English Nature Science

No. 27
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proceedings of a seminar held on
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ENGLISH NATURE

FROG*life*

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Jim Foster
and
Tony Gent
(editors)

Foster, J. & Gent, T. (1996) Reptile survey methods : proceedings of a seminar held on
7 November 1995 at the Zoological Society of London's meeting rooms, Regent's park, London :
English Nature Science series no. 27

Errata :

Contents section : "Howard Innes" should be spelt "Howard Inns"

Page 146 : "Reading, C.J. (1990)" should read "Reading C.J. (1996)"

Contents

Appendices

Introduction

Jim Foster* and Tony Gent[1]
*Herpetofauna Conservation International Ltd and [1]English Nature

Surveying for reptiles can be challenging. This is perhaps the main reason for the largely incomplete knowledge of reptile distributions at a local level. In addition, the confidence with which one can interpret data collected from reptile surveys is generally lacking; what do the observations mean in terms of absolute or relative population sizes and indeed, how reliable are any methods for detecting presence or for indicating the absence of a species? This uncertainty is problematic when trying to compare between sites (perhaps to rank them in order of population sizes) or to compare between samples at one site to show how population sizes vary over time. Changes in population parameters can be related to management (or lack of it) and reveal short term or long term trends that may identify necessary conservation actions. Such data may also be valuable for developing policy or for justifying safeguarding certain sites.

It would be of great benefit for those involved with the conservation of reptiles to be able to survey sites and have some confidence in being able to assess their data. To this end there is a need to develop a survey method, or suite of survey methods, that allow interpretation of the data in an objective and comparative way. The fact that experienced field herpetologists often ascribe a basic evaluation to reptile sites based largely on counts indicates that an objective method is potentially achievable. Such an approach might aim to provide a totally unbiased sample on a site to allow statistical extrapolation. Alternatively it may aim to enhance observations of reptiles such that a maximum number of individuals can be seen. In other cases precise locations of individuals are needed, perhaps to relate to habitat use or for behavioural study. In some cases observers may aim for a method that allows rigorous consistency between visits to allow direct comparison between sites or within a site. Some field workers will argue that a high degree of skill and field craft with a 'feeling' towards the needs of reptiles is a pre-requisite for successful survey, and even then a specialist interpretation is needed to say what they mean. Others would argue that methods that can be applied regardless of ability and that can provide simple numeric comparison are needed to increase the amount of data collected and allow much wider assessment of reptile populations. Although the ecology and behaviour of reptiles mean that they are difficult to survey, our knowledge of these species has advanced considerably over the last 20 or so years.

Opinions on which approach to take vary and may be influenced by both theoretical and pragmatic considerations. For example, survey needs to be sufficient in terms of effort to ensure adequate data are collected but needs to guard against excessive effort, disturbance to animals or damage to their habitats. Indeed the actual objectives of different surveys will vary and these will affect the chosen method and should be the determining factor in deciding which approach to use. Reptile survey is being undertaken countrywide. Data collected by different observers, though, are rarely comparable; indeed there are remarkably few attempts at making such comparisons. In some cases it is even debatable whether the data obtained can serve the function for which it was collected. Can, for example, repeat visits to a reptile site really provide information that allows population changes to be estimated? Do methods employed in some areas allow legitimate assessment of habitat use or are the biases in the way the data are collected so substantial that they preclude such analysis?

With a view to looking at these issues a seminar was held to which a number of herpetologists involved with reptile survey were invited. Those invited represented professional scientists

and nature conservationists, students and experienced amateur herpetologists. The objective of the seminar was to exchange ideas and to report on current and recently undertaken work.

Such an exchange of views was considered an important first step in developing further a standard methodology or some form of standardisation (or calibration) of method. Indeed it offered an opportunity to discuss whether such standardisation was considered necessary. The length and nature of the papers presented in these proceedings varies. Some papers report on work that is part of a larger project or are summaries of observations that will be reported elsewhere; other papers are fuller and are using this as a vehicle to report on information that will otherwise not be made widely available. We have also included some papers not reported at the seminar where they complement the papers presented or further the objective of the seminar.

This report collates a diversity of opinions and experience, drawing together information pertinent to those wishing to study reptile behaviour and distribution. However, it is not the intention of this report to provide a critique of the work described here. Nor do we attempt in this volume to formulate a method or series of methods to provide a standard for reptile survey. Recommendations for such standard methods will be addressed in due course, and it is hoped that the information contained herein will prove a valuable aid towards that objective.

Main proceedings

A statutory perspective on monitoring reptiles

Steve Gibson
Joint Nature Conservation Committee, Monkstone House, City Road, Peterborough PE1 1JY

The single largest influence on conservation policy in Britain in the next few years will be the Biodiversity Convention.

Article 7 of the Convention states that:

Each contracting party shall, as far as possible and appropriate, for the purposes of *in situ* and *ex situ* conservation, and the sustainable use of components of Biological Diversity, undertake the following:

❑ identify the components of Biological Diversity important for conservation and sustainable use;

❑ monitor through sampling and other techniques the components of biodiversity.

Signatory parties to the convention were required to produce an 'action plan' that laid down how they would meet the requirements of the Convention. Chapter 9 of the UK Governments plan, Biodiversity: the UK action plan, states that the Government and its agencies will:

❑ develop a set of guidelines for standard systems of data collection;

❑ seek to establish baselines for key components of biodiversity;

❑ develop thresholds for conservation action in relation to species population and habitat change.

There are two threads that run through this. These are the need to be able to monitor species and the need to set thresholds of acceptable change.

Conservationists therefore need to know about the biology of species to determine when a change is an insignificant fluctuation or a significant change (increase or decrease). They also need to develop techniques for assessing the status of populations and their habitats and identifying at least pointers to causes of unacceptable change. Finally, recommendations for remedial action will aid in policy formulation. There is also the issue of improving the current status of species. Monitoring plays a part here as well since it provides a means of assessing the effectiveness of any rehabilitation techniques being deployed.

The answers to some of the above, particularly the techniques, depend upon the geographical scale at which information is needed, and the policy questions that need to be answered. Thus different techniques will be necessary to determine national and regional status and inform SSSI 'areas of search' and planning to those used to quantify specific populations for designation purposes.

The ultimate goal for conservationists is to produce a cost-effective monitoring system for reptiles that identifies when real changes are occurring, why and where, and is able to provide advice for policy makers, and to develop a system for identifying important sites in need of greater protection.

Discussion following the talk by Steve Gibson from JNCC on a statutory perspective on reptile survey

Keith Corbett: What should we use as a baseline upon which to measure changes in reptile abundance? Should it be based on today's figures or historical data? If we are going to use today's figures then we overlook the substantial losses of populations and of ranges that have already occurred.

Steve Gibson: The objective of setting a baseline is to determine successive change. Relative changes can be detected by looking at differences in any time-series data collected by a consistent method. Therefore, there is no need to have precise data on population size before implementing a monitoring programme.

For many conservation actions determining current populations as a 'baseline' may be less important than identifying a 'target' population size as a goal to work towards. This 'goal' could then form the basis of monitoring studies.

Tony Gent: If we know what we've got today and decide that we need twice as many, then the baseline figure is worth stating. This will form the basis of the 'success criteria'.

Training courses and translating survey data into conservation

Jim Foster
Froglife (Herpetofauna Conservation International Ltd), Triton House, Bramfield, Halesworth, Suffolk IP19 9AE

1.   Reptile survey: what's the problem?

Snakes and lizards are challenging to survey for a variety of reasons. They tend to be secretive, fast-moving and cryptically coloured, may be inactive and inaccessible for long periods, occur at low population densities, and unlike amphibians there is usually no marked seasonal breeding aggregation. Combined with the fact that reptiles do not generally have the high profile accorded to some other species groups, this means that the local distribution and status of reptiles is often inadequately understood or documented.

The lack of this information has important consequences in terms of the conservation of reptiles. Sites are lost because no knowledge of reptiles existed before a change in land use or beacuse inadequate survey methods were used; habitat management may not take reptiles into account if their presence or use of a site is unclear.

The fact that there has been no adequate guidance on reptile survey has meant that even those with a keen interest in reptiles have faced problems in terms of maximising time spent surveying, and making comparisons within and between sites. Although the ecology and behaviour of reptiles results in their being difficult to survey, a standard methodology (or guidelines) should be achievable which allows objective assessment of reptile populations. The exact format, precision and applicability of such a methodology will be discussed in the remainder of this seminar. Once this has been agreed upon, it needs to be promoted for wide use amongst those involved in reptile conservation. Furthermore, the ways in which survey data can be transformed into conservation on the ground also need promoting, since the status of reptiles and certain aspects of their ecology mean that this is not always straightforward.

2.   What information do we need from reptile surveys?

Those conducting surveys for reptiles are usually wishing to fulfill one or more of the following objectives:

a.   to determine the presence or absence of reptiles;
b.   to determine an indication of population size (either absolute, or - more realistically - relative population size);
c.   to determine changes in the size (or other character) of a population [monitoring].

The methodologies used to reach these objectives may differ, and there are implications in terms of the amount of resources and time needed to fulfill them.

3.   Training courses

There is clearly a need for a standard, recognised training course syllabus. The contents should be easy to follow, unambiguous and factually correct. Froglife have been developing

and gradually updating such a course since 1994, primarily for use through the Herpetofauna Groups of Britain and Ireland network.

Who needs to know?

