -	- -
Posture 3	6.076	*	13.0	NS	22.0	*	28.0	NS
Posture 4	4.667	NS	- -	- -	- -	- -	- -	- -
Posture 5	NA	NA	NA	NA	NA	NA	NA	NA

Table 5.12: **Interspecific comparison of body temperatures recorded for the body coiling posture categories in the laboratory.**

Comparisons between all 3 species have been made with the Kruskal-Wallis test (statistic = χ^2). Comparisons between 2 species have been made with the Wilcoxon/Mann-Whitney pairs test (statistic = U).

NS = $p > 0.05$
* = $p < 0.05$
** = $p < 0.01$
*** = $p < 0.001$
NA = not applicable due to small sample size

		Body coil posture			
		1	2	3	4
Natrix natrix	1	- -			
Body coil posture	2	NA	- -		
	3	NA	638.5 *	- -	
	4	NA	539.0 ***	4039.0 *	- -
	5	NA	173.5 ***	1260.5 ***	1415.5 ***

Table 5.13: **Intraspecific comparisons of body temperatures recorded for the body coiling posture categories in the laboratory during thermally unlimiting conditions (heatlamp on).**

Note that no significant differences were found between the body temperatures of the coiling posture categories in *Coronella austriaca* or *Vipera berus.*

Significance levels are provided with Wilcoxon/Mann-Whitney pairs test statistics (U).

NS = $p > 0.05$
* = $p < 0.05$
** = $p < 0.01$
*** = $p < 0.001$
NA = not applicable due to small sample size

		Body coil posture			
		1	2	3	4
Vipera berus	1	- -			
Body coil posture	2	NA	- -		
	3	NA	14.5 **	- -	
	4	NA	0.0 *	2.0 NS	- -
	5	NA	NA	NA	NA

Table 5.14: **Intraspecific comparisons of body temperatures recorded for the body coiling posture categories in the laboratory during thermally limiting conditions (heatlamp off).**
Note that no significant differences were found between the body temperatures of the coiling posture categories in *Coronella austriaca* or *Natrix natrix.*

Significance levels are provided with Wilcoxon/Mann-Whitney pairs test statistics (U).

NS = $p > 0.05$
* = $p < 0.05$
** = $p < 0.01$
*** = $p < 0.001$
NA = not applicable due to small sample size

snakes (Kruskal-Wallis chi-squared = 8.581, $n = 131$, $p > 0.05$). The same result was found in smooth snakes (chi-squared = 6.564, $n = 234$, $p > 0.05$). A significant difference was found in grass snakes (chi-squared = 33.022, $n = 266$, $p < 0.001$) so therefore a series of Mann-Whitney tests was performed on all the possible body posture combinations, the results of which are given in Table 5.13.

When conditions were thermally limiting, no significant differences were found in the body temperatures of the body coil postures of smooth snakes (chi-squared = 1.320, $n = 19$, $p > 0.05$) or grass snakes (chi-squared = 3.468, $n = 9$, $p > 0.05$). Significant differences were found in adders (chi-squared = 12.004, $n = 25$, $p < 0.01$) and the results of the subsequent body coil posture pairwise tests are provided in Table 5.14. Note that comparisons were only possible between body coil postures 2 and 3, 2 and 4, and 3 and 4.

5.3.4. Body Posture: Aspect

The aspect of the snakes' bodies in relation to the incoming solar radiation was assessed during the outdoor vivaria experiments. Records were not made between 1030 and 1430 hours when the sun was too high in the sky to categorise the body aspect. Body aspect was scored on a scale of 1 to 4 (see Fig. 2.8) for snakes engaged in basking or mosaic basking activity.

Results are provided in Table 5.15. The results give frequencies and proportions of body aspect observations recorded when conditions were sunny or clouded. In most cases, there were small sample sizes of observations in particular body aspect categories. Combining adjacent categories together to allow G-test comparisons to be performed on the data was judged to be unsatisfactory. Instead, comparisons were made through straight-forward examination of the data.

A body aspect of 1 (i.e. body aspect at right angles to incoming solar radiation) would theoretically allow snakes to increase heat absorption. Body aspects of 1 were more frequently observed for all 3 species when conditions were sunny than when conditions were clouded. Body aspects of 4 (body posture tightly coiled and no specific body aspect in relation to the sun.) were the most commonly observed postures during both conditions for all 3 species, although they were less frequent when conditions were sunny. The data suggests that there is some degree of postural heliothermic behaviour in relation to body aspect with body aspect 1 and 3 (body aspect at 45° to incoming radiation) more frequently observed than body aspect 2

		Coronella austriaca		*Natrix natrix*		*Vipera berus*	
		n	%	n	%	n	%
1. Sunny conditions	Body aspect 1	2	7.1	17	26.2	26	14.6
	Body aspect 2	2	7.1	5	7.7	6	3.4
	Body aspect 3	5	17.9	11	16.9	28	15.7
	Body aspect 4	19	67.9	32	49.2	118	66.3
	Total	**28**		**65**		**178**	
		n	%	n	%	n	%
2. Clouded conditions	Body aspect 1	1	3.0	5	13.5	7	7.9
	Body aspect 2	0	0	4	10.8	1	1.1
	Body aspect 3	1	3.0	4	10.8	8	9.0
	Body aspect 4	31	94.0	24	64.9	73	82.0
	Total	**33**		**37**		**89**	

Table 5.15: Frequency and percentage frequency of observations for the body aspect categories during the outdoor vivaria experiments.

(body aspect parallel to incoming solar radiation), especially for adders and grass snakes. During observations in the outdoor vivaria, adders and grass snakes were usually seen in body aspect 1 shortly after emergence during the heating phase when body coil postures were also relatively loose. When body temperatures reached selected body temperatures, body coil postures tended to become tighter and body aspects were then classed as 4.

5.3.5. Use of Cover in Thermoregulation

Outdoor Vivaria Experiments

The amount of body surface area not in the shade of cover (e.g. vegetation) was estimated for snakes engaged in mosaic basking. When the sky was overcast the percentage snake body area not under cover (rather than shade of cover) was estimated. The degree of exposure was placed on a scale of 1 to 3 (1 = 5-35% exposure, 2 = 36-65% exposure, 3 = 66-95% exposure). In some of the analysis which follows, data from observations of basking snakes that were completely exposed (>95% exposure) have also been used. Data from snakes classed as 'hidden' have not been used as it was not always possible to know whether a snake was totally submerged below cover or if it was involved in another activity but hidden from the observer.

The frequencies of observations during thermally limiting and unlimiting conditions for the different exposure categories are given in Table 5.16. The results are also provided in Fig. 5.14, with basking (i.e. fully exposed) behaviour included. A series of G-tests have been carried out on the frequency data and the results are given in Table 5.17. The table includes details of where some of the frequencies had to be combined to allow G-tests to be undertaken. Interspecific comparisons revealed that there were significant differences in the frequencies of the observed body exposure categories between smooth snakes and grass snakes and between smooth snakes and adders during thermally limiting and unlimiting conditions (whether or not basking frequencies were taken into account). Grass snakes and adders tended to have greater proportions of their body areas exposed than smooth snakes, especially when conditions were thermally unlimiting. No significant differences were found between grass snakes and adders, except when basking (>95% exposure) was included from data collected when conditions were thermally limiting. When the basking results were included, adders were observed basking for 52.8% of the observations compared to 20.8% for grass snakes.

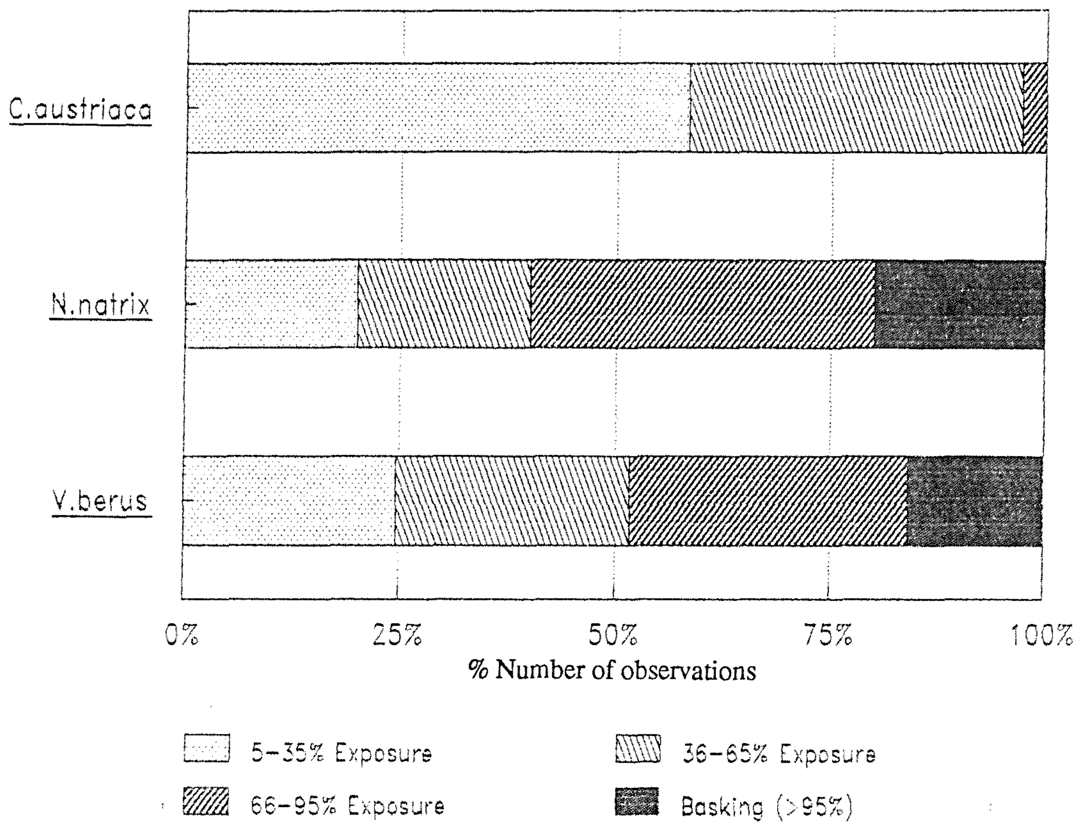
An intraspecific comparison of frequencies (see Table 5.17) revealed there were significant differences for all 3 species between data from thermally limiting and thermally unlimiting conditions (whether or not basking frequencies were taken into account). In all cases, the amount of body area exposed was greater when conditions were thermally limiting.

During some of the observations of body exposure behaviour, body temperature measurements were also made. Summary statistics of the results are presented in Table 5.18 and Fig. 5.15. Statistical comparisons of data were carried out using the same techniques as those used in Section 5.3.3.

An interspecific comparison showed that body temperatures were not significantly different between species for each body exposure category when conditions were thermally limiting, except between basking (>95% exposure) grass snakes and adders (see Table 5.19). When conditions were thermally unlimiting, significant differences occurred for each exposure category between grass snakes and adders, and for exposure categories 1 and 2 between smooth snakes and adders. Adders had higher mean and median body temperatures in all the categories.

Intraspecific comparisons of body temperature for the different exposure categories were investigated during the different thermal conditions. Smooth snakes were found to have no significant differences between the different exposure categories when conditions were thermally unlimiting (chi-squared = 1.692, $n = 36$, $p > 0.05$) but significant variation did occur during thermally limiting conditions (chi-squared = 35.262, $n = 116$, $p < 0.001$). Note, however, that no body temperature measurements were available for smooth snakes engaged in basking (>95% exposure) when conditions were thermally unlimiting. Grass snake body temperature measurements were significantly different when conditions were thermally unlimiting but not significantly different during thermally limiting conditions (chi-squared = 12.005, $n = 56$, $p < 0.01$ and chi-squared = 6.078, $n = 117$, $p > 0.05$ respectively). The body temperatures of adders were significantly different between body exposure categories during both conditions (chi-squared = 28.930, $n = 134$ for thermally unlimiting conditions, chi-squared = 26.715, $n = 266$ for thermally limiting conditions, $p < 0.001$ in both cases). Where significant variation was found between body exposure categories within species, a series of Mann-Whitney comparisons was performed on each pairwise combination (see Tables 5.20 and 5.21).

1. Thermally unlimiting conditions



2. Thermally limiting conditions

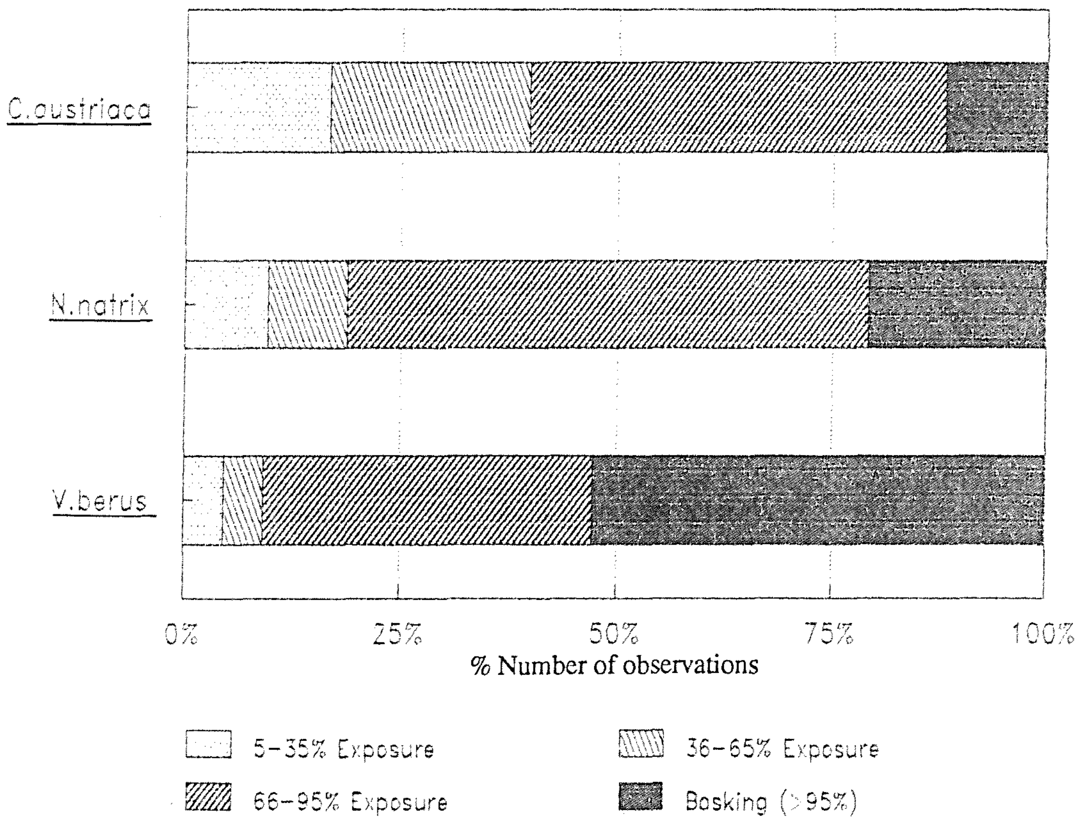
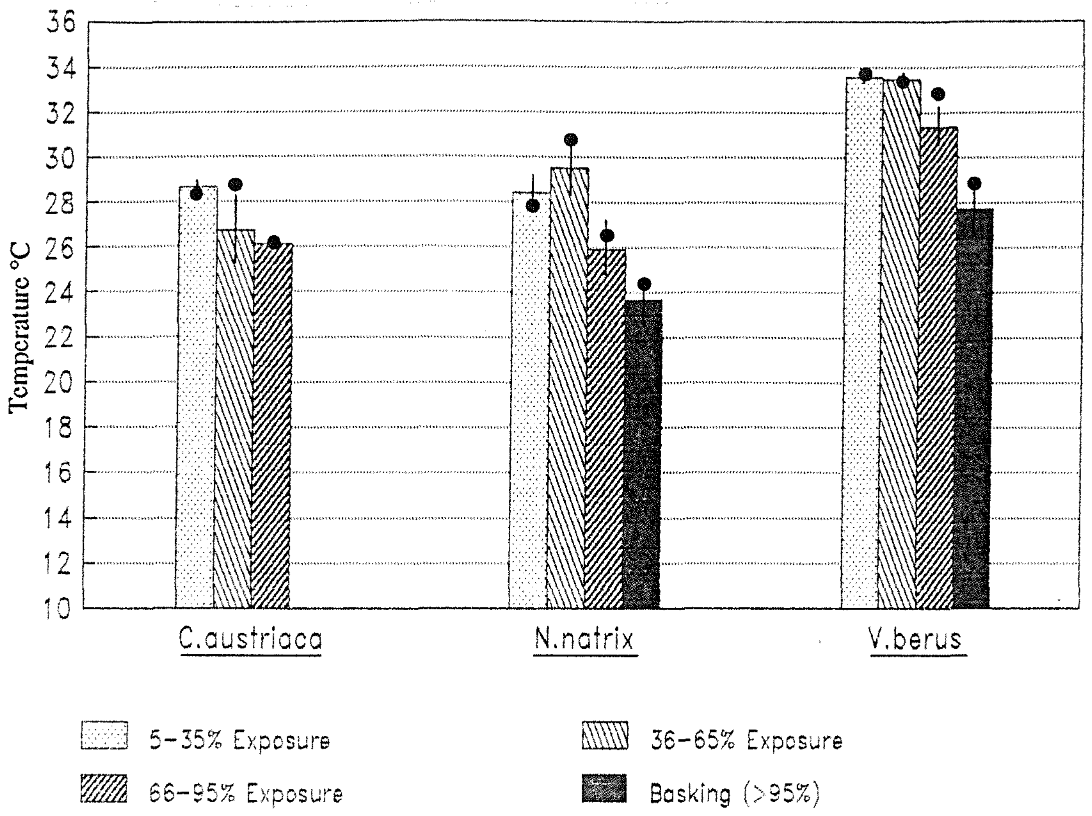


Fig. 5.14: Percentage number of observations assigned to each of the 'body area exposed' behavioural categories during thermally unlimiting and limiting conditions for the outdoor vivaria experiments.