Various categories of organisation can benefit from an understanding of reptile survey techniques and their application to conservation. For each group, the information required may be subtly different according to their aims and remit. Promoting sound guidelines on reptile survey can be done in various ways. Perhaps the two most effective methods are via written guidance which can be easily circulated, or by dedicated training courses delivered to appropriate groups. The principal groups who have an interest in reptile survey are:

a. *Volunteers* (members of local amphibian and reptile groups, Wildlife Trusts, etc). Mainly to survey their area of coverage, to compile lists of the most important sites and those under threat, etc;

b. *Reserve wardens/ managers*. To monitor resident populations and assess changes in status (perhaps linked to management regimes), to assess the success of reintroductions, etc;

c. *Environmental consultants*. Most commonly, to determine presence/absence on a given site under consideration for a change in land use; also determining relative importance of site, key areas within a site, etc.

Format and contents

The course consists of a lecture-style presentation, with slides to demostrate key points. Course notes are provided. A field visit to put the techniques into practice following the main session is also recommended; although the success of these visits in terms of finding the animals is unpredictable (since courses are generally arranged far in advance), they are indispensable for pointing out key habitat features and certain survey techniques.

The main components of the course are: the purpose of reptile surveys; identification; biology, ecology and behaviour; planning a survey; survey techniques and survey effort; assessing site importance; translating survey results into conservation; legislation; welfare considerations; safety and code of conduct. A copy of the course notes is provided in Appendix 3.

Up to the time of writing, this course has been delivered to many local amphibian and reptile groups, as well as a few local authority ranger services involved in specific reptile surveys. The course content is modified in the light of feedback from participants as well as wider developments in conservation. It is hoped that this will provide the model for the promotion of standard techniques for reptile survey, at least within the voluntary sector. This will not only promote the most effective survey methods, but will also help to ensure that surveys conducted in different regions will be more comparable.

4.   Using survey data for conservation

At the most fundamental level, all sightings arising from reptile surveys should be converted into records and sent to the appropriate local recorder/records centre, which usually means the local reptile and amphibian group, county museum, environmental records centre or similar. It is important that this local recorder also copies the information to the national repository for records (the Biological Records Centre). This simple action can result from the most basic of surveys (or even chance sightings), so long as there is positive species

identification and the location is known. Depending on local circumstances, records will allow various further uses of the data, including to flag up proposed threats in the planning process; use in compiling of regional atlases; use for compiling lists of important sites (see below); assisting with habitat management plans; helping to determine trends in populations locally; helping to determine habitat associations locally; assisting with enquiries about where reptiles are found locally.

The effectiveness of many of the functions listed above will depend to a large degree on the way in which data is stored, and the way in which it is accessed, on a local level. The data needs to be available (directly or indirectly) to various organisations, most notably the local planning authority. The most effective, and increasingly the most popular, way for data to be stored is on a personal computer running a database such as Recorder. The use of biological records in general will not be dealt with in depth here, but direct applications of survey results are covered below.

If the information resulting from the survey amounts to more than a few records, further possibilities for analysis and conservation action arise. It is often useful to discern areas of special importance on a particular site. For example, given sufficient sightings in relation to habitat features, it may be possible to identify hibernacula, favoured foraging and basking areas, breeding sites (especially for grass snakes) or other seasonal changes in use of the habitat. These, along with other important areas, of the site, can be studied more closely with a detailed map showing topography and habitat type overlayed with reptile sightings. In terms of the area of the site occupied, features such as hibernacula or breeding sites may have a disproportionate significance for the integrity of the resident reptile population. It is therefore helpful to make a note of these features on any records made.

Habitat management can have profound effects on reptile populations, and carefully planned surveys can help to assist with the production of management plans or to assess their effectiveness whilst in operation. A substantial and protracted decrease in numbers, a lack of breeding success, or skewed demographic profile detected by monitoring may offer evidence of unsympathetic management. Conversely, increased breeding success etc may show that the population is responding positively to habitat manipulation. Given appropriate historical data concerning reptiles on a particular site, it may even be possible to deduce the effects of management in previous years. It is worth reiterating however that in terms of survey, reptiles do tend to be unpredictable and one should be cautious about deriving causal relationships between modifications to the site and apparent population changes as indicated by monitoring.

Survey results can be used to help rank sites in terms of their importance on a local or regional level. This can be useful in terms of prioritising conservation resources (for example, allocating valuable management time and resources to sites in particular need). Ideally, it can also lead to a system whereby locally important sites can be given designations so that they are recognised in the planning system. Adopting this approach can be extremely beneficial for assemblages of common reptiles in particular, since these species are not afforded any degree of habitat protection in law. All counties (or appropriate administrative area) have a system for designating notable wildlife sites which do not meet national criteria (or for which notification has not occurred), but unfortunately reptiles are very rarely considered. Compiling lists of notable reptile sites can feed into existing designation initiatives to ensure that reptile interest is flagged up in the planning process. A model for this system has been developed by Froglife, including guideline criteria for site selection (see section on Key Reptile Site Register in Appendix 3).

Thermal ecology 1: Thermal ecology of reptiles and implication for survey and monitoring

Martin J Gaywood[1] and Ian F Spellerberg[2]
[1]Scottish Natural Heritage, Research Advisory Services Directorate, 2 Anderson Place, Edinburgh EH6 5NP and [2]Centre for Resource Management, PO Box 56, Lincoln University, Canterbury, New Zealand

Abstract

A brief summary of reptile thermal ecology is provided and its relevance to the surveying of reptiles discussed. Definitions of key terms commonly used in the field of thermal ecology are given.

The results of a case study on the thermal ecology of the adder *Vipera berus*, grass snake *Natrix natrix* and smooth snake *Coronella austriaca* illustrates the difficulty of determining when thermal environmental conditions may limit reptiles from reaching selected body temperatures. The use of physical models or 'animal thermometers' to estimate operative temperatures is described.

Physiological performances of reptiles vary with body temperature and therefore this affects their overall performance and fitness. The thermal environment can have a significant effect on reptile behaviour and this should be taken into account in devising a survey methodology. Factors that should be considered in producing a standardised survey methodology are discussed.

1. Introduction

Reptiles are ectothermic, that is they depend on external sources of heat to thermoregulate. Most species of reptiles have complex behaviour patterns which have evolved to ensure that they can exploit heat sources. There is therefore an inextricable link between the thermal environment and reptile physiology and behaviour.

Most people, if asked, would suggest that warm and sunny weather might provide the best conditions to see a reptile in the British countryside. Experienced herpetologists may go further and provide a more detailed response, for example suggesting cloud cover conditions and times of the day. This illustrates that understanding the thermal ecology of reptiles helps surveyors identify those periods when reptiles are most likely to be seen. The purpose of this paper is to provide a background to the subject of thermal ecology and to indicate its relevance and the implications to the surveying of reptiles.

There is an extensive terminology used in the field of thermal ecology and reptile thermoregulation, much of which is often used inaccurately and inconsistently. The following section attempts to provide a definition of a few key terms. Most of the thermoregulatory terminology is based on Pough and Gans (1982) who produced a unified set of terms in order to reduce confusion.

☐ **Thermoregulation (= temperature regulation):** the maintenance of body temperature within a restricted range despite variation in ambient temperature.

☐ **Thermoconformity (= temperature conformity):** variation in body temperature that parallels variation in the thermal environment.

❏ **Ectothermy:** the mode of thermoregulation in which body temperatures depend primarily on the absorption of heat energy from the environment, ie body heat is derived mainly from external sources (used by reptiles).

❏ **Endothermy:** the mode of thermoregulation in which body temperatures depend on balancing the rate of production of heat by metabolism and its dissipation to the environment, ie body heat is derived mainly from internal sources (used by mammals and birds which tend to have high metabolic rates).

❏ **Heliothermy:** form of ectothermy in which thermoregulation is achieved through basking in the sun.

❏ **Thigmothermy:** form of ectothermy in which thermoregulation is achieved through absorbing heat by contact with warm surfaces.

The terms warm-blooded and cold-blooded tend not to be used in the scientific literature any more as they are archaic and frequently inaccurate, for example body temperatures of some species of lizards during activity may be 5-10°C higher than that of endotherms. Some of the larger reptiles are known to use endothermic means of thermoregulation to a degree, for example the leatherback turtle which can maintain constant, high body temperature through their large body size, low metabolism and use of peripheral tissues as insulation.

It was originally thought that reptiles were thermoconformers and that their body temperatures passively followed those of the environment. However, a series of studies as long ago as 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. These early studies therefore demonstrated that reptiles were able to regulate body temperatures, sometimes with great precision, using behavioural strategies such as heliothermy (ie basking) and thigmothermy (absorbing heat by contact with warm surfaces). Figure 1 shows a thermoregulating reptile maintaining its body temperature significantly higher than the shade air temperature and at a relatively precise level.

Cowles and Bogert (1944) went on to describe a number of discrete temperature ranges or set points of particular significance in reptile biology which can usually be measured only in a laboratory environment. Similar terms are still frequently used today and are listed below and indicated in Figure 2.