1. Thermally unlimiting conditions (heatlamp on)



2. Thermally limiting conditions (heatlamp off)

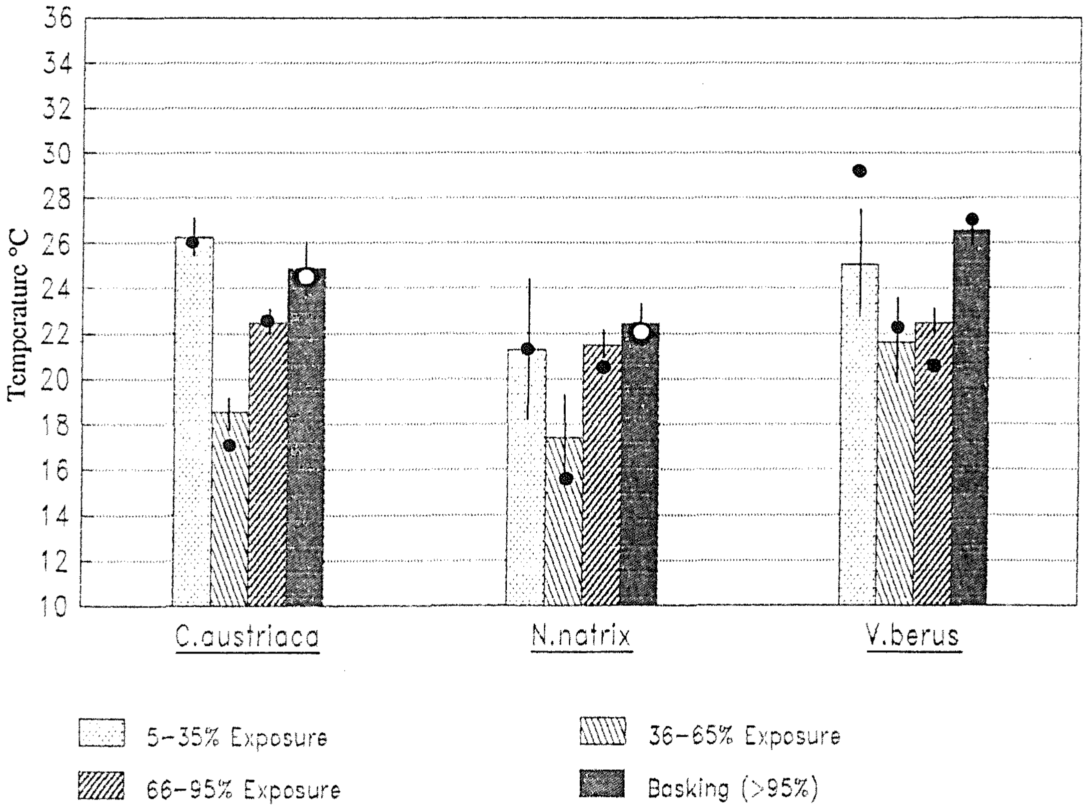


Fig. 5.15: Mean body temperatures (± 1 s.e.) of snakes recorded for the 'body area exposed' categories in the outdoor vivaria during thermally unlimiting and limiting conditions. Median body temperature values are marked as •.

	Coronella austriaca			*Natrix natrix*			*Vipera berus*		
1. Thermally unlimiting conditions	n	%*	%†	n	%*	%†	n	%*	%†
5-35% exposed	21	58.3	58.3	13	20.0	25.0	51	24.6	29.3
36-65% exposed	14	38.9	38.9	13	20.0	25.0	56	27.1	32.2
66-95% exposed	1	2.8	2.8	26	40.0	50.0	67	32.4	38.5
Basking (>95% exposed)	0	0	- -	13	20.0	- -	33	15.9	- -
Total	**36**			**65**			**207**		
2. Thermally limiting conditions	n	%*	%†	n	%*	%†	n	%*	%†
5-35% exposed	21	16.7	18.9	20	9.7	12.2	14	4.6	9.7
36-65% exposed	29	23.0	26.1	19	9.2	11.6	14	4.6	9.7
66-95% exposed	61	48.4	55.0	125	60.4	76.2	116	38.0	80.6
Basking (>95% exposed)	15	11.9	- -	43	20.8	- -	161	52.8	- -
Total	**126**			**207**			**305**		

%* including basking
%† excluding basking

Table 5.16: **Frequency and percentage frequency of observations for the 'body area exposed' behavioural categories during the outdoor vivaria experiments.**

	Excluding 'basking' category					
	Thermally unlimiting conditions			**Thermally limiting conditions**		
Groups for comparison	**Combined groups**	**G**	**p**	**Combined groups**	**G**	**p**
(i) *Coronella austriaca, Natrix natrix*	1/2+3	10.024	**	None	14.322	***
Coronella austriaca, Vipera berus	1/2+3	10.614	**	None	19.848	***
Natrix natrix, Vipera berus	None	2.207	NS	None	0.861	NS

	Excluding 'basking' category								
	Coronella austriaca			*Natrix natrix*			*Vipera berus*		
	Combined groups	**G**	**p**	**Combined groups**	**G**	**p**	**Combined groups**	**G**	**p**
(ii) Thermally unlimiting, thermally limiting conditions	1/2+3	19.303	***	None	12.234	**	None	59.810	***

Table 5.17: Continued on next page.

		Including 'basking' category					
		Thermally unlimiting conditions			Thermally limiting conditions		
		Combined groups	G	p	Combined groups	G	p
(i)	*Cornella austriaca, Natrix natrix*	1/2+3+4	15.079	***	None	18.798	***
	Cornella austriaca, Vipera berus	1/2+3+4	15.293	***	None	88.920	***
	Natrix natrix, Vipera berus	None	2.769	NS	None	55.974	***

		Including 'basking' category								
		Coronella austriaca			*Natrix natrix*			*Vipera berus*		
		Combined groups	G	p	Combined groups	G	p	Combined groups	G	p
(ii)	Thermally unlimiting, thermally limiting conditions	1/2+3+4	22.976	***	None	12.252	**	None	135.764	***

Table 5.17: **Comparison of frequencies of 'body area exposed' behavioural categories observed during the outdoor vivaria experiments.** Part (i) presents the results of interspecific comparisons, part (ii) the results of intraspecific comparisons for different environmental conditions. For some comparisons, the sample sizes were <5 for particular 'body area exposed' categories. Where this occurred, the frequencies of adjacent categories were combined. For example, 1/2+3 means that the frequencies of 'body area exposed' categories 2 and 3 were combined into one group. 'Body area exposed' categories are coded as follows: 1: 5-35% exposure 2: 36-65% exposure 3: 66-95% exposure 4: Basking (>95% exposure).

Significance levels are provided with the G-test statistic (G)
NS = p>0.05 * = p<0.05 ** = p<0.01 *** = p<0.001

			Body temperatures (°C)				
1. Thermally unlimiting conditions		n	Mean	SD	Median	Min	Max
5-35% exposure	*Coronella austriaca*	21	28.66	1.194	28.40	26.8	31.3
	Natrix natrix	12	28.39	2.590	27.80	24.0	33.1
	Vipera berus	42	33.53	1.349	33.75	30.3	35.6
36-65% exposure	*Coronella austriaca*	14	26.71	5.104	28.75	15.3	32.1
	Natrix natrix	11	29.49	3.421	30.90	21.4	32.5
	Vipera berus	36	33.46	1.974	33.45	28.7	39.0
66-95% exposure	*Coronella austriaca*	1	26.10	- -	26.10	26.1	26.1
	Natrix natrix	22	25.90	5.715	26.60	14.6	34.5
	Vipera berus	40	31.38	4.804	32.85	21.1	39.9
Basking (>95% exposure)	*Coronella austriaca*	0	- -	- -	- -	- -	- -
	Natrix natrix	11	23.66	3.703	24.35	16.0	30.2
	Vipera berus	16	27.72	4.493	29.05	17.8	33.7

			Body temperatures (°C)				
2. Thermally limiting conditions		n	Mean	SD	Median	Min	Max
5-35% exposure	*Coronella austriaca*	19	26.25	3.153	26.10	20.7	32.4
	Natrix natrix	6	21.28	6.901	21.30	13.9	28.7
	Vipera berus	14	25.04	8.946	29.35	13.6	34.5
36-65% exposure	*Coronella austriaca*	27	18.59	3.604	17.20	14.8	26.9
	Natrix natrix	5	17.44	3.949	15.70	14.6	24.3
	Vipera berus	14	21.64	7.235	22.35	12.4	30.6
66-95% exposure	*Coronella austriaca*	61	22.48	3.983	22.60	12.7	30.0
	Natrix natrix	73	21.49	4.947	20.60	9.5	32.3
	Vipera berus	101	22.49	6.334	20.50	9.2	34.2
Basking (>95% exposure)	*Coronella austriaca*	9	24.86	3.712	24.60	20.3	29.5
	Natrix natrix	33	22.46	4.793	22.20	10.6	30.8
	Vipera berus	138	26.60	5.505	27.10	9.8	36.1

Table 5.18: Summary statistics of body temperatures recorded for 'body area exposed' categories in the outdoor vivaria during thermally unlimiting and limiting conditions.

Species combinations for statistical comparison

	Coronella austriaca *Natrix natrix* *Vipera berus*		*Coronella austriaca* *Natrix natrix*		*Coronella austriaca* *Vipera berus*		*Natrix natrix* *Vipera berus*	
(i) Results from thermally unlimiting conditions	χ^2	p	U	p	U	p	U	p
5 - 35%	50.278	***	106.0	NS	8.0	***	21.0	***
36 - 65%	34.924	***	44.5	NS	14.5	***	39.5	***
66 - 95%	14.232	***	10.0	NS	7.0	NS	189.0	***
Basking (>90%)	NA	NA	NA	NA	NA	NA	40.5	*
(ii) Results from thermally limiting conditions								
5 - 35%	1.574	NS	- -	- -	- -	- -	- -	- -
36 - 65%	1.503	NS	- -	- -	- -	- -	- -	- -
66 - 95%	1.738	NS	- -	- -	- -	- -	- -	- -
Basking (>90%)	16.297	***	100.5	NS	474.5	NS	1272.5	***

Table 5.19: **Interspecific comparison of body temperatures recorded for the 'body area exposed' categories in the outdoor vivaria.**
Comparisons between all 3 species have been made with the Kruskal-Wallis test (statistic = χ^2).
Comparisons between 2 species have been made with the Wilcoxon/Mann-Whitney pairs test (statistic = U).

NS = $p > 0.05$
* = $p < 0.05$
** = $p < 0.01$
*** = $p < 0.001$
NA = not applicable due to small sample size

		Exposure		
		5-35%	36-65%	66-95%
Natrix natrix	5-35%	- -		
	36-65%	47.0 NS	- -	
	66-95%	102.0 NS	75.0 NS	- -
	Basking (>95%)	17.0 **	13.5 **	80.5 NS
Vipera berus	5-35%	- -		
	36-65%	701.0 NS	- -	
	66-95%	603.5 *	549.5 NS	- -
	Basking (>95%)	40.5 ***	48.0 ***	158.5 **

Table 5.20: **Intraspecific comparisons of body temperatures recorded for the 'body area exposed' categories in the outdoor vivaria during thermally unlimiting conditions.**
Note that no significant differences were found between the body temperatures of the exposure categories in *Coronella austriaca.*

Significance levels are provided with Wilcoxon/Mann-Whitney pairs test statistics (U).

NS = $p > 0.05$
* = $p < 0.05$
** = $p < 0.01$
*** = $p < 0.001$
NA = not applicable due to small sample size

		Exposure 5-35%	 36-65%	 66-95%
Coronella austriaca	5-35%	- -		
	36-65%	36.0 ***	- -	
	66-95%	289.5 ***	363.0 ***	- -
	Basking (>95%)	71.0 NS	29.0 ***	185.5 NS
Vipera berus	5-35%	- -		
	36-65%	61.5 NS	- -	
	66-95%	604.0 NS	658.5 NS	- -
	Basking (>95%)	937.5 NS	577.5 *	4246.5 ***

***Table 5.21:* Intraspecific comparisons of body temperatures recorded for the 'body area exposed' categories in the outdoor vivaria during thermally limiting conditions.**
Note that no significant differences were found between the body temperatures of the exposure categories in *Natrix natrix.*

Significance levels are provided with Wilcoxon/Mann-Whitney pairs test statistics (U).

NS = $p > 0.05$
* = $p < 0.05$
** = $p < 0.01$
*** = $p < 0.001$
NA = not applicable due to small sample size

	Coronella austriaca		*Natrix natrix*		*Vipera berus*	
	n	%	n	%	n	%
Vegetation (excluding heather)	151	91.5	220	85.0	362	85.6
Heathers	1	0.6	11	4.2	33	7.8
Logs	4	1.2	6	2.3	14	3.3
Litter/decomposing vegetation	11	6.7	22	8.5	14	3.3
Total	**165**		**259**		**423**	

Table 5.22: **Frequency and percentage frequency of cover types that were observed being used by mosaic basking snakes during all periods in the outdoor vivaria.**

When snakes were mosaic basking, a record was made of the type of cover they used. The frequencies and proportions of observed cover types are presented in Table 5.22 from all the data collected during the outdoor vivaria experiments. The results are likely to have been affected by the amount of cover type available. This would have been particularly relevant when the sunlit areas of the vivaria were relatively small and the range of cover types available in such areas were restricted.

Live vegetation (excluding heathers) was the most commonly used cover type when mosaic basking. 'Live vegetation' was usually grass although dock (Rumex sp.), ribwort plantain (Plantago lanceolata) and other herbaceous species were occasionally used as cover. The piles of decomposing vegetation in the northwest corners tended to be used for mosaic basking when the snakes had been hidden in them overnight. They were the first areas of the vivaria to receive the sun, and the snakes would sometimes mosaic bask in the litter for a few minutes before emerging completely. In the case of the heathers, there were only 2 bushes in each vivaria and they were not always in sunlit areas. Adders appeared to use them to a greater degree than the other 2 species.

Laboratory Experiments

The amount of body area exposed during refuge basking in the laboratory experiments was measured on a scale of 1 to 4 (1 = head only exposed, 2 = 25% body area exposed, 3 = 50% body area exposed, 4 = 75% body area exposed). Table 5.23 presents the total time durations that the 3 snake species were observed in each of the body exposure categories plus durations for basking behaviour (both 100% exposure). Fig. 5.16 presents a graphical version of the results.

During thermally unlimiting conditions (i.e. when the heatlamp was on) adders were very rarely observed refuge basking (only 1% of the time of basking and refuge basking combined). When they did refuge bask, it was usually just the head that was exposed. The other 2 species also basked for longer periods than they refuge basked. Smooth snakes refuge basked for 17.1% of the total time spent engaged in combined refuge basking and basking. They were most frequently observed refuge basking in the 75% exposure category. Grass snakes were observed refuge basking for 37.1% of the time of refuge basking and basking combined with roughly the same proportion of time engaged in each of the refuge basking exposure categories.

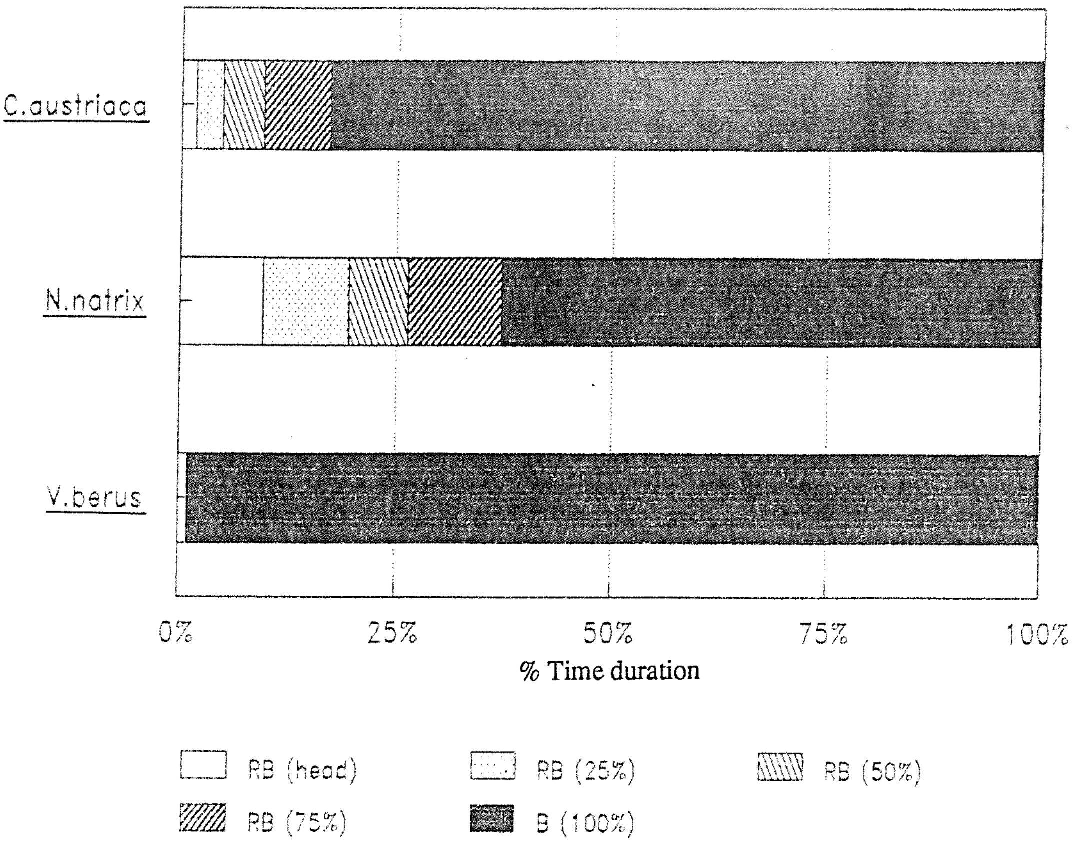


Fig. 5.16: Percentage time duration assigned to each of the 'body area exposed' behavioural categories during thermally unlimiting conditions (heatlamp on) for the laboratory experiments.

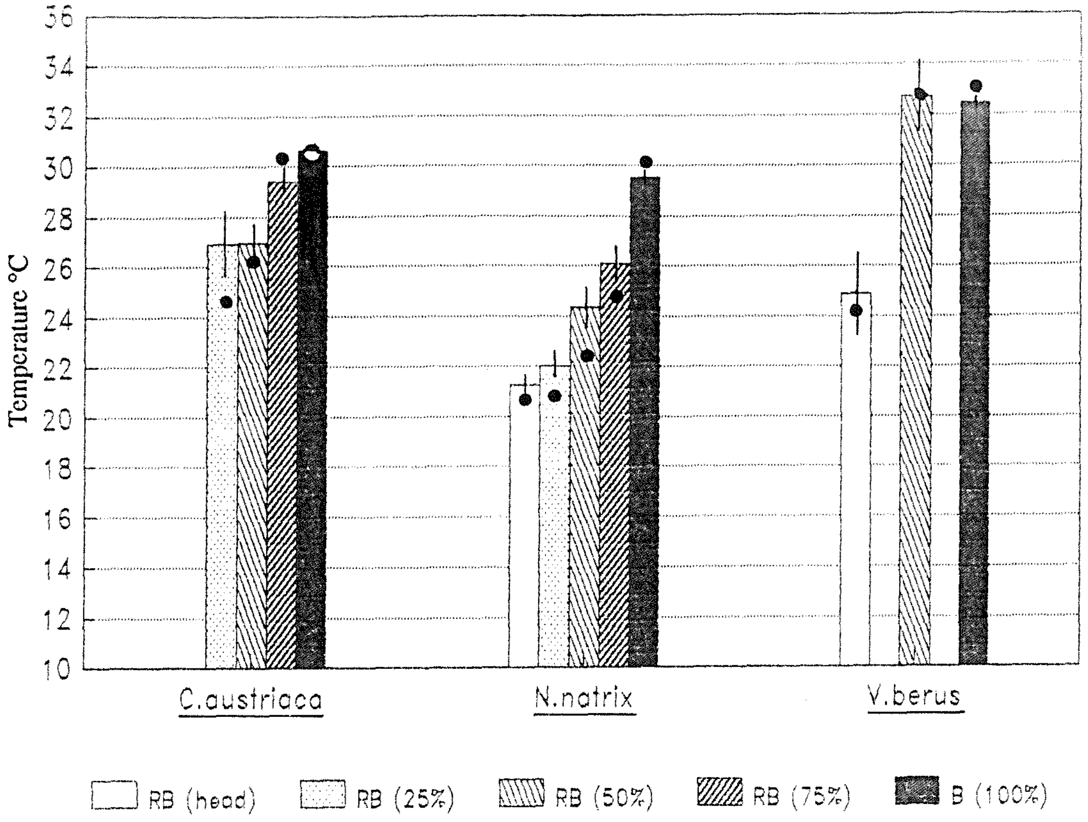


Fig. 5.17: **Mean body temperatures (± 1 s.e.) of snakes recorded for the 'body area exposed 'categories in the laboratory during thermally unlimiting (heatlamp on) conditions.** Median body temperature values are marked as •.

	Coronella austriaca			*Natrix natrix*			*Vipera berus*		
	Duration (mins)	% duration	% duration excluding 100% exposure	Duration (mins)	% duration	% duration excluding 100% exposure	Duration (mins)	% duration	% duration excluding 100% exposure
Head only exposed	166	1.7	9.8	1012	9.5	25.7	153	1.0	82.3
25% exposed	298	3.0	17.6	1056	10.0	26.8	16	0.1	8.6
50% exposed	470	4.7	27.8	723	6.8	18.4	10	0.07	5.4
75% exposed	759	7.7	44.8	1147	10.8	29.1	7	0.05	3.8
Basking (100%) exposed	8206	82.9	- -	6673	62.9	- -	14749	98.8	- -
Total	9899			10611			14935		

***Table 5.23:* Overall time duration and percentage time duration of 'body area exposed' behavioural categories during thermally unlimiting conditions (heatlamp on) in the laboratory.**

			Body temperatures (°C)					
		n	Mean	SD	Median	Min	Max
Head only exposed	*Coronella austriaca*	0	- -	- -	- -	- -	- -
	Natrix natrix	49	21.28	2.741	20.80	17.8	31.8
	Vipera berus	6	24.88	4.806	24.05	20.0	32.3
25% exposed	*Coronella austriaca*	8	26.89	3.969	24.60	22.9	32.6
	Natrix natrix	27	22.02	3.117	20.90	18.5	32.1
	Vipera berus	0	- -	- -	- -	- -	- -
50% exposed	*Coronella austriaca*	15	26.97	3.132	26.20	21.7	32.6
	Natrix natrix	27	24.38	4.757	22.40	19.2	35.1
	Vipera berus	2	32.70	2.263	32.70	31.1	34.3
75% exposed	*Coronella austriaca*	30	29.37	2.570	30.35	21.4	31.9
	Natrix natrix	38	26.08	4.648	24.85	18.4	34.2
	Vipera berus	0	- -	- -	- -	- -	- -
Basking (100% exposed)	*Coronella austriaca*	234	30.63	1.468	30.55	25.1	35.3
	Natrix natrix	266	29.53	3.838	30.20	17.0	37.1
	Vipera berus	141	32.42	3.028	33.10	19.8	37.2

Table 5.24: Summary statistics of body temperatures recorded for 'body area exposed' categories in the laboratory during thermally unlimiting conditions (heatlamp on).

	Species combinations for statistical comparison							
	Coronella austriaca *Natrix natrix* *Vipera berus*		*Coronella austriaca* *Natrix natrix*		*Natrix natrix* *Vipera berus*		*Natrix natrix* *Vipera berus*	
	χ^2	p	U	p	U	p	U	p
Head only	NA	NA	NA	NA	NA	NA	72.0	*
25%	NA	NA	NA	NA	NA	NA	72.0	*
50%	8.760	*	119.0	*	2.0	NS	3.0	*
75%	NA	NA	357.5	**	NA	NA	NA	NA
Basking (100%)	92.591	***	27049.0	*	7657.5	***	9269.0	****

***Table 5.25:* Interspecific comparison of body temperatures recorded for the 'body area exposure' categories in the laboratory.**

Comparisons between all 3 species have been made with the Kruskal-Wallis test (statistic = χ^2).
Comparisons between 2 species have been made with the Wilcoxon/Mann-Whitney pairs test (statistic = U).

NS = $p > 0.05$
* = $p < 0.05$
** = $p < 0.01$
*** = $p < 0.001$
NA = not applicable due to small sample size

		Exposure			
		Head only	25%	50%	75%
Coronella austriaca	Head only	- -			
	25%	NA	- -		
	50%	NA	51.5 NS	- -	
	75%	NA	89.5 NS	131.5 *	- -
	Basking (100%)	NA	522.0 *	620.0 ***	2550.0 *
Natrix natrix	Head only	- -			
	25%	535.5 NS	- -		
	50%	404.0 **	294.0 NS	- -	
	75%	337.0 ***	235.0 ***	388.0 NS	- -
	Basking (100%)	906.0 ***	703.0 ***	1481.0 ***	3023.0 ***
Vipera berus	Head only	- -			
	25%	NA	- -		
	50%	1.0 NS	NA	- -	
	75%	NA	NA	NA	- -
	Basking (100%)	74.0 ***	NA	135.5 NS	NA

Table 5.26: **Intraspecific comparisons of body temperatures recorded for the 'body area exposed' categories in the laboratory during thermally unlimiting conditions (heatlamp on).** Significance levels are provided with Wilcoxon/Mann-Whitney pairs test statistics (U).

NS = $p > 0.05$
* = $p < 0.05$
** = $p < 0.01$
*** = $p < 0.001$
NA = not applicable due to small sample size

The summary statistics of body temperature measurements for snakes exhibiting refuge basking and basking behaviour are provided in Table 5.24 and graphical interpretations are given in Fig. 5.17. Note that body temperatures were generally higher the greater the body area that was exposed. The results of an interspecific comparison of body temperatures for each refuge basking exposure category and basking are given in Table 5.25. Note that small sample sizes prevented the comparison of some of the categories. For those where comparisons were possible, body temperatures were significantly different in all cases except between smooth snakes and adders for the 50% exposure category.

An intraspecific comparison of body temperatures for each of the exposure categories within each species was also performed. Significant variation of body temperatures was found in each of the 3 species (Kruskal-Wallis chi-squared = 25.439, n = 287, $p < 0.001$ for smooth snakes, chi-squared = 145.101, n = 407, $p < 0.001$ for grass snakes, chi-squared = 11.696, n = 149, $p < 0.01$ for adders). The analysis was therefore extended and a series of Mann-Whitney tests carried out on each of the exposure category pairwise combinations. The results of this analysis are given in Table 5.26.

5.3.6. Shuttling Heliothermy

To investigate this aspect of thermoregulation, data from thermally unlimiting conditions during the laboratory experiments (i.e. when the heatlamp was on) were examined. Much of the analysis referred to below was presented in Section 4.3.3.

The results of overall time budgets for the main behavioural categories given in Section 4.3.3 showed that adders in particular spent much of their time basking (73.2%) and most of the rest of their time moving (21.3%). The median duration of a basking period was 11 mins (n = 574) and the median duration of a movement period was 6 mins (n = 561). Although basking formed the greater part of the overall behavioural time budget, the number of times either of the 2 behavioural categories were displayed was about the same (45.4% for basking, 44.4% for moving). The body temperature data shown in Fig. 4.8 indicates that although significant differences existed between basking body temperatures and those of other behavioural categories, and between moving and 'in refuge' body temperatures, the differences between them were not as great as the body temperatures of the behavioural categories of the other 2 species. Overall this suggests that adders displayed a degree of shuttling heliothermic behaviour. Body temperatures were kept at relatively high levels throughout the thermally unlimiting periods (overall mean body temperature of 31.09°C ± 3.84, n = 228) through frequent and relatively short basking periods.

Grass snakes were observed basking and refuge basking for 44.9% of the time and moving for 13.7% of the time. Median durations for each of these behavioural categories were also relatively short (12 mins, n = 163 for basking, 10 minutes, n = 161 for refuge basking, 6 minutes, n = 330 for moving). The differences between body temperatures during basking behaviour and the other main behavioural categories was much greater than that displayed in adders (see Fig. 4.8). They also spent more time hidden under refuges (16.3% of the time) and 'refuge stationary' away from the heatlamp (22.5% of the time). The overall mean body temperature of grass snakes was 23.19°C ± 5.15 (n = 983).

Smooth snakes tended to bask for longer periods at any one time (median duration 45.5 mins, n = 74) than grass snakes and adders although their overall basking time budget was less than adders (41.5% of the time). An additional 8.6% of the time was engaged in refuge basking. Movement was least often observed in this species than the others (6.1% of the time) and hiding under a refuge was more often observed than in grass snakes or adders 25.2% of the time). The mean body temperature was 27.44°C ± 4.63 (n = 416). Shuttling was not very evident in this species.

The data of basking and refuge basking behaviour were combined into one category and the data of all the other behavioural categories were made into a second category. The results are provided in Table 5.27. They further suggest that adders displayed the greatest degree of shuttling heliothermic behaviour between the 3 species. The basking/refuge basking behavioural actions tended to be short, frequent and formed 74.1% of the overall time budget in adders. Body temperatures were high during basking/refuge basking behaviour (mean value 32.12°C ± 3.42). Other behavioural categories were also short and frequent but formed a much smaller portion of the overall time budget (25.9%). Although body temperatures were significantly different between basking/refuge basking and other behaviour (Wilcoxon/Mann-Whitney U = 2876.5, n_1 = 149, n_2 = 129, $p < 0.001$) they were still relatively high in the case of the latter (29.24°C ± 3.82).

It is worth noting that shuttling heliothermy did not seem to be a major part of the thermoregulatory repertoire of adders in the outdoor vivaria. Adders tended to bask for relatively long periods in the same site until they became shaded at which point they would often seek out a new site. Grass snakes were most frequently observed moving in the outdoor

		Time (mins)									Body temperature °C					
		n	%n	Sum	%Sum	Mean	SD	Median	Min	Max	n	Mean	SD	Med	Min	Max
1. Basking + refuge basking	*Coronella austriaca*	134	34.9	9899	50.1	74.4	111.64	14.5	1	476	287	30.21	2.091	30.50	21.4	35.3
	Natrix natrix	324	32.5	10629	44.9	32.8	57.46	11.0	1	455	407	27.37	4.971	28.90	17.0	37.1
	Vipera berus	617	48.9	14935	74.1	24.2	45.12	10.0	1	427	149	32.12	3.420	33.00	19.0	37.2
2. All other behavioural categories	*Coronella austriaca*	250	65.1	9855	49.9	39.2	82.43	10.0	1	720	129	21.30	2.155	20.80	18.0	32.5
	Natrix natrix	672	67.5	13039	55.1	19.8	39.82	6.0	1	332	570	20.15	2.428	19.90	16.5	33.4
	Vipera berus	646	51.1	5217	25.9	8.1	9.98	6.0	1	128	78	29.24	3.820	30.35	18.4	36.3

Table 5.27: **Body temperature and time summary statistics for basking/refuge basking and non-basking behaviour during thermally unlimiting conditions (heat lamp on) in the laboratory.**

vivaria, often basking between periods of movement. Shortage of time has prevented a more detailed analysis of these observations.

5.3.7. Basking Sites

All the data used in this section were recorded during the outdoor vivaria experiments. The records refer to measurements taken when snakes were observed basking or mosaic basking.

Basking Site Slopes.

Smooth snakes were observed basking/mosaic basking on a slope >20° on 45 of the 169 observations (26.6%). This compares with 43 out of 209 observations for grass snakes (20.6%) and 53 out of 518 observations for adders (10.2%). It should be noted that the number of basking sites in the outdoor vivaria with slopes >20° was limited and the snakes may have made more use of sloping bask sites if they had been available. When a snake was observed basking on a site sloping >20°, a record was made of the direction the slope was facing and an estimate was made of the angle of the slope.

It was hypothesized that the snakes would bask on slopes which faced the direction of the sun's incoming radiation. To examine if this effect was true, the daily pattern of basking site slope selection was investigated. Data were separated into 3 categories; basking site slope observations from the earliest records of the 'lit' phase until 1159 hours, from 1200 hours until 1500 hours and from 1501 hours until the last records of the 'lit' phase. The results are presented in Fig. 5.18 in the form of adapted 'wind rose' diagrams. Such diagrams are usually used to present wind direction, frequency and velocity data. In this case, the diagrams provide information on basking slope direction, basking slope angles and proportions of observations.