Key

●—●—●—● snake body temperature

———— shade air temperature

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

—·—·—·— maximum model temperatures

— — — — minimum model temperatures
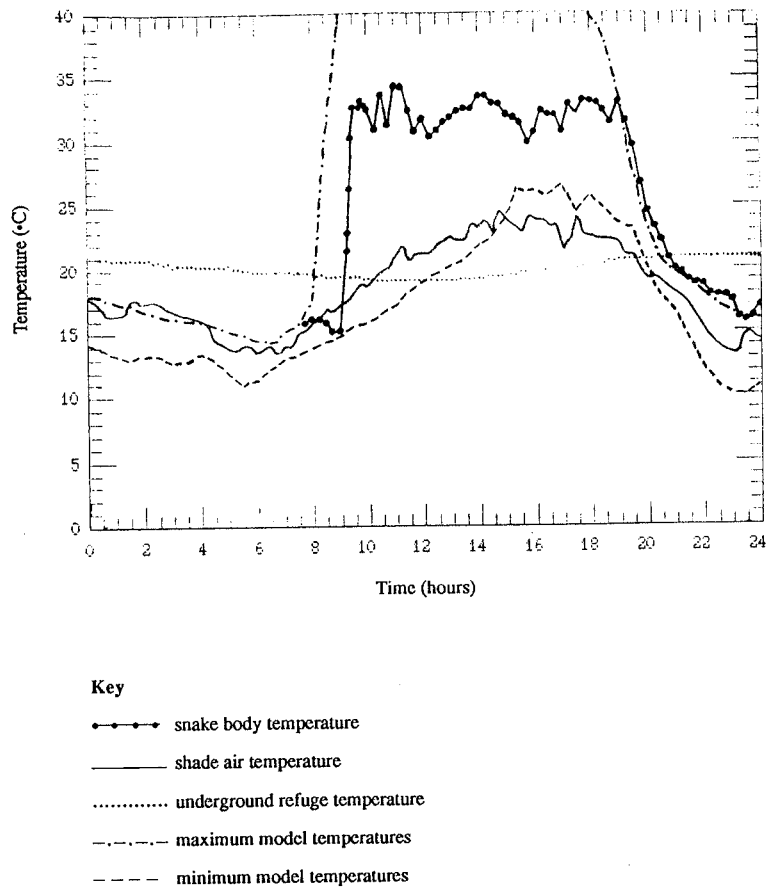
Figure 1: Body temperature pattern of an adder, *Vipera berus*, on a sunny day. Note the distinct heating phase, followed by a period of precise thermoregulation (the 'plateau phase') and then the cooling phase of the snakes body temperature. An explanation of 'model temperatures' is provided in Sections 3.2-3.4. (From Gaywood 1990).
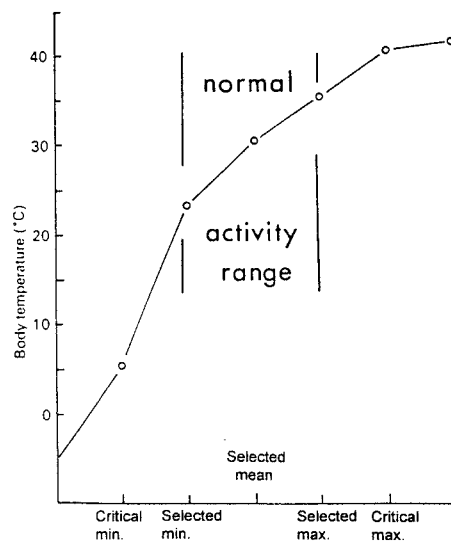
Figure 2. Graphic representation of the ranges of possible body temperatures for a hypothetical reptile. (Adapted from Spellerberg 1982).

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Critical minimum temperature: the low body temperature at which a reptile loses its power of locomotion and is thus an ecologically lethal temperature if it has not found shelter.

Selected minimum temperature (= voluntary minimum or minimum tolerated): the body temperature at which a reptile seeks conditions that will raise its body temperature, or conditions which will protect it from very low ambient temperatures.

Selected body temperature range: this is the range of body temperatures between the selected minimum and selected maximum temperatures. They mark the extremes of the body temperatures maintained by an ectotherm in a laboratory temperature gradient or equivalent apparatus which provides conditions that would permit an animal to extend its body temperature above and below the activity temperature range.

Activity temperature range (= normal activity range): the body temperatures at which a free-ranging animal engages in its ordinary routine.

Selected maximum temperature (= voluntary maximum or maximum tolerated): the body temperature at which a reptile avoids conditions that will further raise its body temperature.

Critical maximum temperature: the high body temperature at which a reptile loses its power of locomotion and is thus an ecologically lethal temperature if it has not found shelter.

These temperatures categories will tend to vary between different species and also within a species depending on physiological condition. Some temperature categories are frequently used in intra-species and inter-species comparative studies, especially the 'mean selected' body temperature which is the arithmetic mean of the temperatures measured in a selected body temperature range. The terms 'mean voluntary' or 'mean preferred' body temperature or just 'preferred body temperature', are synonymous in some studies but some workers think the latter term has anthropocentric connotations and that it should be avoided. The term 'selected' body temperature will therefore be used in the rest of this paper.

The terminology that should be employed in the case of non-laboratory based work on body temperatures tends to be less clear. Field body temperatures (ie body temperatures recorded in the field) are often recorded but are not directly comparable with body temperatures measured in the laboratory. This is because environmental conditions frequently restrict the ability of a reptile to select a body temperature, particularly in a country with a temperate climate characterised by frequent changes in the weather. For example an adder may have a mean selected temperature of around 32°C in a laboratory thermal gradient, but in a field situation there may simply not be the thermal conditions to permit it to reach 32°C, sometimes for several days on end. Therefore its thermal environment can be restrictive. We will look into this problem in more detail further on.

2.   Why do reptiles thermoregulate?

Physiological performances of reptiles vary with body temperature. At a certain 'optimal' temperature, a particular physiological function will perform most efficiently, for example food digestion, auditory sensitivity and immunological response. This will affect the overall performance of the 'whole-animal' and therefore the fitness of the reptile. Many studies, most of which have been on lizards, have suggested that physiological processes proceed optimally near the mean selected body temperature for many species.

An example is a study from Greece which involved the measurement of movement speeds of grass snakes *Natrix natrix* at 5°C intervals (Hailey and Davies 1986). The highest speeds were

recorded when the snakes had a body temperature of 30°C. The influence of varying temperatures on the gastric digestion of grass snakes (from Poland) has also been investigated (Skoczylas 1970). Digestion rates were measured at 5°C, 15°C, 25°C and 35°C and the fastest rates were recorded at 25°C. At 35°C digestion occurred at the same or a slightly slower rate. In both these studies, the physiological parameters measured were optimal in the region of the mean selected body temperatures measured for grass snakes from the New Forest by Gaywood (1990) .

Another example concerns one of the most intensively studied snake species, the garter snake *Thamnophis elegans*. Various performance parameters of the snake have been measured, such as digestion, crawling speed, swimming and tongue flick rate (Stevenson *et al* 1985, Figure 3), and related to body temperature. In most cases the performances are optimal in the region of their mean selected body temperature of approximately 30°C. Interestingly, swimming performance is optimal across a broader range of temperatures and this may be an advantage to feeding in cold water.
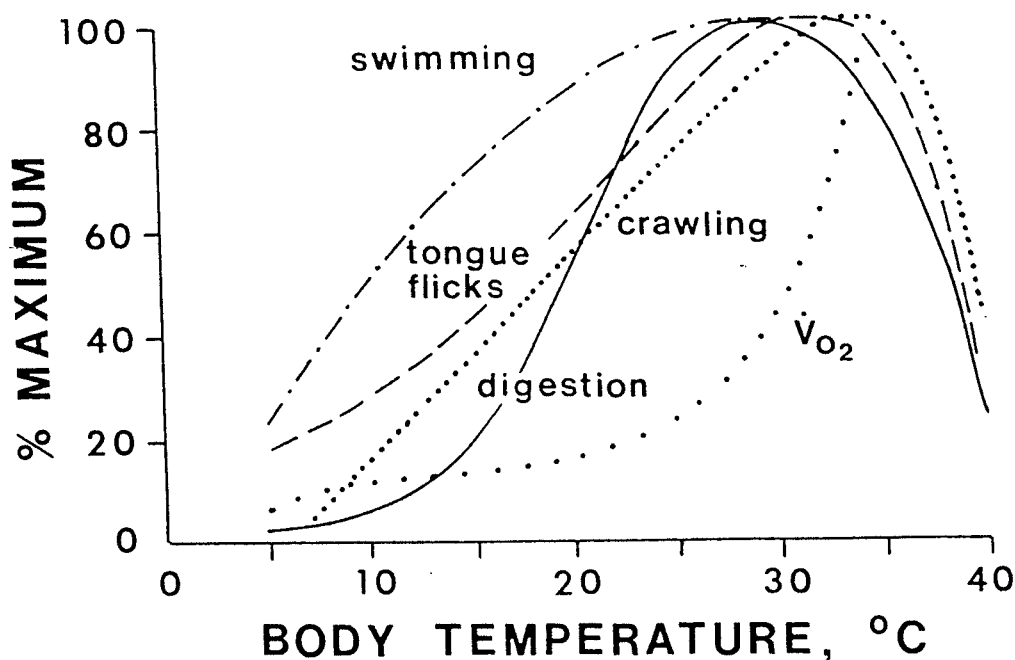
Figure 3. The effects of body temperature on various performance functions, determined from statistical models for the garter snake *Thamnophis elegans*. (From Stevenson *et al* 1985).

In summary, many physiological performance parameters are therefore likely to be greatest when reptiles are able to maintain body temperatures at selected levels. In order to maintain selected body temperatures in a temperate climate such as that of Britain, reptiles have to spend much of their time thermoregulating through behavioural means, such as shuttling

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between sun and shade. Understanding this requirement for reptiles is useful in planning reptile surveys.

3. A case study: Measurements of thermal conditions and body temperatures.

3.1   Introduction

Field surveyors do not need to go as far as defining the selected temperatures of reptiles if they are undertaking straightforward counts, but they do need to know if the thermal conditions are likely to affect their activity. The activity of reptiles is, in turn, related to the visibility of reptiles and consequently will influence the results of survey counts. Any survey procedure which aims to provide data which can be comparable must have certain standardised protocols. In the case of reptile surveying, it is the thermal environmental conditions which are a critical element in any standardisation. The function of this section is to illustrate some of the problems involved in describing the thermal conditions and to make surveyors aware of them.

At the end of section 1 it was stated that calculating selected body temperatures for reptiles from field data can be difficult as it is not always possible to know when the thermal environmental conditions are limiting (eg too cold) for the reptiles. We will illustrate some of the problems involved in the measurement of thermal characteristics outside the laboratory situation with a project which was undertaken on the thermal ecology of the three British snakes (Gaywood 1990). Some of this work was undertaken using snakes kept temporarily captive in outdoor vivaria. A mixture of body temperature recording, environmental temperature recording and behavioural observation was employed during the study.

The problem that had to be faced during the project was determining when and if the thermal environmental conditions were limiting for the snakes. Information was needed which indicated when the thermal conditions were unlimiting thus allowing the snakes the opportunity to select the body temperatures they wanted. Usually some form of mean body temperature measurement is calculated for reptiles in field or vivaria-based studies. However, these are often calculated from a collection of one-off 'spot' body temperature recordings and tend to be lower than corresponding mean selected temperatures obtained from reptiles in laboratory thermal gradients.

To illustrate this, Gent (1988, Gent and Spellerberg this volume) 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 from a laboratory thermal gradient. Unlike the situation in the laboratory temperature gradient, thermal conditions in the field were often limiting and therefore the snakes were sometimes simply unable to maintain higher body temperatures. Thus the mean body temperature of 23.48°C by itself tells us little about the ecology and behaviour of the snake as it is the mean result of many measurements, some recorded when conditions were limiting, some when they were unlimiting. Other factors are also likely to contribute towards such a discrepancy but thermal limitation is likely to be of great importance.

3.2   Operative Temperatures

More information on snake body temperatures can be obtained when they can be related more accurately to the thermal conditions available to the snake. Measurements of only air and substrate temperatures are insufficient to characterise thermal environments. A number of other factors are also important in affecting reptile body temperature levels. The routes of

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heat exchange (through convection, radiation, evaporation and conduction) involve an animal's physiological and morphological characteristics (eg shape, colour, skin relectance/texture and metabolic rate) as well as environmental variables (eg 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 `experienced' 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 one can assume that the metabolic heat production is about equal to the heat loss through the evaporation of water, and so this cancelling out of factors associated with T_Δ leads to $T_b = T_e$. 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. Alternatively, a simpler method is to use 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 one method as to how to make such a physical model.

3.3 Methods

Gaywood (1990) initially made models for all three snake species from copper tubing as the material has a rapid response to temperature change. Copper tubes were cut to the mean body lengths of adult snakes and painted. 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. 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 one type of model for all the vivaria experiments to measure estimates of operative temperatures from a wide range of thermal microhabitats.

Figure 4 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 during identical environmental conditions. The experiment entailed attaching temperature-sensitive transmitters to four snakes. The four snakes were placed in empty, glass tanks positioned in the open on a mild August morning. A snake model was placed in an identical tank positioned nearby. 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 the risks of anaesthesis to the snakes were not acceptable. Instead the snakes tended to move around, searching for a means of escape.
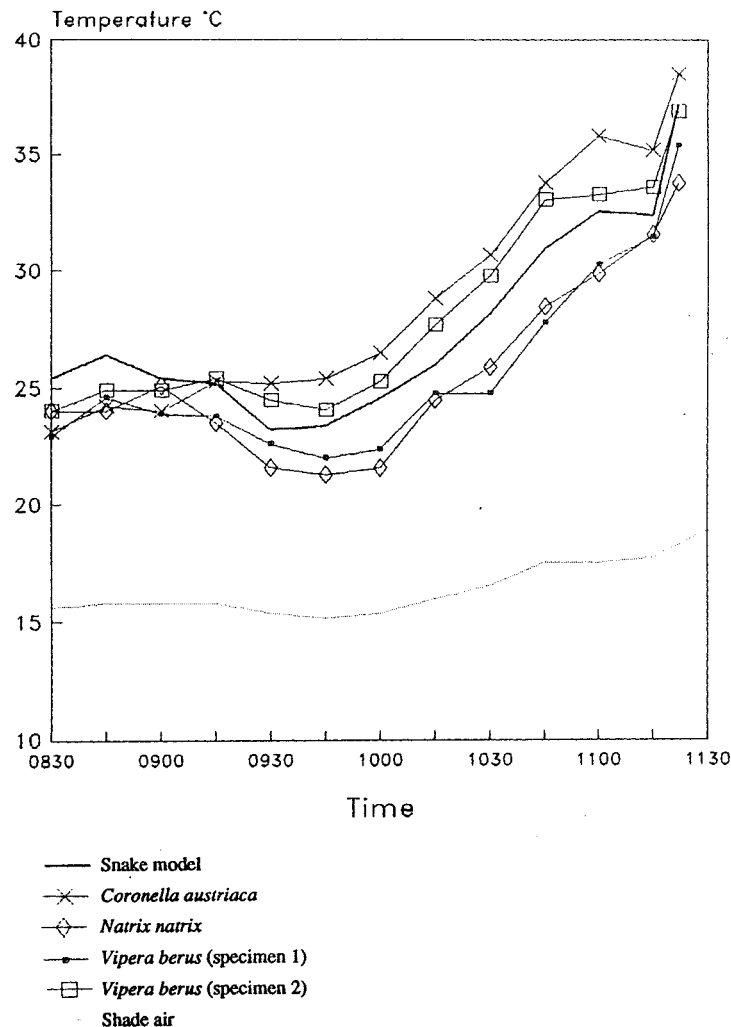

Figure 4. Comparison of body temperatures of a smooth snake *Coronella austriaca*, grass snake *Natrix natrix* and two adders *Vipera berus* with the temperatures of a snake model. (From Gaywood 1990)

During the first half hour shown on the graphs, the sky was overcast. The sun broke through the cloud 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.

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). Note that shade air temperature was shown to be a poor predictor of body temperature.

After this comparative test, the animal thermometer models were placed in various locations around the landscaped vivaria, the aim of which was to estimate what operative temperatures were available to the snakes. A temperature probe was also placed in an

underground refuge. This information was intended to show how the snakes utilised the thermal environment during their normal activity. Environmental temperatures were recorded every 30 minutes from six sites in the outdoor vivaria at any one time by automatic loggers. Snake body temperatures were recorded using thermo-sensitive radio transmitters attached to the snakes (externally mounted with a lead mounting a thermistor bead inserted into the cloaca). Behavioural observations were recorded from behind a hide.

The Squirrel loggers that were available during the project worked by averaging 100 readings over the previous 30 minutes and recording the average value. They had a temperature range 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 over 40°C are lethal and therefore avoided by the snakes.

3.4   Results

The graph illustrated in Figure1 shows the type of body temperatures that were recorded on a day when conditions were not thermally limiting to the snake (from periods when maximum model temperatures measured in the vivaria were always greater than 37°C and were usually much higher).

Note that after an initial heating phase, the snake maintained its body temperatures at a relatively precise level. This latter pattern has been called the 'plateau phase' or the 'thermal preferenda' of body temperatures by some workers, where as Gaywood (1990) called them the 'field selected body temperatures' as they were judged to represent a field equivalent to the selected body temperatures measured in a laboratory thermal gradient.

The mean field selected body temperature calculated for each species were as follows:

Smooth snakes: 30.3°C +/- 1.64 (n=377, median = 30.3°C)
Grass snakes: 29.3°C +/- 2.63 (n=291, median = 29.1°C)
Adders: 33.2°C +/- 1.86 (n=491, median = 33.4°C)

The 95% probability limits of these selected temperatures were calculated for each species, the higher limit of which was used to represent a more precise estimate of the operative temperatures above which the environmental conditions were considered to be thermally unlimiting and would therefore allow snakes to maintain selected body temperatures.

Therefore, the following model temperatures (which were used to estimate the operative temperatures) were used to estimate thermally unlimiting conditions available to snakes in the vivaria:

≥ 34°C for smooth snakes
≥ 35°C for grass snakes
≥ 37°C for adders

Calculating these estimates of the thermal conditions available to snakes (ie either thermally limiting or thermally unlimiting) meant it was possible to analyse the data collected from the outdoor vivaria in such a way as to provide more meaningful conclusions.

Full results of the outdoor vivaria experimental work are provided in Gaywood (1990) but a summary of some points relevant to this discussion are provided below:

i.   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 sunlight periods between April and
      September (note that 'sunlight period' was defined as the phase beginning in the
      morning when at least part of the floor of the vivaria moved out of shadow until the
      time in the evening when the vivaria was totally in shadow; this included periods
      when the sun was behind cloud).

ii.   When periods were thermally unlimiting, adders maintained body temperatures [3]
      mean field selected body temperatures for longer periods than the other two species.
      Smooth snakes in turn, maintained body temperatures [3] mean field selected body
      temperatures for longer periods than grass snakes.