Basking Site Position

For many of the basking and mosaic basking observations in the outdoor vivaria, a record of the site position was noted. This was measured according to which of the 9 grid squares the snake was basking/mosaic basking in. It was hypothesized that the snakes would move to

	Coronella austriaca		*Natrix natrix*		*Vipera berus*	
1. All periods	n	%	n	%	n	%
Logs	11	6.3	22	6.9	63	9.8
Stones	7	4.0	15	4.7	43	6.7
Bare soil	74	42.5	29	9.1	26	4.0
Live vegetation	63	36.2	202	63.7	363	56.5
Litter/decomposing vegetation	13	7.5	44	13.9	123	19.2
Any of the above plus metal wall	6	3.4	5	1.6	23	3.6
Total	**174**		**317**		**641**	
2. Thermally unlimiting conditions	n	%	n	%	n	%
Logs	0	0	7	10.8	25	11.4
Stones	0	0	1	1.5	5	2.3
Bare soil	25	64.1	0	0	8	3.6
Live vegetation	14	35.9	44	67.7	144	65.5
Litter/decomposing vegetation	0	0	9	13.8	32	14.5
Any of the above plus metal wall	0	0	4	6.2	6	2.7
Total	**39**		**65**		**220**	
3. Thermally limiting conditions	n	%	n	%	n	%
Logs	9	7.3	15	7.1	24	7.7
Stones	7	5.7	14	6.6	36	11.5
Bare soil	43	35.0	27	12.8	9	2.9
Live vegetation	45	36.6	129	61.1	154	49.4
Litter/decomposing vegetation	13	10.6	26	12.3	77	24.7
Any of the above plus metal wall	6	4.9	0	0	12	3.8
Total	**123**		**211**		**312**	

Table 5.28: Frequency and percentage frequency of substrate types that were observed being used by basking/mosaic basking snakes during the outdoor vivaria experiments.

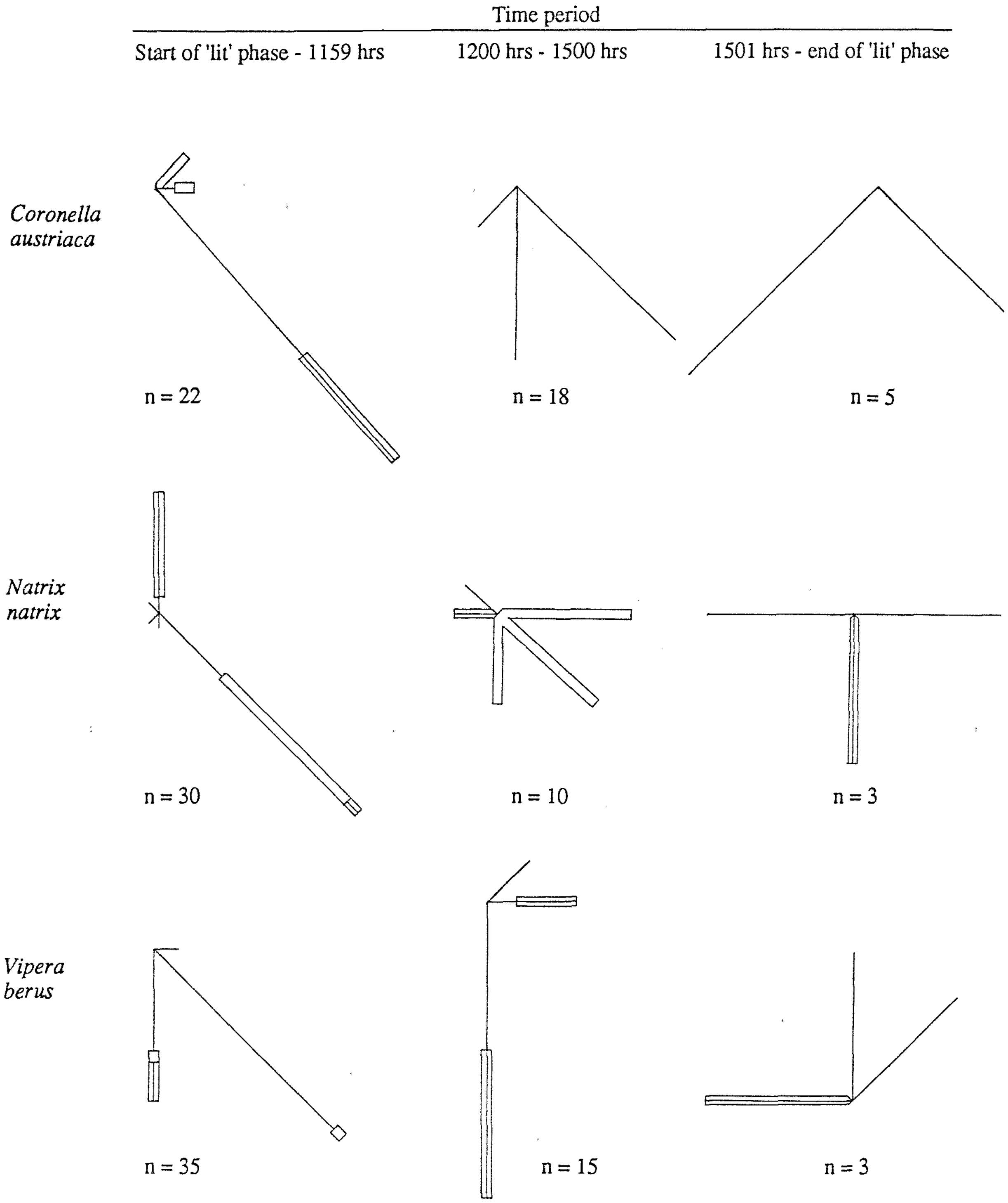
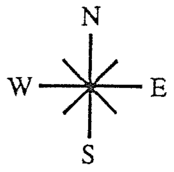


Fig 5.18: **Diagramatic representation of diel patterns of basking/mosaic basking site slope selection observed during the outdoor vivaria experiments.**

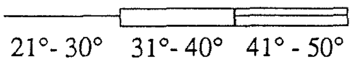
Figures are in the form of modified 'wind rose' diagrams:



(a) The arrows indicate the direction of the slope.

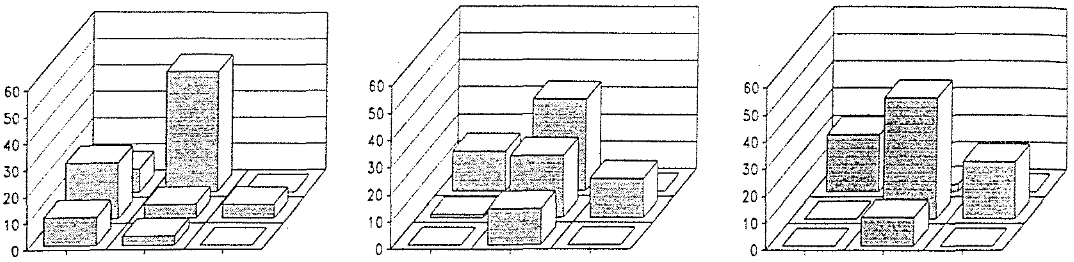
(b) The lengths within the arrows indicate proportion of observations for the particular time period.

(c) The basking/mosaic site slope angles are coded as follows:



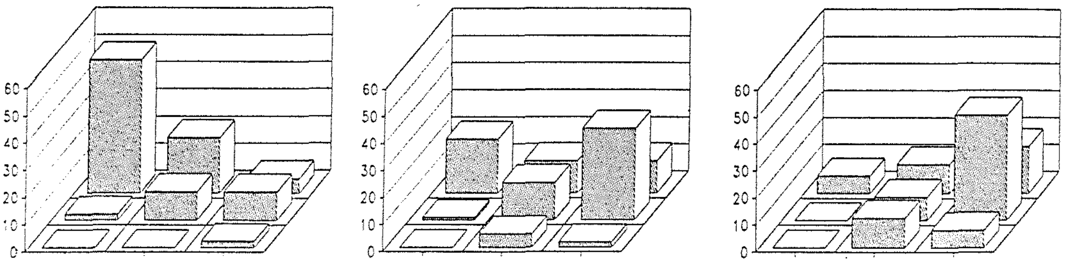
(d) The number of observations is indicated.

Coronella austriaca



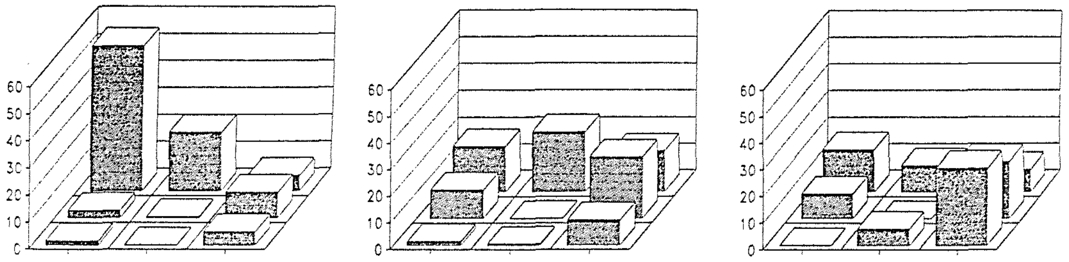
1. Start of 'lit' phase - 1159 hrs (n = 57)
2. 1200 hrs - 1500 hrs (n = 83)
3. 1501 hrs - end of 'lit' phase (n = 38)

Natrix natrix



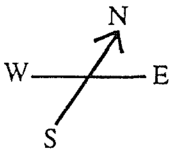
1. Start of 'lit' phase - 1159 hrs (n = 133)
2. 1200 hrs - 1500 hrs (n = 100)
3. 1501 hrs - end of 'lit' phase (n = 46)

Vipera berus



1. Start of 'lit' phase - 1159 hrs (n = 283)
2. 1200 hrs - 1500 hrs (n = 234)
3. 1501 hrs - end of 'lit' phase (n = 131)

Fig. 5.19: **Diel patterns of basking/mosaic basking site selection observed during the outdoor vivaria experiments.**



The grids represent the floor of a vivarium, divided into 9 segments. The vertical bar in each segment indicates the relative proportion of observations during the particular time period under consideration.

different basking/mosaic basking sites throughout the day to avoid the shade of the vivaria walls as the sun's position in the sky altered.

To see if such a daily pattern existed, data were separated into the same 3 basic time categories as used in the basking site slope analysis above. The proportion of basking/mosaic basking observations for each grid square is illustrated in Fig 5.19. The northwest areas of the vivaria were the first to receive direct sunlight in the mornings and note that adders and grass snakes were most commonly observed in this area before midday. The north segments were totally in the sun by 1000 hours (earlier in mid-summer) and smooth snakes were most often observed basking in that area before midday. Central, east, and southeast (the last area of the day to receive direct sun) areas were the most sunlit areas late in the day and basking/mosaic basking behaviour was also most often observed in those sites at those times.

Basking Site Substrate

A brief description was made on the range of substrates the snakes were observed using during basking/mosaic basking behaviour. Some substrate types were only present in certain parts of the vivaria (e.g. stones were only in the northwest segment). Therefore it is likely that selection of substrate type must have been influenced by the abundance of the substrate, especially with regards as to whether they were available in sunlit areas.

Table 5.28 provides frequency and proportional frequency data for substrate use. Live vegetation, the most widely available substrate, was also the most frequently used substrate by grass snakes and adders. Smooth snakes were most commonly observed basking/mosaic basking on bare soil. Decomposing vegetation was usually used in the mornings as the pile of dead vegetation in the northwest corner was the first site to receive the direct sun. Adders, grass snakes and (to a lesser extent) smooth snakes were sometimes observed basking on the pile during their heating phases.

Snakes were occasionally seen basking on litter or vegetation with parts of their bodies touching the metal vivaria walls. This was possibly a thigmothermic strategy of thermoregulation.

5.4. Discussion

5.4.1. Regression Analysis of Thermoregulation

The purpose of investigating the relationship between ambient temperatures and snake body temperatures was to identify temperature regulation and to see if interspecific differences existed. The usefulness of this analysis was also assessed. The slope of the linear regression of body temperatures on ambient temperatures provides a useful index of thermoregulatory strategy (Huey and Slatkin 1976, Huey 1982). A slope of 1 suggests thermoconformity (body temperature dependent on ambient temperature) whereas a slope of 0 suggests perfect thermoregulation (body temperature independent of ambient temperature). Previous studies have shown that near perfect thermoregulation can occur in some species of lizards when active (Stebbins and Barwick 1968, Marquet et al. 1989).

In the laboratory, shade air temperatures were used to estimate ambient temperatures. Shade air temperatures are often used to estimate ambient heat loads on reptiles but this is usually out of convenience. Huey and Slatkin (1976) suggested that the temperatures of reptiles tethered in the shade would be the most appropriate measures of ambient heat loads but that it would be generally impractical. In the present study, shaded model temperatures were used in the outdoor vivaria experiments as an estimate of 'ambient operative' temperatures.

When conditions in the outdoor vivaria were thermally unlimiting, the slope of the adder data was most shallow ($b = 0.655$) suggesting thermoregulation was more prevalent than in the other 2 species. The slope of the smooth snake data was slightly more shallow than grass snakes but still close to 1 suggesting thermoconformity.

Gent (1988) found that the slope of smooth snake body on shade air temperatures during all conditions was 0.916, which compares with a slope of 0.936 for smooth snakes in the present study during all conditions. During thermally limiting conditions in the outdoor vivaria, the regression slopes of all 3 species were close to 1 and again suggested thermoconformity. The slopes of data from 'unlit' periods (which included nocturnal measurements) were actually slightly more shallow than the slopes of data from thermally limiting periods ('lit phase' measurements only) and therefore suggested that some degree of thermoregulation was taking place.

It appears from the outdoor vivaria results that using regression coefficients of the overall data from varying conditions oversimplifies the situation. For example, a look at the plot for adder data during thermally unlimiting conditions (Fig. 5.1) reveals a dense collection of data between model ambient temperatures of 15-25°C and body temperatures of 31-35°C. This group of data relates to periods of thermoregulatory behaviour and by itself would result in a slope much closer to zero. However, there were some periods during thermally unlimiting conditions when snakes remained submerged below cover, especially during early morning periods when the temperatures of their refuges were much cooler than the maximum operative temperatures that were measured in the vivaria. This data 'drags' the slope towards a value of 1. The same phenomenon can be observed in the smooth snake and, to a lesser extent, grass snake plots (Fig 5.1).

During thermally limiting conditions, it would have been more difficult for the snakes to maintain selected body temperatures. During thermally unlimiting conditions there was always an area within the vivaria where selected body temperatures could be maintained, whereas during thermally limiting conditions the maximum model temperatures available in the vivaria could vary considerably but were always <34°C. This meant that if a snake was attempting to thermoregulate by basking in areas of maximum operative temperature, its body temperature could vary likewise. Model ambient temperatures however, did not show the same degree of variation. This is reflected in the data plots for thermally limiting conditions (Figs. 5.2)

An example of this can be seen in the data for adders (Fig. 5.2). At lower model ambient temperatures (<15°C) there appears to be a general pattern of thermoconformity. Above that level, body temperatures vary considerably reflecting thermoregulatory behaviour but varying maximum operative temperatures. Fig. 5.7 illustrates a situation where an adder was observed engaged in thermoregulatory behaviour but it was unable to maintain body temperatures at relatively precise levels. The maximum operative temperatures (estimated by model temperatures) varied considerably and so the adder body temperature varied similarly. Therefore even though the adders attempted to thermoregulate during many of the thermally limiting periods, this is not suggested by the regression slope value of 1.286. The same was true to a lesser extent for the smooth snake and grass snake data.

Slope values from 'unlit' conditions seemed to indicate that the snakes did not simply thermoconform as might be expected. Body temperatures were generally above model ambient temperatures suggesting they used some form of cover. It is interesting to note that for all species, body temperatures were higher than model ambient temperatures at cold temperature levels than at higher temperature levels. This could indicate that the snakes submerged below ground at lower ambient temperatures and thus maintained body temperatures at relatively higher levels. This was especially the case for grass snakes. The regression line suggests they maintained body temperatures about 5°C above model ambient temperatures at approximately the 5°C model ambient temperature level. At ambient model temperatures of about 22°C, grass snake body temperatures were about the same.

The laboratory arena was not as thermally heterogeneous as the outdoor vivaria and body temperatures were recorded over a smaller range of ambient (shade air) temperatures. During thermally unlimiting periods, the slopes of all 3 species implied a degree of thermoregulation was occurring. The slope of the adder data was the most shallow ($b = 0.241$), followed by smooth snakes and grass snakes ($b = 0.427$ and 0.464 respectively). The slope of the smooth snake data was not significantly different from zero. During thermally limiting periods (heatlamp off) the regression lines indicated that body temperatures were generally about 1-2°C higher than ambient temperatures and that thermoconformity was the norm.

The analysis which has been performed gives an overall impression of thermoregulation in the snakes during the laboratory and outdoor vivaria experiments and during various conditions. It is important, however, not to just rely on the regression slope as a measure of thermoregulation. The examples given here come from the pooled data of several animals performing a variety of behavioural activities over many days. This form of analysis is probably of more use when examining the data of an individual animal on a particular day, when any patterns can be more easily identified (e.g. Huey and Slatkin 1976). There is also the question of whether this form of regression analysis should be used on body temperature measurements which are not independent of eachother. It should also be noted that random movements (i.e. non-thermoregulatory behaviour) into areas with high operative temperatures could result in high body temperatures giving an impression of thermoregulation (Huey 1982). Direct observations of behaviour help to avoid this problem and therefore form the basis of the rest of this discussion.