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

iv.   Unsurprisingly, 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 two species during thermally
      unlimiting conditions and smooth snakes had higher body temperatures than grass
      snakes. Significant differences were detected between the data of all three species.

v.   Adders displayed a greater ability to temporally utilise thermally unlimiting
      conditions. They basked in the open for relatively long periods. Adders emerged
      earlier and submerged later, emerged on a greater number of occasions and had a
      wide repertoire of thermoregulatory behaviour (eg dorso-ventral flattening, alteration
      of body aspect, body coiling, adjustment of body area exposure, basking site selection,
      thigmothermy).

vi.   Smooth snakes were also heliothermic and were capable of very precise
      thermoregulation. Mosaic basking (ie basking partly in the shade of vegetation or
      some other form of cover) was observed far more than basking in the open and
      movement was observed less than in the adders or grass snakes. This can be related to
      the smooth snake's cryptic lifestyle.

vii. 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.

3.5   Discussion

One of the results of the project was the observation that snakes are only visible at certain
limited times and their complex behaviour consequently makes them difficult animals to
survey. Some key points that are particularly relevant to reptile surveys can be identified.
First of all there is the observation that for the majority of the time when operative
temperatures were recorded during sunlight hours, the thermal conditions were estimated to
be limiting for the snakes and thus would not allow them to reach their selected body
temperatures. This is quite apart from the night time periods and the period of inactivity
between October and March when thermal conditions will usually be thermally limiting.

Secondly, there are differences in the overall behaviour observed in different reptile species. In the case of the three British snake species, one of the most striking examples of this is the cryptic behaviour of smooth snakes in comparison with the other two species. Adders and grass snakes often engaged in mosaic basking (ie basking partially in the shade of vegetative cover) and when they were seen basking out of shade, it was usually in close proximity to some form of cover to which they could quickly retreat in the event of danger. However, smooth snakes were hardly ever seen in the open, were very often totally hidden and when they did bask it was nearly always partially in the shade of cover and yet they were still able to maintain high body temperatures on warm days.

It is also worth noting that behaviour, especially thermoregulatory behaviour, will also depend on other factors, such as the physiological condition of individual animals. Snakes which have just fed will spend more time basking in order to maintain body temperatures at optimal levels and speed the digestion process. Also, seasonal variation in behaviour can be linked to the reproductive development. Gravid female adders tend to be more visible and bask for longer periods than other adders during late summer and early autumn. Adders of both sexes which have recently emerged from hibernation in late March or early April also tend to bask a lot and be more visible. Behavioural thermoregulation is also believed to be a primary mechanism through which reptiles compensate for geographic variations in the thermal environment (Avery 1978). Reptiles at higher latitudes tend to spend longer periods of time engaged in thermoregulatory activities than those from the warmer conditions of lower latitudes.

4.   Implications for survey/monitoring

One of the aims of this paper was to demonstrate the difficulties in defining the thermal environment for the purposes of standardising surveys. This is also a problem in the survey of animals from other taxa, for example butterflies. The UK Butterfly Monitoring Scheme (Pollard et al 1986) therefore ensures comparable information is collected along butterfly transects by requiring that surveys are undertaken during certain set environmental conditions only;

❏   Recording takes place from the beginning of April until the end of September.

❏   Counts should start after 1045 hrs BST and completed before 1545 hrs.

❏   Counts are not carried out with shade air temperatures below 13ºC.

❏   During periods when shade air temperature is 13-17ºC there must be at least 60% sunshine. When it is above 17ºC it can be sunny or cloudy.

Inevitably there are various potential problems in this type of system but the methodology has to be fairly simple as it has to take into account the practicalities of surveys being undertaken by many people in the field of varying experience across the UK.

In designing a standardised survey methodology for reptiles a number of different issues will have to be taken into account but defining the thermal environment is likely to be one of the most difficult. Experienced herpetologists will know that reptiles are likely to be hidden under cover in cool or very hot conditions but are more visible at other times. Before searching for reptiles they may use a mixture of assessing certain weather parameters and 'gut feeling', but in order to set up a standardised survey methodology, a more structured approach is required. Therefore two key issues need to be addressed; the means by which to measure thermal parameters of the environment and which thermal parameters to measure.

Ideally the best way of measuring the thermal environment for reptiles is to estimate operative temperatures from animal thermometer models which duplicate the heat exchange properties of the real animal. These models would effectively take into account the air temperature, substrate temperature, the radiative effect of the sun (which in turn is linked to latitude, time of day, time of year and cloud cover), effects of wind movement, and so on and provide a single operative temperature reading which would have to be above and/or below certain limits for a standardised survey to take place.

There are, however, various practical problems in using such models. For example a standard model would have to be designed, the models produced and then made easily available to reptile surveyors. Also a decision would have to be made as to the operative temperatures which would define the thermal conditions suitable for surveying for reptiles (these could be different for different species of reptile). It may be that the use of such models will only be practical at certain permanent long-term monitoring sites where more detailed ecological information about resident reptile populations are required.

The alternative to using animal thermometer models is to use a similar system to the Butterfly Monitoring Scheme and to define a range of environmental conditions during which reptile surveying should take place. A number of interlinked factors, which are used in describing a thermal environment, need to be taken into account, such as:

❑ time of year (linked to solar radiation intensity and related factors);

❑ time of day (linked to solar radiation intensity and related factors);

❑ latitude (linked to solar radiation intensity and related factors);

❑ solar radiation (direct measurement would require a meter, otherwise could provide simple measurement of cloud cover - this will not take into account solar radiation variation resulting from latitude, time of day and year, cloud type, cloud height etc.);

❑ air temperature (shade air temperature most frequently used. Figs. 4 and 5 demonstrate how simple measurements of shade air temperature by themselves relate little to the operative temperatures 'experienced' by reptiles and the body temperatures they exhibit);

❑ substrate temperature (will vary depending on substrate type);

❑ air movement (simple measure can be made e.g. on Beaufort Scale, will vary depending on height above ground at which it is recorded, eg reptile level or human level);

An attempt at defining what limits to set for these various parameters is dealt with by Inns (this volume). These initial guidelines could be backed up through setting up a small project which concentrates on defining thermal limits for easily measurable environmental characteristics in relation to operative temperatures estimated from animal thermometer models which may not normally be available to reptile surveyors.

Thermal ecology is therefore of fundamental importance to reptile biology. Their daily and seasonal patterns of behaviour are linked to their thermoregulatory ability to maintain body temperatures at such levels that their physiological processes can proceed at optimal or near optimal levels. This is an important consideration when designing a standardised survey methodology as the visibility of reptiles will therefore be linked to the thermal environment.

5. Acknowledgements

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Thermal ecology 2: The thermal ecology of the smooth snake *Coronella austriaca* and its application to conservation and survey

A.H. Gent* and I.F. Spellerberg[1] (reporting on research at Department of Biology, University of Southampton, Highfield, Southampton SO9 5NH)
* English Nature, Northminster House, Peterborough, PE1 1UA and [1]Department of Resource Management, Lincoln University, Canterbury, New Zealand.

Abstract

Body temperatures of smooth snakes *Coronella austriaca* in the wild were recorded immediately upon capture using a quick acting mercury thermometer. Body temperatures ranged between 10.5° and 31.6°C (mean value of 23.48°C ± 3.95 (n= 327)). There was a strong positive correlation between body temperature and ambient temperature.

The body temperatures of captive animals (provided with a wide range of ambient temperatures at all times) were recorded each hour by telemetry. Body temperatures ranged from 19° to 38°C with a mean value of 29.6°C ± 3.15 (n= 324). The lower thermal limit to body temperature was determined; the critical minimum temperature was 1.98°C ± 1.14 (n= 7).

The relationship between metabolic rate (measured as oxygen consumption rate) and temperature was almost semi-logarithmic. More rapid rates of change of oxygen consumption were shown at the lower (5° to 10°C) and higher (25° to 35°C) temperature ranges than over the intermediate range. This suggested a level of metabolic homeostasis over the body temperature range most commonly encountered in the field.

Smooth snakes were most often captured in the field with body temperatures below the laboratory determined 'preferred temperature'. This indicates that snakes were being detected prior to achieving their optimal temperature. When optimal temperatures are achieved they will be active and more difficult to detect. It is proposed that smooth snakes have evolved a strategy where there is a trade off between achieving optimal temperatures and cryptic (anti-predator) behaviour. Survey effort should best be targeted at times when weather conditions allow basking but do not permit optimal temperatures to be achieved. Implications for habitat management and captive breeding are also considered.

Introduction

The smooth snake *Coronella austriaca* is at the north-western limit of its range in southern Britain. It is probable that the distribution in the British Isles has always been restricted and this has been related to climate (Beebee, 1978). In Britain the smooth snake is considered to be endangered and thus conservation measures are needed to safeguard the species (Whitten, 1990). The smooth snake has been protected in Britain since 1975.

Smooth snakes, like all reptiles, are ectothermic; that is their body temperature is determined by exchange of heat between their bodies and the environment. Oxidative metabolism makes little or no contribution to body temperature. Active maintenance of body temperature therefore is essentially a behavioural process; this is termed thermoregulation (Gans and Pough, 1982). Since *C. austriaca* is at the limit of its geographic range in Britain, it may be

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expected that the species will be in a 'delicate balance' with its thermal environment. This will be manifested directly by the need to regulate body temperature and indirectly through food requirements and over-wintering conditions. These thermal requirements have implications for the habitat types occupied. Similarly the precision of temperature regulation (*sensu* Gibson and Falls, 1979) will also influence and be influenced by habitat selection. *Coronella austriaca* is an elusive animal and one that is difficult to find and to observe. Little is known about the animal that can form the basis for designing the management of habitats for the conservation of the species. The significance of the thermal environment for ectothemic species means that, in order to understand the habitat requirements of *C. austriaca*, a knowledge of its thermal ecology is therefore needed. Such information will also be of value when considering conservation management both in the field and, should it be considered necessary, when developing captive breeding programmes. Through an understanding of this aspect of the species' ecology, it will be possible to evaluate the 'quality' of an area of habitat via thermal, rather than botanic, assessment. Understanding the thermal ecology of the species will help when designing survey or monitoring projects. This will allow a better assessment of conditions during which survey should be undertaken to yield best returns for effort and a means of evaluating results on the basis of the weather conditions under which a survey was undertaken.

Previous work has been undertaken on the thermal ecology of *C. austriaca*. These studies looked variously at body temperatures in either field (Goddard, 1981; Bont, van Gelder and Olders, 1986) or laboratory conditions (Spellerberg, 1976) or both (Spellerberg and Phelps, 1975). The field studies by Goddard (1981) and Spellerberg and Phelps (1975) recorded cloacal temperatures taken with quick acting mercury thermometers; the studies of Bont *et al* (1986) employed thermal transmitters placed in the guts of free ranging snakes; the laboratory studies of Spellerberg and Phelps (1975) and Spellerberg (1976) were based on two and three animals respectively. Subsequent to this study a study of the thermal ecology of the three native British snakes has been undertaken (Gaywood 1990).

The primary objective of this research was to investigate body temperatures of *C. austriaca* in the field and to compare these with those measured in controlled laboratory conditions. Body temperatures recorded in the field will represent the combination of the thermoregulation behaviour of the animals, the current environmental conditions and other (possibly conflicting) behavioural needs of the animals. The laboratory studies allowed a determination of any inherent 'preferred' body temperatures and, through the 'critical minimum' the physiological limits imposed upon snakes by environmental conditions. The combination of the studies of the 'voluntary temperatures' in the laboratory and in the field will therefore allow surveyors to understand the thermal 'aspirations' of active smooth snakes and the likely limitations imposed upon them in the field.

A second objective was to investigate the relationship between body temperatures and oxygen consumption rate. Thus the species' physiology can be related to its thermal ecology and in turn used to understand its behaviour. For example, these data can be used for modelling food requirements; this will help explain why an animal behaves as it does and also allow an assessment of whether food is a limiting factor in any habitat. This can further assist those involved in survey and conservation management of *C. austriaca*.

Methods

a.   Field measurements

Body temperatures of snakes in the field were taken with a fast acting 'Shultheis' type mercury thermometer inserted into the cloaca of the snake immediately upon

capture. Shaded air temperature (at a height of 1.5 metres above the ground in the experimenter's shadow) and the ground temperature at the point of capture were taken. All temperatures were taken to the nearest 0.1°C. The degree of cloud cover was noted (scored as a value between zero and eight eighths). Other information recorded included sex, length and weight and its slough condition, breeding status (for females) and feeding state.

b.   **Laboratory measurement of body temperature**

The thermal gradient consisted of a metal tank 215 centimetres in length, 38 cm wide and 38 cm high, with a false floor covering heating and cooling elements (hot plates and Grant cooling coils respectively) and a thick layer of sand to dissipate the heat evenly. The false floor was covered with a thin layer of 'vermiculite', a substratum that allowed the animal to burrow and provided some insulation. A strip of hardboard 15 cm wide and supported 1.5 cm above the substratum by wooden block ran the full length of the apparatus. This offered cover for the snake and allowed the animal to select any position along the length of the gradient without coming into the open. Drinking water was provided in four petridishes at different points along the gradient chamber.

The surface temperature was monitored using a Yellow Springs Instrument Co (YSI) telethermometer via a series of thermistors that were taped flush to the false floor. Alteration of the thermostats on the hot plates allowed a gradual thermal gradient between 0°($\pm$ 2°) and 40° ($\pm$ 4°) C to be established and maintained. The thermal gradient was established at least 24 hours before introducing animals to the chamber.

Animals were exposed to light:dark cycles approximating natural conditions at the time of the experiment. This was done using four anglepoise lamps with alternate 40 and 60 watt bulbs. The chamber was covered with a net curtain to ensure even, diffuse light and to reduce disturbance from outside. The light:dark periods were 11:13 (n= 2), 13:11 (n= 4) and 16:8 (n= 1).

Body temperature was measured by telemetry using small externally mounted radio-transmitters (type SS-1, 173 MHZ; Biotrack Ltd, Wareham, Dorset) with a thermistor probe attached. The pulse frequency of the transmitter was proportional to the temperature of the thermistor bead. The thermistor was inserted into the snakes cloaca to a depth of 2 to 3 cm and the transmitters were taped onto the snakes tail with a plastic surgical tape. Radio signals were received on a Mariner 57 'Biotag' receiver via an aerial wire that ran the length of the gradient chamber and recorded on a chart recorder. Both the receiver and the chart recorder were powered by a 12 volt car battery which allowed the former to run continually. The chart recorder was activated for a period of 20 seconds each hour by a timer, thus body temperature were recorded at fixed, discrete times during the day.

Seven experiments were carried out with snakes being left in the chamber for varying periods of time ranging from 36 to 75 hours. The relationship between temperature and pulse frequency was calibrated both before and after each experiment. Due to slight inconsistencies between these readings it was only possible to record body temperature to the nearest 1-2°C.

c.   **Critical Minimum**

The critical minimum is the temperature at which a snake, on having its body temperature cooled, becomes immobile. As such it may be considered an 'ecologically lethal' body temperature.

Critical Minimum Temperature was investigated by slowly cooling a snake in a deep freezer. Animals were contained in a small metal tin which provided a flat surface and offered little thermal insulation. Body temperatures were measured continually using a fine YSI probe inserted into the animals cloaca and a telethermometer. The temperature at which an animal was just no longer able to right itself after successively turning over on its back was considered to be that at which it had lost its ability to move. This body temperature was recorded and taken as the Critical Minimum Temperature.

d.   **Determination of temperature - metabolism relationships**

A double chamber volumetric system, maintained at experimental temperatures by immersion in a water bath, was used to determine the rate of oxygen consumption of *C. austriaca* at different temperatures following the methods of Al-Sadoon and Spellerberg (1985).

The first measurement in any experiment was discarded since this may have been affected by residual carbon dioxide in the system. The procedure was repeated until about ten readings were recorded. The four lowest, but consistent, values were used to determine rate of oxygen consumption since these are considered to best reflect resting metabolism (Al-Sadoon and Spellerberg, 1985). The values were converted to standard temperature and pressure (STP), ie. $0^{\circ}C$ and 760 mmHg (1013.25 mB), and divided by the animals body weight to give weight-specific oxygen consumption rate ($ml\ O_2 \cdot g^{-1} \cdot h^{-1}$).

The temperature of chambers was then altered, increasing or decreasing by $5^{\circ}C$. The apparatus was left for a minimum of two hours between experiments to ensure the animals had become rested following the change in temperature. Temperatures investigated were at five degree intervals from 5° to $35^{\circ}C$ inclusive. Snakes were not allowed to acclimatise to the test temperatures.

Results

a.   **Field body temperatures**

The frequency distribution of observed body temperatures (to the nearest $1^{\circ}C$) recorded in the field during all seasons are presented in Figure 1. This allows a general overview of all the body temperature data recorded in the field. Males exhibited a mean body temperature of $23.30^{\circ}C \pm 3.89$ (range= 13.1 to $31.6^{\circ}C$, n= 152) and females had a mean value of $23.63^{\circ}C \pm 4.01$ (range= 10.5 to $31.1^{\circ}C$, n= 175). These were not significantly different (F_{max} test shows homogeneity of variances, F= 1.06, $p>0.05$; Student's t-test, t= 0.74 with 325 d.f., $p>0.05$), nor were the two frequency distributions shown to be different (Kolmogorov-Smirnov two-tailed test, D= 0.60, n_1=152, n_2= 175, $p>0.05$).
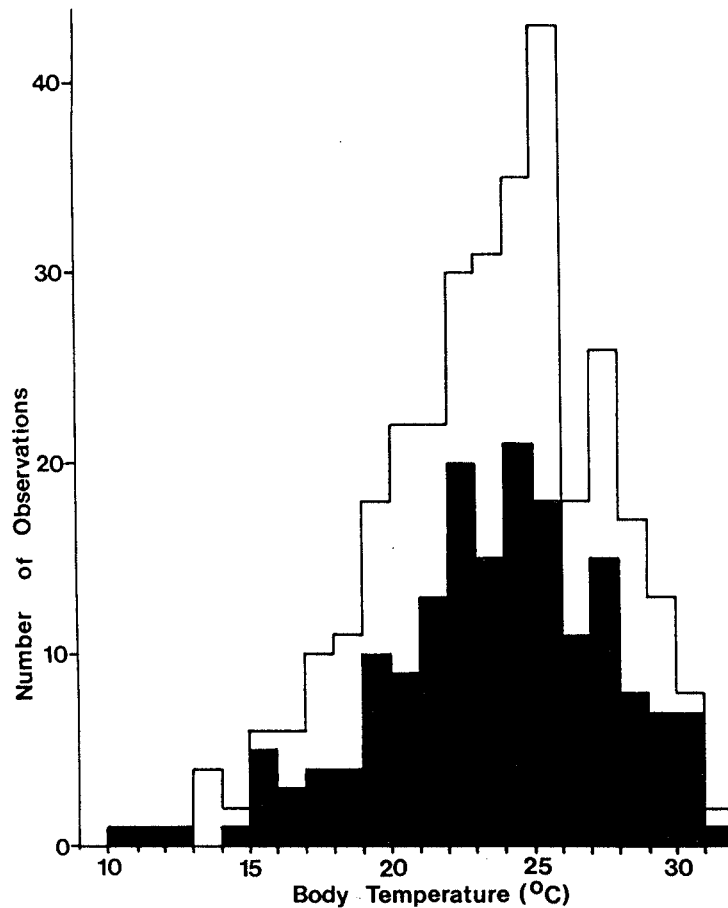
Figure 1: Frequency distribution of body temperatures (°C) of *C. austriaca* observed in the field between April 1984 and October 1986 inclusive, showing those observed for males (unshaded, n= 152) and females (shaded, n= 175).