In Chapter 3, selected body temperatures were calculated from periods when body temperatures were precisely maintained (a 'plateau' pattern). The variation of these body temperatures gives an impression of the precision with which the snakes could thermoregulate during such periods. Maximum model temperatures indicated conditions were thermally unlimiting for periods from which the selected body temperatures were calculated. Smooth snakes had the smallest standard deviations for the overall, pooled selected body temperature data during outdoor vivaria and laboratory experiments (1.64°C and 1.25°C respectively). Grass snakes had standard deviations of 2.63°C and 2.10°C respectively, and adders 1.86°C and 2.27°C. Adders probably had higher variation in the laboratory due to the shuttling-type behaviour that was employed in those experiments (see Section 5.4.4). Peterson (1982) measured a median standard deviation value of 1.32°C for free-ranging garter snake from body temperature plateau patterns.

5.4.2. Body Posture

The dorso-ventral flattening of the body observed in adders was a postural heliothermic method of increasing the surface area exposed to incoming solar radiation. Such behaviour was most often observed in the outdoor vivaria soon after emergence. After locating a suitable bask site, the adders positioned themselves and flattened their bodies. The body temperature varied considerably at the commencement of flattening after emergence (mean 12.88°C ± 3.303, n = 20, range 7.4-17.3°C). This would have been related to night time operative temperatures (and therefore the time of year).

The body temperatures that the snakes attained and the length of the flattening periods were related to environmental conditions. During sunny periods, the length of flattening behaviour times were generally shorter. Also, the last recorded body temperatures of the flattening behaviour were much higher than when conditions were clouded/changeable (28.8°C ± 5.43, n = 12 when sunny, 22.4°C ± 5.49, n = 5 when clouded/changeable). It should be noted however that the operative temperatures that existed during sunny and clouded/changeable conditions could vary (as discussed in Section 5.2.2) and this would affect heating rates and the body temperatures that the snakes could achieve.

It was very noticeable how flattening behaviour was nearly always observed when the sun was shining directly. As soon as the sun became clouded over, the adders were usually observed to cease flattening. On a sunny day the only time that flattening might be observed was soon after emergence during the snake's heating phase. However, during periods of cooling operative temperatures, a period of sun later in the day could be utilised to full effect with the adder flattening to take full thermal benefit of it. If the sun became clouded over again, flattening would cease.

Observations of flattening in adders has also been recorded by Appleby (1971) and Saint Girons (1978). The latter author observed 6 species and 9 sub-species of European Vipera but only observed flattening in the adder, Vipera ursinii, and Vipera seoanei. However, flattening behaviour in Vipera seoanei was altogether exceptional and it was concluded from this that flattening was a behavioural rather than an anatomic difference between the vipers. There is also one record of a smooth snake engaged in flattening behaviour (Goddard 1981) but this was not observed in the present study.

Body flattening is well known as a form of postural heliothermy in lizards (Heath 1965, Cogger 1974, Avery 1979). However, it has only been observed in a handful of snake species; Crotalus spp. (Norris 1967), Notechis scutatus (Heatwole 1970, 1976) and Pseudechis porphyriacus (Heatwole and Johnson 1979, Heatwole and Taylor 1987) and Vipera spp. as has already been noted. During the study by Heatwole and Johnson (1979), flattening was observed in Pseudechis porphyriacus during initial periods of basking when body temperatures needed to be raised. It was also observed during the late afternoon when ambient temperatures were dropping and the snakes were attempting to retard heat loss. Saint Girons (1978) also noted that flattening in adders tended to be associated with sunny periods in 'cool' weather. These observations correspond to those of the present study.

Specimens of Pseudechis porphryiacus have also been observed to tilt their flattened bodies so that the dorsal surface is more at right angles to the suns rays (Heatwole and Johnson 1979). During one occasion in the present study a 'flattened' adder was observed engaged in interesting behaviour which may have played a role in augmenting thermal gain. On 29.7.88 at 0858 hours, specimen Vb4 was observed basking on a heap of vegetation in the northwest corner of a vivarium. The snake, which was flattened, was seen arching a quarter to a third of its body and holding it in position for at least 20 seconds (see Fig. 5.20). It is possible that the snake was holding the body in a position which would have been more at right angles to the incoming solar radiation. It may also have been some other form of behaviour. The snake was in a pre-slough condition and it could have been arching the body to help loosen the old skin. Unfortunately I had to leave it and did not observe for how long the position was held.

The body coiling postures of snakes were observed during outdoor vivaria experiments. Results were analysed from thermally unlimiting and limiting conditions and from sunny and clouded conditions.

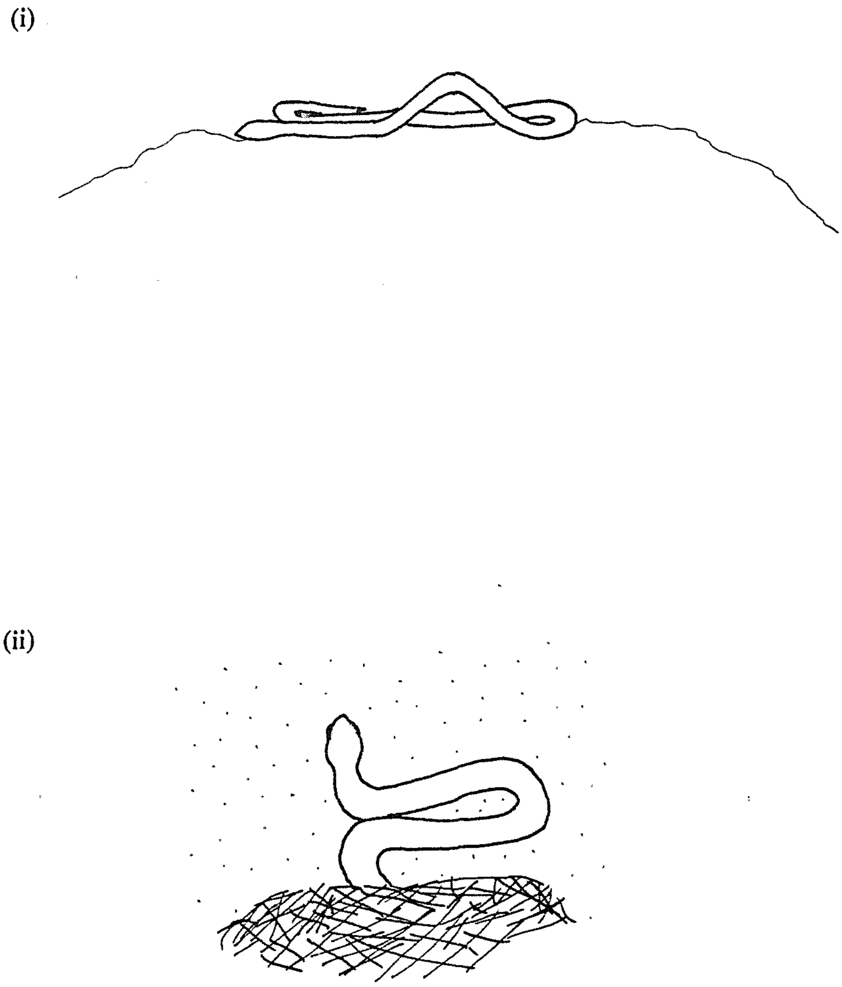


Fig. 5.20: **(i) Body posture of adder specimen Vb4 on 29.7.88.**
The snake was observed to arch its body and hold it in position while basking on the heap of dead vegetation in the northwest corner.

(ii) Body posture of adder specimen Vb6 on 31.3.89.
The adder was on the heap of dead vegetation with its body supported and pressed up against the metal vivarium wall. The snake was in the shade but the metal was being heated by the sun from the other side.

During thermally unlimiting conditions, adders and smooth snakes were observed using posture 4 most often but the most tight postures of 5 and 6 were also frequently used (83.8% for smooth snakes and 73.4% for adders for postures 4,5,6 combined). Grass snakes tended to use looser coil postures (70.4% for postures 1,2, and 3 combined). Tighter coiling appeared to be associated with higher body temperatures, especially in adders and smooth snakes (except a slight decrease from posture 5 to 6), but no significant differences were detected.

When conditions were thermally limiting, smooth snakes showed an increase in looser coil posture frequency and a decrease in posture 4 frequency. Grass snakes and adders showed a general increase in tighter coil postures than when conditions were thermally unlimiting. Adders displayed the tightest coil postures and grass snakes the loosest coil postures among the 3 species. During these occasions the pattern of increasing body temperatures with increasing tightness was more pronounced in the adder data. Body temperatures were significantly different between all postures except 3 and 4, 3 and 5, and 4 and 5. A small sample size probably resulted in the high temperatures recorded for postures 1 and 2 in smooth snakes, but the rest of the data showed a similar pattern to the adder data. Significant differences existed between postures 3 and 4, 3 and 5, 3 and 6, 2 and 6, and 4 and 6. The pattern in the grass snake data was not as pronounced and body temperatures were not significantly different between postures.

Data from sunny periods indicated that tighter body coil postures were used by adders and smooth snakes than by grass snakes. In all 3 species there appeared to be a pattern of increasing body temperatures with increasing tightness of coil postures, although the differences were only significant for adders and smooth snakes. Intraspecific differences (i.e. comparison of body temperatures of coil postures within each species) occurred between postures 2 and 6, 3 and 4, 3 and 5, and 3 and 6 for smooth snakes and 2 and 4, 2 and 5, 2 and 6, 3 and 5, and 3 and 6 for adders.

For smooth snakes and grass snakes there was little difference in coil posture frequencies between sunny and clouded conditions. During the latter periods, there was a slight increase in the tighter body coil postures. For adders, there was an increase in the proportion of coil posture 6 observations and a decrease in the looser postures. For smooth snakes and adders there was again an increase in body temperatures with coil tightness and the differences were significant. The pattern was slightly disrupted by high body temperatures recorded for coil posture 1 (adders and smooth snakes) and 2 (smooth snakes only) but this was probably a result of extremely small sample size ($n \leq 3$ in all cases). Significant differences occurred between postures 3 and 4, 3 and 5, 3 and 6, 4 and 6, and 5 and 6 in smooth snakes and between postures 2 and 3, 2 and 4, 2 and 5, 2 and 6, 3 and 6, 4 and 6, and 5 and 6 in adders. No significant differences existed between the body temperature data of grass snake postures.

In adders and smooth snakes there was a definite relationship between body coil posture and body temperature. The pattern in grass snakes did not appear to be so pronounced. The only occasion when body temperatures of the different coil postures did not show significant differences in smooth snakes and adders was when conditions were thermally unlimiting. During those conditions the snakes could have been maintaining body temperatures close to selected levels when engaged in basking/mosaic basking behaviour. The exception to this would have been when snakes emerged during thermally unlimiting periods but even then body temperatures could have increased rapidly. The slightly lower body temperatures of the looser coil postures (especially in adders) could be a result of such post-emergence basking behaviour when the snakes were often observed using loose coil postures during the heating phase.

When conditions were classed as sunny or clouded, the pattern of increased body temperature related to increased tightness could be detected in smooth snakes and adders. The maximum operative temperatures available to the snakes in the vivaria could vary during both sunny and clouded conditions. For example, sunny periods could result in relatively low operative temperatures in early morning periods. However, in general sunny periods tended to produce higher operative temperatures than clouded periods (see Section 5.2.2). Body temperatures for the different coil postures also tended to be higher when conditions were sunny.

The pattern of increasing body temperature with increased tightness of coil posture appeared to be stronger in adders than smooth snakes. Significant body temperature differences occurred between more adder coil postures than between smooth snake postures. An examination of the graphs (Figs. 5.10, 5.11) also indicates greater contrasts between coil posture data for adders. This might imply that adders use more precision when altering body coil posture behaviour in relation to temperature factors. Adder body temperatures of the body coil posture categories also tended to be higher and significantly different to those of smooth snakes and grass snakes during the different conditions. The latter 2 species tended not to show significant differences.

Body coil posture appears to be used as a form of thermoregulatory behaviour. This behaviour was most pronounced in adders and least pronounced in grass snakes. It was used in conjunction with other thermoregulatory behaviour during 'basking' or 'mosaic basking'. Loose coiling postures tended to be used soon after emergence during the heating phase. Adders used relatively loose postures when they were 'flattened'. Such behaviour results in an increase in the amount of body surface area exposed to incoming radiation thus decreasing the time necessary to raise body temperatures. At higher body temperatures, body coil postures tightened, reducing the body surface area exposed. This was usually in conjunction with a move to cover (mosaic basking or totally 'hidden'). As well as tightening when body temperatures were high (and thus reducing the surface area available for heat-gain), they also tightened during periods of cooling operative temperatures. Heat loss is thus prevented by reducing the surface area from which back-radiation can occur. Note that all 3 species were observed in postures 5 and 6 more often during thermally limiting conditions than during thermally unlimiting conditions.

In the laboratory, the results of body coil posture monitoring did not appear to match those of the outdoor vivaria. When the heatlamp was on (thermally unlimiting conditions) tighter coil postures (postures 4 and 5) were used by smooth snakes most often and adders least often. There was no significant difference in the body temperatures of the body coil postures in adders or smooth snakes whereas significant differences existed between all the possible posture combinations in grass snakes. Tighter coiling postures were marked by increasing body temperatures in the latter species. This appears to be a reversal of the situation in the outdoor vivaria where grass snakes appeared to show the least distinct relationship between body temperature and coil posture.

For all body coil postures adders had higher and significantly different body temperatures than the other 2 species during the thermally unlimiting conditions in the laboratory. Smooth snake body temperatures were higher and significantly different to those of grass snakes except for posture 5. As stated previously in Section 4.4.2, adders in particular were observed performing different patterns of behaviour to those of the outdoor vivaria. Shuttling heliothermy (and possibly positional changes under the heatlamp) appeared to be the main thermoregulatory strategy of adders in the laboratory. Smooth snakes did not shuttle but when they did bask, it tended to be for relatively longer periods and may have involved positional changes under the heatlamp. Grass snakes basked periodically but it was not true shuttling. They appeared to use postural alterations of coiling posture when basking.

Records of body coil posture were also made when conditions were thermally limiting in the laboratory (heatlamp off) and the snakes were observed engaged in thigmothermic behaviour.

In theory a tight body coil would act to reduce heat loss once the heatlamp was off. Adders were observed using tight coil postures least of all whereas smooth snakes used posture 5 for 64.7% of the time. Smooth snakes maintained higher and significantly different overall body temperatures than grass snakes or adders and tight coil postures may have been a factor in that.

The role of body coiling posture in snakes as a thermoregulatory mechanism has been discussed in previous studies. Cogger and Holmes (1960) noted that carpet pythons (Morelia spilotes variegata) displayed loose coil postures when the weather was 'fine' and tighter coils when conditions were excessively hot or bask sites became shaded. It was estimated that the surface area exposed when tightly coiled was only 30-50% of that of the surface area when the snake was uncoiled. The same species was studied by Johnson (1972) and he noted similar observations to the previous workers. He observed 'outstretched' body postures after emergence, loose coils when body temperatures approached the 'preferred' range (30.7-32.0°C) and tight coils once the preferred temperature had been reached. The latter behaviour was in conjunction with a move into the shade. The temperature was kept at preferred levels by shifting between sun-shade interface (termed as shuttling). These observations are very similar to those recorded in the present study.

Lillywhite (1980) observed alterations in body coil postures among 7 species of Australian snakes of the Elapidae but gave no quantitative data. He considered coil posture, alterations in body orientation and shuttling behaviour to be their main methods of behavioural thermoregulation during experiments in a laboratory thermal gradient. Slip and Shine (1988) noted loose body coil postures in Morelia spilota during basking behaviour (characterised by the heating phase) and tighter coil postures when under cover.

Spellerberg and Phelps (1977) observed that smooth snakes appeared to display tight coils in cool weather and loose coils when very warm. Goddard (1981) made similar observations and Gent (1988) demonstrated that significant variation existed between the body temperatures of different coil postures of free-ranging smooth snakes. He used the same scale of body coiling posture as the one employed in the present study and noted that tighter coils tended to relate to warmer body temperatures. The results of the outdoor vivaria experiments in the present study confirm his observations.

The orientation of the body aspect of reptiles in relation to the sun is another postural heliothermic strategy of thermoregulating used by some species (Heath 1965, Heatwole and

Taylor 1987). The categorisation of body aspect used in the present study was a crude scale of the relative solar azimuth angle (RAZ, Muth 1977). The RAZ can be defined as the horizontal angle of the sun relative to the head and frontal plane of the snake. Another way for a snake to change the angle of its body in relation to incoming solar radiation is to bask on a slope. However, this relates to bask site choice rather than varying body posture and is discussed later on.

During sunny and clouded conditions, observations where no definite body aspect in relation to the sun could be defined were most frequently observed (body aspect 4, see Fig 2.8). These observations were made when snakes were tightly coiled. Body aspects 1-3 could only be defined when the coil postures were relatively loose. As we have seen above, loose body postures were generally observed during periods when body temperatures were being raised (in particular the post-emergence heating phase) and it was then that some patterns could be observed.

Unfortunately records of body aspect were relatively small in some cases. When conditions were sunny, smooth snakes were generally observed in body aspect 4 and a fair proportion was observed at 45° to the sun but it was difficult to state whether or not body aspect was utilised as a form of postural heliothermy. For grass snakes and adders, body aspect 4 was the most frequently observed body aspect once again. However, when body coil postures were loose, there was a definite tendency to use body aspects at 45° or 90° angles to the sun rather than lying parallel to incoming radiation.

During overcast conditions one might not expect to see such distinct patterns. Certainly body aspect 4 was more frequently observed (i.e. no distinct body aspect to the sun) when overcast. When loose body postures were observed, the sample were too small to make any definite conclusions. Adders did appear to display body aspects at 45° and 90° angles to the sun more frequently whereas no pattern was discernible in grass snakes. It may have been that the pattern observed in adders could have occurred on days of changeable conditions. For example, a period of sun could have resulted in a body aspect of 90°. This may have been followed by a period of cloud during which another record was taken but the snake remained with the same body aspect.

5.4.3. Use of Cover in Thermoregulation

When conditions were thermally unlimiting in the outdoor vivaria, smooth snakes were the least exposed of the 3 species. On 58.3% of the observations, the snakes were only 5-35% exposed. Adders and grass snakes did not differ significantly in the amount of cover they used. The 66-95% exposure category was most frequently seen in the latter 2 species. There was a general pattern of decreasing body temperatures with increasing body exposure. The body temperatures of the different exposure categories in smooth snakes did not differ significantly whereas significant differences did exist within the data for grass snakes and adders. The body temperatures of the different exposure categories were higher and significantly different in adders from smooth snakes (except 66-95% exposure category where n = 1 for smooth snakes) and grass snakes. No significant differences existed in the latter 2 species.

The exposure of all 3 snake species increased when conditions were thermally limiting. Adders were the most exposed and smooth snakes the least exposed. When basking (>95% exposure) was not included, there was no significant difference between grass snakes and adders in the degree of exposure used when mosaic basking. The body temperatures showed a general reversal of the pattern observed during thermally unlimiting conditions with an increase in relation to increasing exposure. The exception to this in all species was the least exposed category (5-35% exposure). This had relatively high body temperatures. No significant differences were detected between the body temperatures of the exposure categories in grass snakes. Significant differences were found in the smooth snake and adder data. There were no interspecific differences in body temperatures except between grass snakes and adders for the basking (>95% exposure) category.

The observation that the frequency of basking increased in adders and (to a lesser extent) smooth snakes when conditions were thermally limiting has already been discussed in Section 4.4.2. This was matched by a general move to the shade of cover when conditions were thermally unlimiting. However, it appears that this is an oversimplification. The results presented here suggest that once they are under cover and mosaic basking, the snakes actually alter the degree of body that is exposed. Rather than just using sunny areas or shaded areas for thermoregulatory purposes, mosaic basking allows them to combine the two at the same time.

For smooth snakes there were no significant differences in the body temperatures of the different exposure categories when conditions were thermally unlimiting. This could suggest that as body temperatures reached the same particular level, the snakes retreated more into cover. There were significant differences in grass snakes and adders though, and this could have been because the snakes progressively retreated into cover as their body temperatures got higher. However, a more valid explanation for low body temperatures of the most exposed categories relates to the inclusion of heating phase temperatures. During periods of heating (particularly the post-emergence heating phase) the snakes were most exposed and it was during these periods that body temperatures were at their lowest. When body temperatures had increased close to selected levels, the snakes retreated more into cover to prevent them increasing further. Therefore the inclusion of relatively cold body temperatures of the heating phase tends to lower the overall mean body temperature of the most exposed categories.

When conditions were thermally limiting, the snakes had to expose themselves more during basking/mosaic basking behaviour in order to raise body temperatures. This was reflected by an increase in body temperatures as body exposure increased. The exception to this was the least exposed category (5-35% exposure) for which relatively high body temperatures were recorded. This high degree of cover tended to be used when operative temperatures were particularly high. The high body temperatures recorded for this category during thermally unlimiting conditions appear to support this. It is possible that brief periods of cloud could have lowered operative temperatures for short periods during which the snakes remained well covered and body temperatures could have remained high. They would have the effect of increasing the overall mean body temperature value of the least exposed category. An alternative or additional explanation is that if a snake needed to conserve heat during a period of cooling operative temperatures, the best strategy would be to coil up tightly and move under dense cover. Relatively high body temperatures could result from such behaviour during thermally limiting conditions.

The fact that snakes often retreat into the shade during hot periods has been noted before (e.g. Carpenter 1956, de Bont et al. 1986). Heatwole and Johnson (1979) observed Pseudechis porphyriacus progressively moving into the shade as they began to overheat. After a certain degree of cooling had occurred, the snakes would move back into the full sunlight. This was described as shuttling behaviour and differed from the observations of the present study. Instead of moving to and from full sunlight, the snakes in the present study tended to remain mosaic basking in partial sunlight once body temperatures were at approximately selected levels.

A rare quantitative investigation of the degree of exposure used by thermoregulating snakes was made by Hailey and Davies (1987) on free-ranging Natrix maura. In cool weather (air temperature < 22°C) snakes were observed exposing most of their bodies. In hot weather (air temperature > 26°C) the snakes were less exposed and in some cases completely shaded. The fact that adders and smooth snakes appear to alter the degree of body area exposed in different conditions has also been noted before (Prestt 1971 and Gent 1988 respectively) but no quantitative records have been provided.

Altering the degree of exposure during mosaic basking could be considered to be an extreme form of shuttling heliothermy. Shuttling normally entails a series of movements into and out of the sun. Huey and Slatkin (1976) examined the potential costs and benefits of thermoregulation in lizards, a group that often utilises shuttling heliothermy. They proposed that lizards may opt out of precise thermoregulation if the costs (e.g. in terms of energy) of shuttling are excessively high. For example, Anolis lizards living in shaded (high cost) forests tend to thermoconform whereas those living in open (low cost) tend to thermoregulate through shuttling.

The heterogeneous vegetative structure of the outdoor vivaria provided the snakes with a relatively wide range of operative temperatures (subject to warm weather conditions). By adjusting the degree of body area exposed when mosaic basking, the snakes were able to thermoregulate without the need to shuttle between distinct sunny and shaded sites. Theoretically, such behaviour would be very low cost in terms of energy as locomotion is reduced to a minimum. There is the additional advantage that the snakes also remain relatively cryptic under the partial cover of vegetation and are therefore less vulnerable to potential predators (especially important to smooth snakes, see Section 4.4.2) and more hidden from potential prey (especially for sit-and-wait foraging strategists, see Section 4.4.2).

Smooth snakes were the least exposed of the 3 species during thermally limiting and thermally unlimiting conditions. This is in keeping with the cryptic nature of the species as discussed in Section 4.4.2. The cover type used most by the smooth snakes and the other 2 species in the outdoor vivaria was vegetation (excluding heathers). However, this was also the most abundant cover type available. In the field it was noticed that snakes very often basked on the sunny sides of dense bushes of vegetation. Grass snakes were frequently seen by the edge of Rubus fruticosus clumps, smooth snakes by Calluna or Erica bushes. The snakes used these as a place for retreat when they sensed me approaching. In addition, they were often observed mosaic basking under part of the overhanging vegetation.

In the laboratory, the degree of body surface area exposed during basking/refuge basking behaviour was also investigated. The large extent to which basking was used has been discussed in Section 4.4.3. Body temperatures generally increased with increasing body exposure. This was not unexpected as the hottest area was directly under the heatlamp. The more exposed the snakes were, the closer to the 'hotspot' directly under the heatlamp they became. This was a different situation to snakes mosaic basking in the outdoor vivaria where there was no distinct hot area that the snakes had to move to in order to heat up.

It was difficult to determine whether the degree of exposure during refuge basking in the laboratory was actually a thermoregulatory strategy or if it performed some other function. Smooth snakes and grass snakes were also observed to engage in 'refuge stationary' and 'in refuge' behaviour to a much higher degree than adders (Section 4.4.3). Refuge basking was only rarely observed in adders but when it was, it was usually only the head region that was exposed. 'Head emergence' was often observed in smooth snakes and grass snakes prior to the first emergence of the day and this was looked at in Chapter 4. However, snakes often went under refuges at various times throughout the day and, prior to re-emerging, frequently exposed only the head area before eventually emerging to a greater extent.

5.4.4. Shuttling Heliothermy

As discussed in Section 5.4.3 above, mosaic basking could be considered to be a very extreme form of shuttling behaviour, involving the use of sunny and shaded areas simultaneously rather than making distinct movements between sunny areas and shaded areas. Grass snakes were observed moving to a greater extent than the other 2 species (as discussed in Section 4.4.1) and this was generally interspersed with periods of basking/mosaic basking. However, again this was not shuttling in the strict sense as the movements were not short shuttles between sunny and shaded areas. Instead the movements appeared to be foraging or exploratory behaviour which sometimes lasted for relatively long periods. The grass snakes frequently moved through sunny and shaded areas during a single locomotory session. Distinct shuttling behaviour was not observed in adders or smooth snakes in the outdoor vivaria.

In contrast to the outdoor vivaria, adders in the laboratory did appear to shuttle (Section 4.4.3) for much of the time. Body temperatures were maintained at high levels during basking/refuge basking behaviour (mean 32.12°C ± 3.420, n = 149) and during non-basking/refuge basking behaviour (mean 29.24°C ± 3.820, n = 78) and at relatively precise levels. After a period basking (refuge basking was rarely observed), adders tended to move away to a shaded area but rarely moved under a refuge or performed some other form of behaviour. The artificial environment of the laboratory arena may have stimulated some type of exploratory behaviour (possibly foraging behaviour) which manifested itself in the form of an increased degree of movement. This movement behaviour was therefore incorporated into the adders' shuttling behaviour. It would have been less energetically costly for them to simply shuttle to and from the refuge next to the heatlamp which implies that their behaviour was not totally directed to thermoregulation.

Shuttling behaviour in the laboratory was not as distinct in grass snakes and smooth snakes. Thermoregulatory behaviour was observed in the form of basking/refuge basking (mean body temperatures of 30.21°C ± 2.091, n = 287 for smooth snakes, 27.37°C ± 4.971, n = 407 for grass snakes). Unlike adders however, body temperatures of non-basking/refuge basking behaviour were comparatively low for both species (mean 21.30°C ± 2.155, n = 129 for smooth snakes, 20.15°C ± 2.428, n = 570 for grass snakes). As body temperatures were allowed to drop to such low levels during periods of non-basking/refuge basking behaviour (which tended to be carried out in areas not influenced by the heatlamp), the implication was that shuttling was not used to any great extent.

5.4.5. Basking Sites

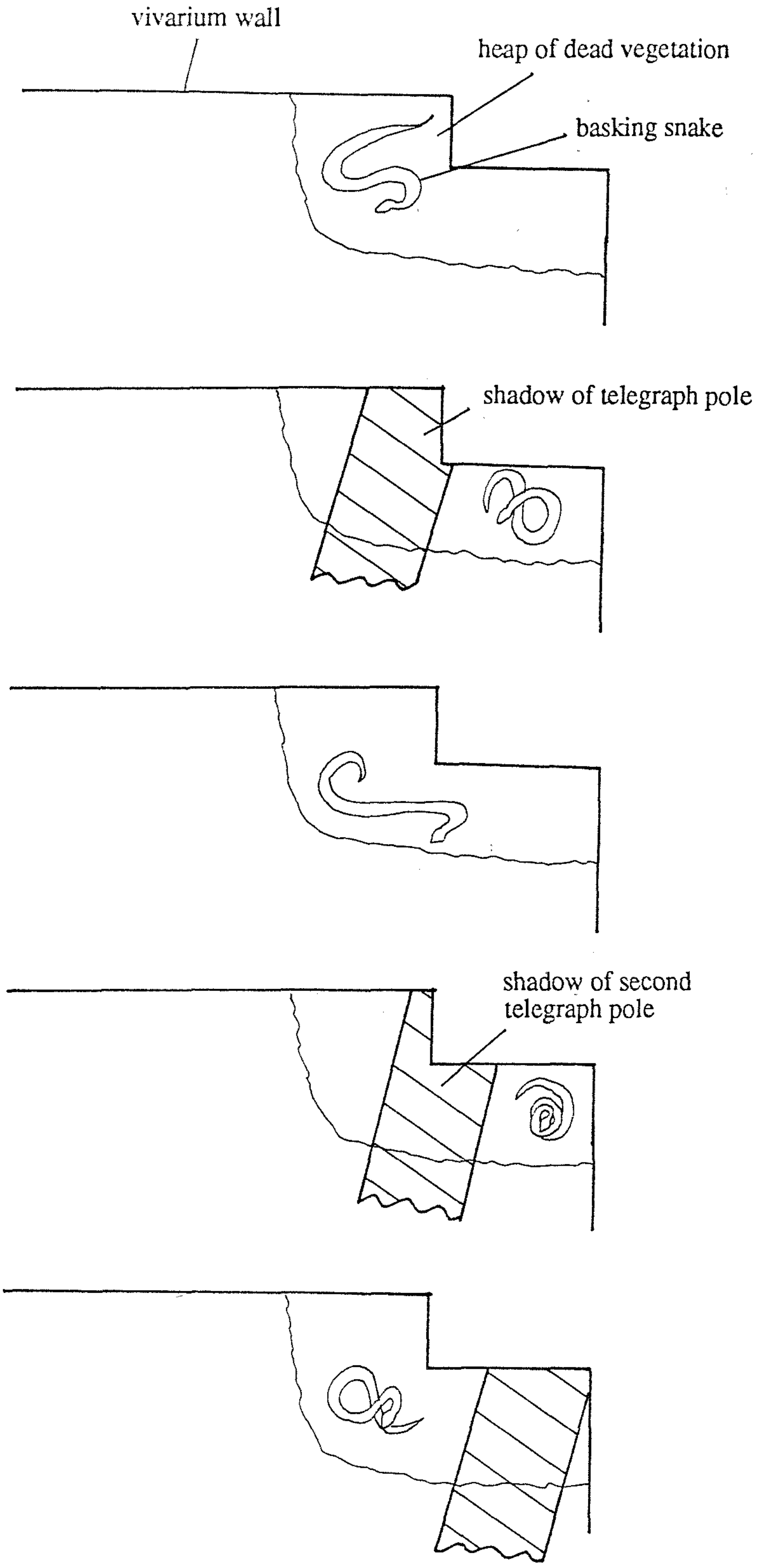
Selection of micro-habitats and micro-climates is likely to play an important part in snakes thermoregulation. It has already been noted how vegetative cover is utilised during mosaic basking behaviour. It was also observed in the laboratory that snakes often adjusted their positions under the heatlamp and it is likely that this contributed in some way to maintaining selected body temperatures. However, the latter aspect has not been examined in detail in the present study.

In Section 5.4.2 above, the horizontal angle of the sun in relation to a snake's body was investigated ('body aspect'). This was considered to be controlled by postural changes. There is also the factor of the vertical angle of the sun in relationship to a snake's body. This aspect can be controlled to an extent by postural changes in some reptiles through tilting (e.g. Bradshaw and Main 1968). The 2 factors are linked and body postures of reptiles reflect this. For example, the Pseudechis porphyriacus basks with the long axis of its body at right angles to incoming solar radiation and with the body tilted so that the dorsal surface is also at right angles to the incoming radiation (Heatwole and Johnson 1979). There was one occasion during the outdoor vivaria experiments when an adder (specimen Vb10, 3.5.89, 1058 hours) was observed basking with the dorsal surface of its body apparently tilted at a 50-60°angle to the horizontal. However, although it appeared that the snake was actually propping itself up in some postural manner, it was difficult to confirm that it was not leaning against some vegetation and using that as support. Otherwise, snakes were not observed tilting their bodies towards the sun (postural adjustment) but instead used slopes to the same effect (basking site selection). The results of the basking site slope selection study (including when mosaic basking behaviour was observed) suggested that all 3 species of snake tended to use slopes that faced the direction of incoming radiation.

The snakes also showed a pattern of microhabitat selection during basking/mosaic basking behaviour in terms of utilising sunny areas and avoiding heavily shaded areas. During the morning periods, grass snakes and adders were most often observed in the northwest sector and smooth snakes in the north sector. These areas were the first to receive the direct sun (the northwest before the north sector). In the afternoon/evening period, adders were most frequently observed in the southeast sector, grass snakes in the east and smooth snakes in the central sectors. These areas were the last to receive the direct sun (the southeast last of all). During the midday period the site basking/mosaic basking site selection did not show such distinct patterns. There did appear to be a general preference for the northern two thirds of the vivaria as these areas were all in the sun at some stage during the midday period.

Adders were observed utilising the sunny areas to the greatest extent, using the northwest segment most in the morning and the southeast segment most in the evening. Some adders were observed basking/mosaic basking in the very last sunny areas of the southeast segment in the evening, confined between the shade of the vivaria walls and the walls of the southeast segment. If a site where a snake was observed basking/mosaic basking became shaded by the vivaria walls, they were often seen moving to a different, unshaded area and resuming their heliothermic behaviour there.