Data for the two sexes were therefore pooled for further analysis. The mean body temperature for all specimens of *C. austriaca* was 23.48°C ± 3.95 (range= 10.5 to 31.6°, n= 327). Body temperature was closely correlated with shaded air temperature (Pearson's correlation coefficient, r= 0.698 with 325 d.f, p<0.001) (Figure 2a) and even more so with the ground temperature at the site the snake was located (Pearson's correlation coefficient, r= 0.818 with 325 d.f, p<0.001) (Figure 2b).

Cloud cover was negatively correlated with body temperature (Spearman's rank correlation coefficient, r_s= -0.304, n= 325, p<0.001).

Mean body temperatures of *C. austriaca* varied between seasons. During Spring (March to May) a mean body temperature of 22.59°C ± 4.91 (n= 55) was recorded. The values of 24.33°C ± 3.23 (n= 192) and 22.08°C ± 4.31 (n= 79) were recorded in Summer (June to August) and Autumn (September and November) respectively. Significantly different body temperatures were recorded during the three seasons (one way ANOVA, F= 11.82 with 2 and 323 d.f., p<0.001) with the highest body temperatures being found in Summer. However, there is significant heterogeneity of variances between season (Bartlett-Box F test, F= 10.028, p<0.001) and thus results of any analysis of variance must be treated with caution.
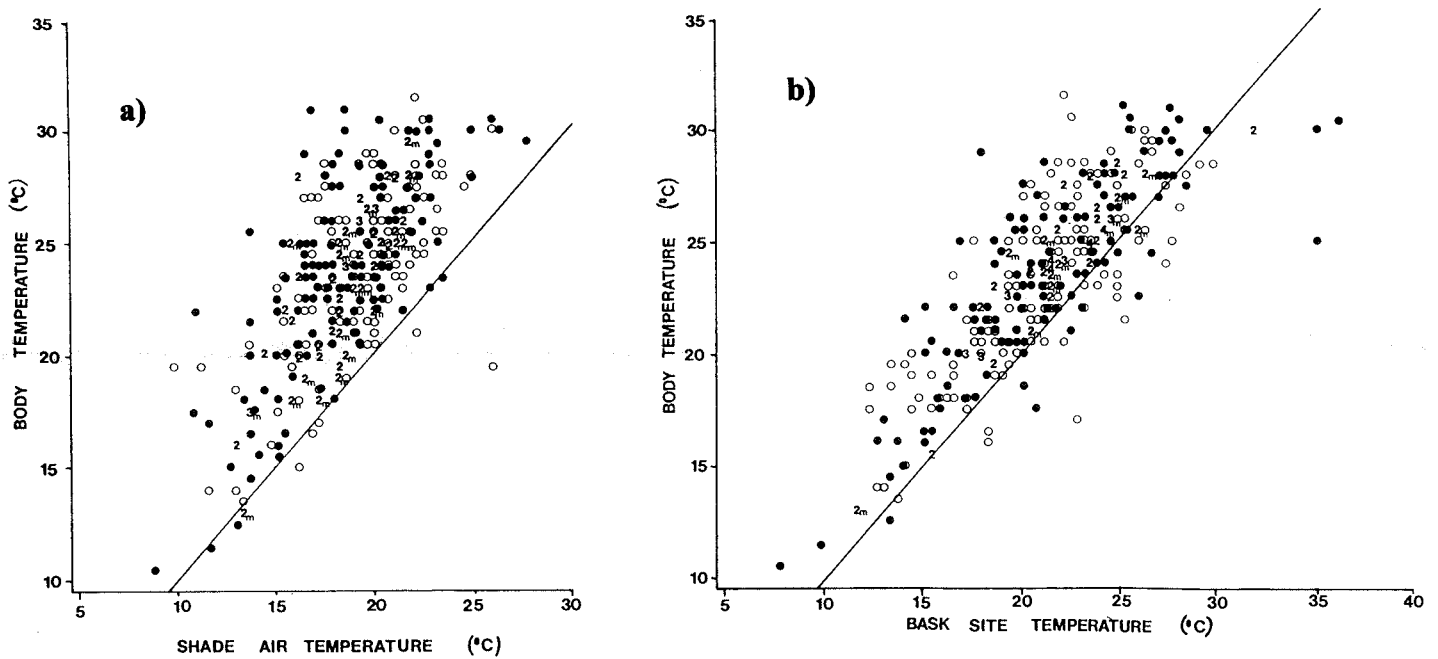
Figure 2: Relationship between body temperature and a. shade air temperature and b. ground temperature at the location of the snake (°C) for male (open circles, n= 152) and female (closed circles, n= 175) *C. austriaca* recorded in the field between April 1984 and October 1986 inclusive. Solid line represents body temperature equalling environmental temperature. Numbers indicate points where more than one record occurs suffix indicates sex, m= male, f= female.

Body temperatures were tested pairwise between seasons. The variances of temperatures in Spring and Autumn were homogenous (F_{max}= 1.298, 54 df., p>0.05) but those for Spring and Summer (F_{max}= 2.311, 54 df., p<0.01) and Summer and Autumn (F_{max}= 1.781, 78 df., p<0.05) were heterogenous. Modified t-tests (Sokal and Rohlf, 1981) were required for the latter two comparisons. A significant difference in body temperatures was observed between Spring and Summer (modified t-test, t= 2.607 with 54 and 191 d.f, p<0.02) and between Summer and Autumn (modified t-test, t= 4.182 with 78 and 191 d.f, p<0.001); the body temperatures recorded in Spring and Autumn were not significantly different (Student's t-test, t= 0.524 with 132 d.f., p>0.05).

Variation in body temperature during the day was analysed by dividing the activity period into arbitrary two hour time blocks. Data were separated by season and, due to small sample sizes, a similar analysis was performed on data from all seasons combined. Mean body temperatures for each time period are given in Table 1. No variation in body temperature was observed between the different time categories in any of the three seasons (one way ANOVA, F= 1.863 with 4 and 50 d.f., F= 1.294 with 6 and 185 d.f and F= 1.080 with 5 and 73 d.f. for Spring, Summer and Autumn respectively. p>0.05 in all cases); in all cases the variances were homogeneous (Bartlett-Box F test, F= 1.992, 0.637 and 1.080 for Spring, Summer and Autumn respectively. p>0.05 in all cases). Pooled data for all seasons showed homogeneity of variances (Bartlett-Box F test, F= 0.056, p>0.05) and indicated no variation in body temperature across the day (one way ANOVA, F= 1.831 with 6 and 320 d.f., p>0.05). Mean values ranged between 17.4° and 24.6°C but quite large standard deviations were associated with each value.

Table 1: Mean body temperatures (°C) of *C. austriaca* in different two hour time blocks during Spring, Summer and Autumn and for All seasons combined, showing standard deviation (s.d.) and number of records (n). Time is indicated a '00 hrs BST

Time	Spring			Summer			Autumn			All seasons		
	Mean	s.d.	n	Mean	s.d.	n	Mean	s.d.	n	Mean	s.d.	n
08-0959	-	-	-	23.6	3.18	16	22.8	5.91	7	23.3	4.07	23
10-1159	23.0	3.39	16	24.1	3.15	34	20.5	4.74	18	22.9	3.92	68
12-1359	21.0	4.68	14	24.3	3.52	37	21.9	3.80	18	23.0	4.03	69
14-1559	21.1	4.95	11	24.8	2.65	32	22.9	4.40	17	23.6	3.89	60
16-1759	25.6	6.54	11	24.8	3.19	44	23.3	2.77	16	24.6	3.82	71
18-1959	20.6	1.37	3	24.0	3.53	28	19.8	6.60	3	23.3	3.89	34
20-2159	-	-	-	17.4	-	1	-	-	-	17.4	-	1

b.   Laboratory measurement of body temperature

Body temperatures were measured from a total of seven animals (four males and three females) over a total of 22 days between May and July in one year (1985) and during June of the following year (1986). Data from seven experiments yielded data suitable for analysis; these lasting between 1.5 and 2.8 days. Measured data are presented to the nearest 1°C (and calculated values to the nearest 0.1°C). However it is should be noted that the method only allowed data to be recorded to the nearest ± 1-2°C.

Mean body temperatures together with the standard deviations, sample size and range of temperatures recorded for each experiment are presented in Table 2. Mean selected body temperatures of the individual animals varied between 28.4 and 31.3°C; although body temperatures between 19 and 38° were recorded. Pooled data indicates a mean selected temperature for the species of 29.6°C ±3.15 (n= 324); however a significantly higher body temperature was shown by females (mean 30.3°C ± 2.17) than by males (29.6°C ± 3.65) (modified t-test, t= 3.382 with 137 and 185 d.f., p<0.001). Body temperatures for females and males were significantly heterogeneous (F_{max}= 2.829, 137 d.f., p<0.01).