A particularly good example of adders maximising their heating rates after morning emergence by avoiding shaded areas was observed in specimen Vb12 on 25.5.89. At this particular time of the year, the vivaria were affected by the shade of 2 telegraph poles during the morning period. The sequence of events is illustrated in Fig. 5.21. The adder was observed basking at 0757 hours on the heap of vegetation in the northwest corner, only a few minutes after the end of the 'unlit' phase (i.e. the sun had begun to shine directly onto the



1. 0757 hours.

2. 0812 hours.
Heap partly in shade of first telegraph pole.

3. 0837 hours.

4. 0848 hours.
Heap partly in shade of second telegraph pole.

5. 0858 hours.
North end of heap partly in shade of second telegraph pole.

Fig. 5.21: **Avoidance of shade by a *Vipera berus* specimen (Vb 12) on 25.5.89.** The snake was basking on the heap of dead vegetation in the northwest corner of a vivarium during its post-emergence phase. Adjustments of basking site position were made to avoid the shadows of 2 telegraph poles.

floor of the vivaria). The shade of the first telegraph pole made the snake 'squash' into the unshaded area of the heap (0812 hours). By 0837 hours the heap was no longer in shade and the snake was once more in a loose coil posture basking in the sun. The shade of the second telegraph pole forced the snake to move itself into the unshaded area of the heap once again (0848 hours). By 0858 hours, there was insufficient space to bask in the sun so it had moved to the other side of the telegraph pole shade and was in the small sunny area there. By 0909 hours there was no longer any shade and the snake was observed basking in a looser posture once more.

Live vegetation was the most frequently observed substrate used by adders and grass snakes engaged in basking/mosaic basking behaviour. Smooth snakes were observed using bare soil to the greatest extent (42.5%) although live vegetation was also commonly utilised (36.2%). Smooth snakes were the most cryptic of the 3 species and it is possible that those basking/mosaic basking on bare soil tended to be easier to see than those positioned on vegetation. Smooth snakes also tended to be kept in a vivarium where there was more bare soil available.

All 3 species have been shown to be heliotherms. Thigmothermy may be used as a thermoregulatory strategy sometimes, but it seems likely that it would only be in a supplementary capacity. Note that stones were used less by all 3 species during thermally unlimiting conditions than during thermally limiting conditions. The operative temperatures available on a stony substrate during thermally unlimiting conditions would be particularly hot and too extreme for the snakes in most cases. However, they were used more in thermally limiting conditions possibly to help increase body temperatures when the snakes were basking/mosaic basking as well. Stones are almost certainly avoided when hot but it is difficult to be sure whether they were actually selected for their thermal properties during cooler conditions. Zuffi (1989) noted similar observations in that adders tended to bask on grass, especially during hot conditions, although rocks were used to a greater extent when conditions were cloudy and windy.

Snakes were also seen pressing their bodies against the metal sides of the vivaria walls during basking/mosaic basking behaviour. Thus heliothermy was being supplemented by thigmothermy to a possibly large extent. Snakes were frequently engaged in what was classed as basking or mosaic basking for the purposes of recording, but during periods of overcast sky and low operative temperatures. Heliothermy would have been a less important strategy as such times and thigmothermy may have performed a comparatively greater one.

There were 2 particular observations when thigmothermic behaviour had a definite effect on snake body temperatures. Adder specimen Vb6 had been observed moving in the shaded northwest of its vivarium at 1519 hours on 31.3.89. Its body temperature at the time was 26.6°C. By 1532 hours it was observed on the heap in the northwest corner with its body supported and pressed-up against the wall in spectacular fashion (Fig. 5.20). The heap was in the shade but the sun was shining and therefore heating the metal wall against which the snake was pressed. At this point the body temperature of the adder was 29.8°C although the model temperature of the site on which the snake was positioned was only 17.6°C (the model was not touching the metal wall). The body temperature of the adder increased to 34.1°C at 1546 hours. By 1647 hours the snake was still in the same position although the body had slumped somewhat and the body temperature had decreased to 27.1°C. It was hidden within the heap by 1703 hours but could just been seen still next to (and probably touching) the metal wall. The last recording was made at 1800 hours when the body temperature had decreased to 21.9°C but was still higher than the model temperature of 13.8°C.

A smooth snake was observed on exactly the same site as the adder had been seen, with only 30% of its body exposed and lying pressed against the metal wall (specimen Ca8, 18.5.89). The time of the observation was 1651 hours and the site was in the shade. The body temperature of the smooth snake was 32.4°C. The model temperature was only 24.2°C. The snake was completely hidden under the heap by 1749 hours and its body temperature had dropped to 25.8°C. However, the snake must still have been touching or was very close to the metal wall as the sun, which had become clouded over, came out again and the body temperature increased to 27.2°C at 1602 hours (model temperature 22.6°C). The insulative properties of the dead vegetation into which it had submerged would also have acted to conserve heat and insulate the snake from cold ambient temperatures. These 2 examples demonstrate that snakes will use thigmothermy as an alternative strategy if an opportunity arises.

5.5. Summary

(i) The slope of the regression lines of body temperature on ambient model temperature suggested that adders thermoregulated to the greatest extent during the outdoor vivaria experiments. During 'unlit' periods, the snakes tended to thermoconform although they avoided particularly cold ambient temperatures, probably by retreating underground.

(ii) During the laboratory experiments, the slopes of the regression lines suggested that adders thermoregulated to the greatest extent, followed by smooth snakes and finally grass snakes.

(ii) Thermoregulation was also assessed through the direct observation of snake behaviour combined with monitoring of body and environmental temperatures.

(iv) Dorso-ventral body flattening was a form of postural heliothermy only observed in adders. It was usually observed during the post-emergence heating phase although it was used later in the day if body temperatures had decreased during thermally poor conditions.

(v) Flattening behaviour was generally restricted to sunny conditions. The mean duration of the post-emergence flattening on sunny days was 22.1 mins ± 14.21 ($n = 17$) and the mean body temperature at which flattening ceased was 26.9°C ± 6.17 ($n = 17$).

(vi) During outdoor vivaria experiments, grass snakes tended to have looser body coiling postures than the other 2 species, although they did tend to tighten when conditions were thermally limiting or clouded.

(vii) Smooth snakes and adders had similar body coiling posture frequencies when conditions were thermally unlimiting or sunny, although adders would tighten more when conditions were thermally limiting or clouded during outdoor vivaria experiments.

(viii) For smooth snakes and adders, tighter body coil postures were associated with higher body temperatures during outdoor vivaria experiments. Loose coils tended to be used during heating phases (increasing body surface area exposed to sun). Tighter coils tended to be used when body temperatures were close to selected levels, and when thermal conditions cooled down (insulative role).

(ix) In the laboratory, grass snakes displayed tighter body coil postures associated with higher body temperatures.

(x) When conditions were sunny and body coil postures were relatively loose (i.e. during heating phases), adders and grass snakes showed a tendency to bask with the long axis of their bodies at 45°/90° angles to the horizontal position of the sun. There were insufficient data available for smooth snakes.

(xi) An examination of the degree of exposure displayed by the snakes in the outdoor vivaria indicated that smooth snakes were the least exposed of the 3 species. Grass snakes and adders did not differ significantly during thermally unlimiting conditions. The latter 2 species also did not differ during thermally limiting conditions in the degree of exposure utilised during mosaic basking behaviour, although adders basked fully in the open more often.

(xii) All 3 species were more exposed during thermally limiting conditions than during thermally unlimiting conditions in the outdoor vivaria.

(xiii) During thermally unlimiting conditions, median/mean body temperatures were higher when less exposed (but not significantly different for smooth snakes). During thermally limiting conditions, body temperatures were lower when less exposed (but not significantly different for grass snakes). The exception in the latter case was the least exposed category, which would have been more sheltered and therefore may have been utilised by the snakes to reduce heat loss during periods of cooling temperatures.

(x) Mosaic basking was considered to be an extreme form of shuttling heliothermy, utilising sunny and shaded areas simultaneously.

(xi) True shuttling heliothermy was not observed in smooth snakes or adders in the outdoor vivaria. Grass snakes interspersed periods of movement with basking/mosaic basking in a crude form of shuttling behaviour.

(xii) Adders maintained high body temperatures in between periods of basking/refuge basking behaviour in the laboratory. This was achieved by frequent and short periods of basking interspersed with frequent and short periods of other behavioural actions. This was a form of shuttling behaviour. Smooth snakes and grass snakes tended not to maintain such high body temperatures when not engaged in basking/refuge basking.

(xiii) All 3 species showed a general daily pattern of basking/mosaic basking on slopes which faced the direction of the sun.

(xiv) All 3 species showed a general daily pattern of basking/mosaic basking in areas which were in the sun for the longest time. Adders in particular were often seen basking in the first sunny areas of the vivaria in the morning and the last sunny areas in the late afternoon.

(xv) Live vegetation was most often used as a substrate during basking/mosaic basking behaviour in grass snakes and adders. Smooth snakes were more often seen on bare soil.

(xvi) Stony substrate was more often used when conditions were thermally limiting. All 3 species were seen basking/mosaic basking while pressed against the metal vivaria walls, suggesting that thigmothermal behaviour was supplementing heliothermic behaviour. Thigmothermy was observed as a main method of thermoregulation in an adder and a smooth snake specimen.

CHAPTER SIX

GENERAL DISCUSSION

6.1. Introduction

A comparative study of the thermal ecology of the three British snake species was undertaken. It incorporated an investigation of the body temperatures attained by the snakes and their relationship with the physical environment. The general behaviour and ecology of the snakes was related to environmental conditions and the body temperatures that could be attained during such conditions. Behavioural thermoregulation formed an important part of the overall behavioural time budgets and this was investigated in greater detail, again with an emphasis on interspecific comparison.

In this discussion, an overview of the relationships between the thermal environment, the body temperatures and the overall behaviour of the smooth snake, grass snake and adder is presented, together with the possible role these factors may play in the distribution of the three species. A section is provided on their conservation and management. The discussion starts with a brief, critical look at the methodology used in the study.

6.2. Discussion of Methodology

It was felt that the outdoor vivaria provided the best means of studying snake behaviour in an environment that was as similar to field conditions as possible. Studying snake behaviour and thermal relations in the field would have been difficult due to their cryptic nature and sensitivity to disturbance. Also, the primary objective of the study was to undertake an interspecific comparison. Any apparent interspecific differences in a field situation may be due to the responses to the respective environments by the different species. Therefore, by undertaking comparisons in similar environments (the outdoor vivaria or the laboratory arena) such problems were avoided.

The use of biotelemetric equipment allowed the continuous monitoring of snake body temperatures over several days of study. The obvious advantage of biotelemetry was that disturbance of the snakes was minimised. Automatic recording, when the observer was not present, could also be carried out thus providing an efficient use of research time. There were problems with the biotelemetric equipment however, especially during the early stages of the study. In the outdoor vivaria, one of the biggest problems was the effect of moisture entering the transmitters and corroding internal wires. This was particularly the case with grass snakes as they were particularly active and probably entered the pond on more occasions. A particular 'weak' spot was where the thermistor lead entered the main body of the transmitter. The silicone sealant covering would eventually wear off and so it was important to ensure that sufficient sealant was used.

The transmitters were externally mounted and this resulted in the snakes occasionally snagging on vegetation as they moved around the vivaria. On one occasion a grass snake had to be removed from the underground refuge after apparently becoming entangled due to the presence of the transmitter. Another grass snake attempted to escape from the vivaria and became caught in the netting (used to keep birds out) but it was removed without any apparent harm having been done. Secure attachment of the transmitters was also important so that they remained in place for as long as possible. Removing the transmitters and the tape with which they were attached, required some care to avoid damaging the snakes' skin. The tape tended to remove the top integument of some of the scales but this appeared to cause no lasting damage and did not break the skin.

The presence of the transmitters did not appear to affect the snakes' behaviour in any significant way. In a previous study, Wilkinson (1988) carried out a study of the possible effect of such transmitters on the behaviour of adders and found no difference in behavioural budgets or sequences between tagged and untagged individuals. Gent (1988) also compared untagged smooth snakes with those attached with externally-mounted transmitters (although without temperature leads). No difference in activity patterns, use of cover and vegetation, movement or rates of change of body weight were detected.

Externally-mounted, temperature-sensitive radio transmitters are not really suited for long-term studies in the field. However, they were ideal for short-term studies in the laboratory and outdoor vivaria as they could be easily attached and replaced with relatively little harm to the snakes. The different types of transmitters available and their method of fixation is discussed in Section 2.3.

Throughout the study, the emphasis has been on the interspecific comparison of snake species. However, it should be noted that intraspecific variation of thermal biology does occur and this has been identified in a number of reptilian species. Selected body temperatures and behaviour associated with maintaining such temperatures can vary between individuals according to physiological states (Regal 1966, Saint Girons 1978, Beuchat 1986, Madsen 1987) and the time of day and year (Gibson and Falls 1979, Peterson 1982, Meek 1988). In the latter case, acclimitisation of the animals to seasonal conditions may result in alterations of selected body temperatures and/or activity temperatures, or the changing constraints of seasonal climatic factors may contribute to such patterns. However, for the purposes of the present study, it was felt that an overall picture of the thermal strategies utilised by the 3 snake species could be best achieved by the pooling of data of individual animals.

Shortage of time prevented a more detailed examination of daily patterns of snake behaviour. Pooling of data from different days inevitably resulted in the loss of some of the finer detail but it allowed overall interspecific comparisons to be made. By using animal models to estimate operative temperatures during the outdoor vivaria experiments, it was possible to make interspecific comparisons for periods of thermally equivalent environmental conditions (at least with respect to the maximum operative temperatures that were available). Simultaneous recording of different snakes in neighbouring vivaria meant that even more direct comparisons could be undertaken. This was also possible for experiments performed in the laboratory where environmental conditions were kept as constant as possible throughout the study.

6.3. Body Temperatures and Lifestyle

Some of the general results that were obtained for the three British species in the present study appear to match those displayed by a wide range of snakes. Lillywhite (1987) commented that for the majority of snake species for which adequate thermal data exists, selected body temperatures (or 'preferred body temperatures' as Lillywhite prefers to use) have been measured to be within the range of 28-34°C and frequently near 30°C. He also pointed out that even high latitude species of Thamnophis have been found to regulate their body temperatures around 30°C (e.g. Gibson and Falls 1979, Peterson 1982, 1987). This appears to be the case for the British snakes, all of which have selected body temperatures in the region of 30°C even though they are at the northern region of their range (especially in the case of smooth snakes and, to a lesser degree, grass snakes).

When body temperatures were maintained at selected levels during thermally unlimiting conditions, (the 'plateau phase' pattern) all three species showed a relatively high degree of precision. They also displayed a variety of thermoregulatory behavioural strategies. In the past the general consensus of opinion has been that snakes are not as precise thermoregulators as lizards (Avery 1982) and that snakes appear to maintain lower body temperatures than do lizards (Brattstrom 1965). The present study, together with some of the more recent investigations of snake thermal biology, suggests that such a suggestion is not entirely valid.

Of the three species studied, adders were found to maintain the highest body temperatures. Their selected body temperatures and the body temperatures attained during thermally unlimiting conditions were higher than that for the other two species. The maximum temperatures of their activity temperature range were also higher than the other two species. Conditions were found to be thermally unlimiting in the outdoor vivarium for all 3 species for only a relatively small proportion of the time. Adders displayed a greater ability to temporally utilise thermally unlimiting conditions, both in the outdoor vivaria and in the laboratory. They were found to display overt thermoregulatory behaviour and basked in the open out of cover for a greater proportion of the time. They also displayed a greater range of thermoregulatory behavioural strategies. Adders tended to emerge earlier and submerge later, emerged on a greater number of days, displayed postural thermoregulatory behaviour (dorso-ventral flattening, alteration of body aspect, body coiling), adjusted the degree of body area exposed, selected basking sites (avoidance of shaded areas, slope direction) and utilised thigmothermal strategies.

Thus adders used a variety of strategies based on the utilisation of the thermal environment in time and space. Avery (1978) suggested that the maintenance of high body temperatures by reptiles in cool climates results in a considerable proportion of their time engaged in thermoregulatory activities. The result of this is a cost in the form of less time spent on feeding. For adders, it is possible that feeding and thermoregulation are combined. A sit-and-wait foraging strategy would mean that they could bask or mosaic bask in a particular site, maintaining body temperatures that permit optimal predatory success (e.g. detection, strike and handling of potential prey).

Adders are distributed as far north as the Arctic Circle. In such areas, ambient temperatures are often likely to be much lower than an adder's selected body temperatures during activity periods. However, sunny periods will result in high operative temperatures in some microhabitats and adders could achieve high body temperatures through basking. If they were to widely forage for prey, the body temperatures would soon drop once they were in areas of cooler operative temperatures. Predatory success would therefore be affected, especially as their main prey items tend to be endothermic and therefore maintain body temperatures more independent of environmental conditions. For snakes, sit-and-wait foraging might be expected to be a more effective means of predation in colder climates.

Saint Girons (1978) commented on the degree of thermoregulatory behaviour displayed by adders compared with other Vipera species, even to the detriment of their safety. In the present study they were seen basking in the open on a much greater proportion of occasions than grass snakes or smooth snakes, although they did bask within close proximity of a refuge. They basked earlier when body temperatures were lower and therefore evasive reactions would be expected to be poorer. On one occasion an adder was observed slowly moving out of an overnight refuge at a body temperature of only 2.8°C. Adders are the only venomous British species and are therefore best able to defend themselves. Like grass snakes, they also seem to be able to detect the presence of predators approaching (e.g. humans) and can therefore retreat under cover in time to avoid danger. Smooth snakes, however, appear to be less able to detect potential danger as they were often caught in the field before they even moved. Adders may also benefit by a more effective cryptic coloration than the other 2 species, but this does not explain their tendency to bask more in the open when compared with other European vipers which have similar markings (Saint Girons 1978).

Smooth snakes had higher mean selected body temperatures than grass snakes in the outdoor vivaria (although slightly lower in the laboratory) but lower body temperatures than adders. They also displayed greater temporal utilisation of thermally unlimiting conditions than grass snakes. They were found to be a heliothermic species capable of very precise thermoregulation (the standard deviation of the selected temperatures calculated from plateau body temperatures was lowest for smooth snakes in the laboratory and the outdoor vivaria) but which tended to be highly cryptic. Mosaic basking was seen far more often than basking in this species. In addition to altering the degree of body area exposed during basking/mosaic basking behaviour, they also altered body coil postures, selected sites on the basis of slope direction, avoided shaded areas, and utilised thigmothermal strategies.

Movement by smooth snakes may have been under cover and therefore more extensive than was observed in the outdoor vivaria but the laboratory investigation supported the view that such behaviour was generally limited. The reliance on cover by smooth snakes may be an important factor in the their distribution. Vegetation may provide a certain degree of protection from predators (especially aerial predators) but there is a possible cost in terms of thermal gain when utilising mosaic basking behaviour, especially when conditions are thermally limiting. This may be an increasingly significant cost at higher latitudes. The alternative behavioural strategy would be to bask in the open to a greater extent but predatory risks may make this unjustifiable.

Grass snakes had the lowest mean selected body temperature in the outdoor vivaria and attained the lowest temperatures during thermally unlimiting conditions in the outdoor vivaria and the laboratory. They displayed a generally wider range of activity temperatures than smooth snakes, and a lower range than adders during thermally unlimiting conditions in the outdoor vivaria.

Movement behaviour in grass snakes was extensive, especially when conditions were thermally unlimiting. This was related to their widely-foraging lifestyle. Behavioural thermoregulation involved body coil posture alterations, body aspect adjustment, adjustment of body area exposed and basking/mosaic basking site selection (slope and avoidance of shaded areas). Thigmothermal behaviour was also probably used to a certain extent, and a crude form of shuttling heliothermy employed. The latter was observed in the form of periods of basking/mosaic basking behaviour used to ‘boost’ body temperatures between periods of movement behaviour.

Widely-foraging behaviour is likely to result in snakes passing through various microhabitats and microclimates. During conditions of warm ambient temperatures and sunny weather, body temperatures may be kept relatively constant. During conditions where varying operative temperatures can occur (e.g. cold, sunny days) the effect on reptile body temperatures can be imposed eurythermy. At higher latitudes the latter situation is likely to be present for a greater proportion of the time. In such circumstances widely-foraging snakes might have to restrict movements to areas of high operative temperatures but, as these would tend to be in sunny, exposed areas, they would be particularly conspicuous to potential predators. An alternative behavioural strategy would be to forage through areas of low operative temperature but at the cost of less predatory success as a result of lower body temperatures. Basking frequency and duration could be increased to help maintain higher temperatures but then less time would be available for foraging. Thus thermal factors and the relationship with the physical environment are likely to be important factors in the distribution of grass snakes and the other species.

6.4. Cold Adaptation and Geographic Distribution

The body temperatures and therefore the behaviour and general ecology of reptiles are tightly coupled with the thermal environment. Those species which inhabit higher latitudes and altitudes have to deal with colder thermal environments. As most physiological processes tend to be optimal around certain body temperatures (usually estimated by selected or 'preferred' body temperatures), it might be expected for reptiles from higher latitudes to have lower and more variable optimal temperatures than those from lower latitudes. This would be reflected in reptiles from higher latitudes having lower selected body temperatures and more variable activity temperatures than those from low latitudes, although resulting in similar levels of performance.

In Section 6.3 above it was noted that the selected body temperatures of snakes appear to show relative uniformity (Lillywhite 1987). The selected body temperatures that Saint Girons (1978) measured for adders and other Vipera species were all very similar, and close to those measured for adders in the present study. Saint Girons studied different Vipera species from varying latitudes and altitudes but as selected and maximum tolerated temperatures did not vary, he concluded that other factors (probably temperature-related) played a role in their distribution.

Spellerberg (1976) considered the lower selected body temperatures ('mean voluntary' and 'voluntary range') of smooth snakes compared to those of the closely related Coronella girondica, a Mediterranean species, to represent a possible adaptation to the colder temperatures of the more northern climatic regions. In the present study the mean selected body temperature of smooth snakes was found to be similar to that measured by Spellerberg for Coronella girondica in the laboratory. However, different methodological techniques were used and so comparisons between the two studies should be treated cautiously. In the same study, Spellerberg compared grass snakes (subspecies Natrix natrix helvetica) with Natrix maura (Mediterranean climatic region). The body temperatures showed the same trend as the Coronella species, with the grass snakes having lower selected body temperatures. Davies and Bennett (1981) measured the acute resting oxygen consumption rates of 27°C-acclimated juveniles of the same species at temperatures from 5-27°C. They suggested that rate-temperature curves derived from their results showed that grass snakes had genotypically differentiated metabolic adaptations to cold climatic conditions. However, Hailey et al. (1982) and Hailey and Davies (1986) considered that the differences may have been the result of different lifestyles between the two species, rather than an effect of latitude. In the latter study, a comparison was made between the activity metabolism of low and high latitude grass snakes (cool temperate Natrix natrix helvetica and warm temperate Natrix natrix persa). Natrix natrix helvetica was found to have elevated and less temperature sensitive aerobic scope which would be useful if they were active with a lower mean and greater range of optimal temperatures. However, an examination by Hailey and Davies (1986) of available data on the activity temperatures of widely foraging natricine snakes indicated no apparent pattern of latitudinal variation. Mean activity temperatures were calculated to be 26°C. In the present study mean activity body temperatures in the outdoor vivaria were slightly higher than 26°C during thermally unlimiting conditions.

The mean selected body temperatures of the three British snakes in the present study do not seem to suggest any patterns of cold adaptation when compared with the few reports of body temperatures measured for the same or closely related species from other geographic areas. It is difficult, however, to make proper comparisons between studies which have used slightly different criteria and methodologies to measure body temperatures. One might expect a comparison between the three British species to show that the species found at the more northerly latitudes to have lower selected body temperatures. However, adders (the most northerly species) actually have higher mean selected body temperatures than grass snakes or smooth snakes. A possible adaptation to colder environments was shown when adders were observed active at the lowest body temperatures, with a minimum measurement of 2.8°C in the outdoor vivaria. A simple comparison between the three species should also take into account that their ecological lifestyles vary and that body temperatures and thermal sensitivity to physiological processes will also be influenced by such factors as well as latitudinal factors.

Some studies have suggested that the thermal sensitivity of physiological processes actually evolve very slowly (Cloudsley-Thompson 1971, Van Damme et al. 1990). These have been described as indicating a 'static' view (as opposed to a 'labile' view, Hertz et al. 1983) of the evolution of thermal sensitivity. Huey (1982) considered that this was the apparent general pattern for most lizards, although thermal physiology was more labile in certain species (Huey and Webster 1976).

Behavioural thermoregulation is believed to be a primary mechanism through which reptiles compensate for geographic variations in the thermal environment (Avery 1978). The fact that adders appear to display the most sophisticated repertoire of thermoregulatory behaviour, and thermoregulate for longer periods and at greater risk from predation, suggests it is likely to be an important factor in their more northerly distribution compared to the other British species (as discussed in the previous section). Other factors, such as mode of reproduction, sexual cycles and feeding strategies, also vary between the three species and will contribute to better adaptation to cold thermal environments. Spellerberg (1975) and Yalden (1980) also considered that historical factors may have played a role in the restricting the distribution of the smooth snake in Britain. However, the scope of the present study has been to examine the body temperatures of the three species and to relate them to general behavioural and behavioural thermoregulatory strategies.

6.5. Conservation and Management

A strategy aimed at the conservation and management of a species must be based around an understanding of its general ecology. For ectotherms, such as snakes, thermal ecological factors are of great importance because the maintenance of suitable body temperatures is necessary for other physiological processes to proceed effectively. For example, circumstances could arise where the translocation of snakes might be considered a useful exercise. The new site could be at the same latitude, altitude and apparently provide the necessary ecological requirements for a successful translocation to take place. The general climatic conditions may be very similar, but the operative temperatures available to the snakes at a microhabitat level may actually be restrictive in terms of achieving selected and activity body temperatures. The costs of thermoregulation in such an environment may be high, possibly resulting in reduced reproductive success and higher mortality. Operative temperatures available at a potential reintroduction site could be assessed using animal thermometers (models).

The provision of a range of microhabitats resulting in a variety of operative temperatures available to the snakes would appear to be an important requirement for effective thermoregulation. The use of vegetative cover was observed to be frequently utilised by all three species as a means of thermoregulation. On a day of thermally unlimiting conditions, a heterogeneous vegetative structure would allow snakes to bask or mosaic bask and alter the degree of body area exposed to direct solar radiation. All three species inhabit heathlands and heather of a medium height and uneven structure would probably be most thermally heterogeneous. Patchy, open areas between clumps would allow fully exposed basking. Areas of dense, mature heather would provide shelter during thermally poor conditions (therefore reducing heat loss) and full shade during very hot conditions. This type of habitat would reduce the need to make energetically costly shuttling movements between sunny and shaded areas. Theoretically, mosaic basking is less costly in terms of energy expenditure.

As well as providing thermal benefits, vegetative cover also provides protection from predators. Even when the snakes were observed basking in the open in the outdoor vivaria or in the field, they were always within easy reach of a refuge into which they could retreat at the sign of danger. The ideal location for a basking snake is where they are totally exposed to the sun but beneath overhanging vegetation which might diminish the chance of being seen by an aerial predator. Snakes were occasionally seen in such positions in the outdoor vivaria and in the field. Grass snakes were frequently observed to use bramble (Rubus sp.) bushes at different field localities during mosaic basking behaviour. Even when basking they were usually at the very edge of the bush or in a gap within the bush. Adders were also observed to use bramble, although to a lesser extent. Snakes basked on the sunny side of bushes and so clumps of vegetation (e.g. brambles) with different edges exposed to the sun throughout the day meant that the snakes could alter basking sites likewise. Numerous, dense 'islands' and interconnecting corridors of cover provide snakes with refuges from predation, areas for mosaic basking, and a range of edges at different orientations to the sun.

Gent (1988) suggested that heathland burning should be restricted to relatively small areas thus ensuring that sufficient areas of cover nearby for all ground-dwelling fauna and a source for subsequent recolonisation. The provision of sufficient and adequate cover in all habitat types in which snakes live would appear to be very important for their survival.

Snakes often seem to inhabit areas close to trees. Forest rides may be managed by ensuring that they are wide enough to provide sufficient sunlight on the ground level to permit snakes to achieve selected and activity body temperatures over a long enough time. Dent (1986) considered that a ride width of 5 m was sufficient for populations of Lacerta agilis to persist. At Site 5 in the present study, adders were commonly found at the junctions of forest rides where trees had been removed except for a few isolated oaks. These relatively open areas also had patchy, grass tussocks providing cover on the ground. However, the snakes became increasingly difficult to find throughout the year which may have been due to the ground vegetation becoming very high and overgrown. The forest rides also became very overgrown, although they were rich in butterflies and other invertebrates. The area may have become too shaded for adders to bask effectively and so some form of management would have been beneficial for the snakes. Cutting areas of dense ground vegetation, especially on northern sides of forest rides (which receive the most sun), will provide bask sites for the snakes.

Other practical management which could improve the thermal environment of snakes might include the construction of south- facing banks with vegetative cover on which the snakes could bask. Ditches also provide slopes and snakes were sometimes observed utilising these in the field. Uneven surfaces to the slopes and patchy vegetation would provide a range of microsites to allow finer adjustment of basking behaviour. Easier to construct would be woodpiles. They could be angled to face the sun and designed so that snakes basking on them could rapidly retreat into the interior of the pile in the event of danger. They could also form sites for night-time or even, if sufficiently sheltered, winter submergence. The small woodpile used in the outdoor vivarium was occasionally used as a basking or mosaic basking site for all three snake species and adders have been observed using woodpiles in the field (pers.ob.).

As well as providing adequate thermal environments, management of habitat for snakes also has to take other factors into account. Nature reserve size and shape, the provision of corridors to link habitat fragments (to reduce the deleterious effects of isolation), the provision of egg-laying sites (e.g. for grass snakes), management of prey species, human and domestic animal disturbance, and consideration for other animal and plant species are examples. Successful conservation also depends upon protective and enforceable legislation, cooperation of interested parties and the raising of public awareness. Conservation is heavily dependent on the raising of money and support so it is important that effective education should be used to rid people of the prejudices that many have towards snakes.

6.6. Additional and Further Research

During the present study, a number of other investigations were undertaken but which have not been incorporated into the thesis due to a shortage of time for analysis and limits of time for writing. These investigations were supplementary to the main investigations which have been presented in the thesis.

On the numerous occasions when excursions into the field were made, details of snake observations were made. These excursions were generally carried out in conjunction with the capture or return of specimens for the purposes of the laboratory or outdoor vivaria experiments. Snakes were measured, scale clipped and body markings recorded. Measurements of behavioural, climatic and microhabitat details were taken and all the data recorded on field cards. About 150 fieldcards were completed. In addition, details of every field trip were taken so that the number of snake sightings could be related to climatic variables. It was the aim of the investigation to provide information on the thermal ecology of snakes in their natural habitat, and to compare results with those of the outdoor vivaria experiments.

The importance of cover in the thermoregulatory behaviour was investigated in a series of laboratory experiments. It was felt that the use of cover may be related to crypsis and the avoidance of predators. Huey and Slatkin (1976) also considered that predation could influence thermoregulatory behaviour. To examine this further, a simple choice-chamber arrangement was set-up in the arena used for the laboratory experiments. One half of the arena of the arena was provided with a poor heat source (thermally limiting) and a nearby refuge, the other with a good heat source (thermally unlimiting) and a distant refuge. The risk of possible predation was enforced by having somebody entering the arena at intervals and waving their arms, thus disturbing the snake.

The costs and benefits of each side of the arena differed for the snakes. Basking on the side with the poor heat source would have meant slow heating rates and difficulty in attaining selected body temperatures, but good protection from potential predation. The other side provided a good heat source but at the risk of greater exposure to predation. The side with the poor heat source was connected to a variac so that heat intensity could be adjusted. Thus a threshold for a shift in behaviour (from one side of the arena to the other) could be identified. It was hypothesized that smooth snakes, because of their preference for cover in the field, would 'sacrifice' thermal benefits for the safety of cover to a greater degree than the other two species. Adders were expected to opt for the more exposed but thermally beneficial site. Only a few of these experiments were completed and technical problems affected some of them. However, it would be an interesting project to continue. Intra-specific variation could be investigated as well, for example the comparison of gravid and non-gravid females.

Another investigation involved the detailed study of body posture during basking behaviour. Individual snakes were placed in a small arena and a heatlamp turned on. As the animals heated up, body temperatures were periodically measured (using biotelemetric techniques) and close-up photographs taken. The photographs will be studied to relate the body area exposed with body temperatures. The amount of body area exposed was adjusted through body coiling postures and (in the case of adders) dorso-ventral flattening.

Many previous studies of snake and general reptilian thermal ecology have tended to be biased towards periods when snakes are active and easier to locate. The increased use of biotelemetry has helped to reduce such a bias. Snakes, especially those from higher latitudes, are inactive for large proportions of the time and therefore a deeper understanding of their thermal ecology during inactivity is required for such an important aspect of their lives.

Comparing body temperatures of snakes recorded during field conditions can result in mistaken assumptions with regards to selected body temperatures. Differences attributed to behaviour and/or physiological factors may, in fact, be the result of thermally limiting conditions. The use of models to estimate operative temperatures provide an easy way of determining the thermal environment. Their application in thermal ecological studies should be encouraged.

There has been a distinct bias towards the study of behavioural strategies utilised by lizards for the purposes of thermoregulation. This is probably due to the more secretive nature of snakes, and the belief that behavioural thermoregulation in this group is not particularly sophisticated. Although there have been a number of studies on snake behavioural thermoregulation using temperature data, there has been extremely few quantitative investigations involving direct observations of snake behaviour. Further studies involving direct behavioural observations would be useful for comparative purposes. Observations of snake behaviour in the field may be difficult and so the use of outdoor vivaria may be the best alternative.

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