Table 2 : Mean body temperatures (°C) of each specimen of C. austriaca recorded in the laboratory thermal gradient (M= male, F= female).

Animal	Sex	Mean body temperature (°C)	s.d.	Number of observations	Range (°C)
H10	M	29.0	2.84	47	20 to 33
H27	M	29.1	4.11	48	20 to 38
B03	M	28.4	3.15	62	19 to 35
B04	M	31.2	4.37	29	20 to 37
H31	F	31.3	1.88	54	27 to 34
S03	F	29.3	1.96	57	23 to 33
L01	F	30.1	2.20	27	25 to 36

Temporal variation in body temperature was studied by dividing the day into six 4-hour time blocks corresponding to the artificial lighting to approximate to dawn (05-0859 hr), morning (09-1259 hr), afternoon (13-1659 hr), evening (17- 2059 hr) and two periods of night (21-0059 hr and 01-0459 hr). Mean selected temperatures for each time period are presented in Figure 3 together with measurement of temperature at two representative fixed points of a series placed along the thermal gradient chamber and laboratory ambient temperature. Males demonstrated significant difference in selected temperature during the day (one way ANOVA, F= 9.237 with 5 and 180 d.f., p<0.001); body temperatures were lowest at dawn (26.4°C ± 3.94) and slowly rose to a peak value in the first period of night (31.5°C ± 2.42). No significant differences were detected in female body temperatures between the six time periods (one way ANOVA, F= 1.015 with 5 and 132 d.f., p>0.05). Pairwise testing showed differences between male and female body temperatures at three of the six time periods, namely dawn, evening and the first period of night (Student's t-test : t= 3.641, 49 d.f., p<0.001; t= 2.217, 60 d.f., p<0.05; t= 2.151, 57 d.f., p<0.05, respectively).
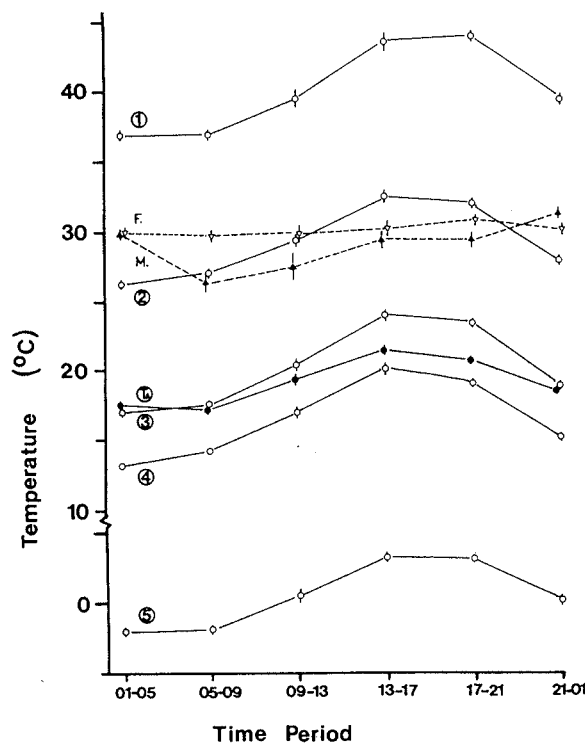

Figure 3 : Mean body temperatures of male (closed circles) and female (open circles) *C. austriaca* recorded in the laboratory thermal gradient during six time periods (Time BST) throughout the day, showing corresponding laboratory air temperature (closed circles, labelled T_A) and temperatures at five positions along the thermal gradient chamber (open circles numbered 1 to 5). Error bars indicate ± 1 s.e.

Significant changes in laboratory ambient temperature and the temperature at five fixed points along the thermal gradient were observed (one way ANOVA, F= 64.09; F= 54.54; F= 65.90; F= 88.56; F= 107.05; F= 46.41: with 5 and 94 d.f. and p<0.001 in all cases).

c. Critical Minimum

The mean critical minimum temperature was calculated as $1.98°C \pm 1.14$ (n= 7; four individuals, all males) (range= 0.6 to 3.86°C). Measurements were taken between April and July 1994).

d. Determination of temperature - metabolism relationships

Values for oxygen consumption rates were obtained from 19 experiments using 17 animals during two successive years; 12 experiments used 10 males and a further seven experiments each used different females. All were adults (snout to vent lengths 360 to 496 mm). Weights, taken prior to each experiment, varied between 31.0 and 66.3g. Five of the females were gravid (no gravid specimens were subjected to temperatures below 10°C). All animals were assumed to be in a post-absorptive state since none showed signs of having recently eaten.

No weight correction equation could be determined for C. *austriaca*. Four of the seven test temperatures showed a significant correlation between Log_{10} Oxygen consumption rate (ml. O_2. g^{-1}. h^{-1}) and Log_{10} weight (g) (Pearson's rank correlation coefficient; r= 0.55, p<0.02, n= 17 at 15°C; r= 0.43, p<0.05, n= 17 at 20°C; r= -0.46, p<0.04, n= 17 at 30°C and r= -0.069, p<0.005, n= 13 at 35°C). Two of these showed positive correlations and two negative correlations. Analysis of weight specific metabolic rates were therefore not further corrected to compensate for differences in body mass between the animals tested.

Pairwise comparisons showed no difference in oxygen consumption rates between gravid and non-gravid females at any temperature except 25°C (t= 2.77 with 5 d.f., p<0.05); thus data for all females were combined in further analysis. Male and female snakes had different metabolic oxygen consumption rates only at 35°C (t= 2.54 with 11 d.f., p<0.05) and thus the data from the two sexes were considered sufficiently homogenous to permit amalgamation.

Mean values of weight specific oxygen consumption rate are presented in Table 3 and in Figure 4. The semi-logarithmic plot shows an approximately linear relationship; however the gradients at low and high temperatures were steeper than those at intermediate temperatures.

Table 3. Mean values of oxygen consumption (ml O_2. g^{-1}. h^{-1}) (of four lowest but consistent values for each animal) for C. *austriaca* in post-absorptive condition for different test temperatures (°C). Combined data for males (n= 11, 10, 10, 10, 10, 10 and 7) and females (n= 3, 7, 7, 7, 7, 7 and 6). Data collected between May and July 1984 and May and July 1985; converted to Standard Temperature and Pressure (STP)

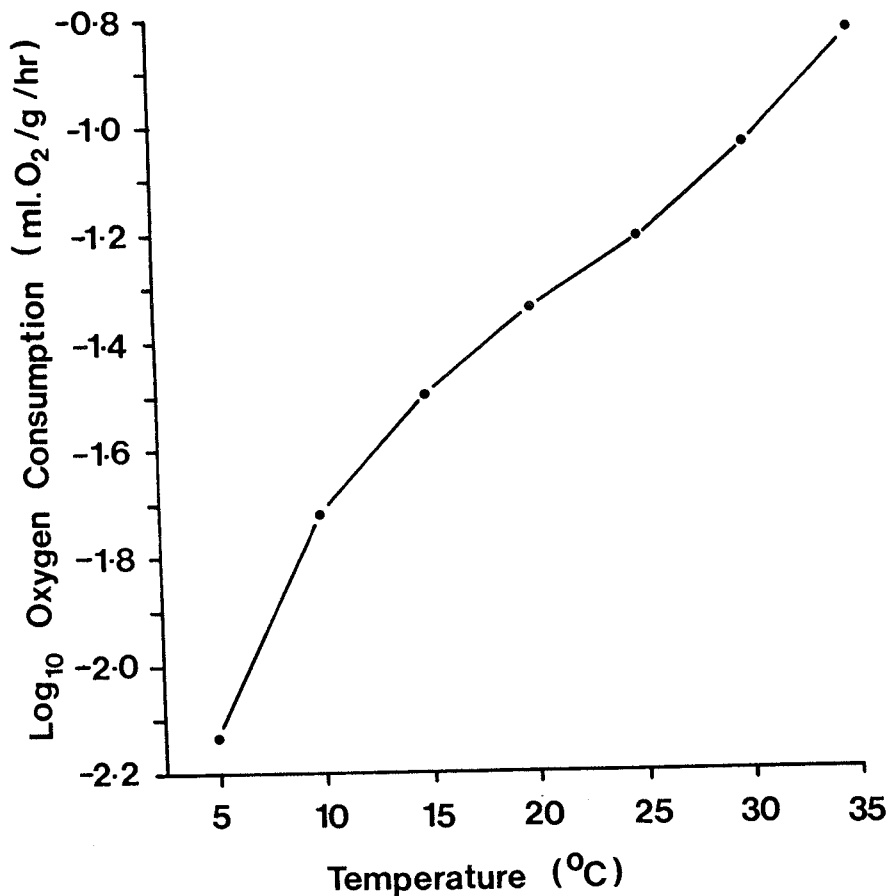| Statistic	Experimental temperature (°C)						
	5	10	15	20	25	30	35
Mean	0.008	0.021	0.034	0.048	0.063	0.094	0.150
s.d.	0.002	0.010	0.015	0.018	0.014	0.024	0.030
Log_{10} mean	-2.131	-1.722	-1.501	-1.340	-1.211	-1.041	-0.832
sample size	14	17	17	17	17	17	13

Figure 4 . Log_{10} Oxygen consumption rate (ml O_2. g^{-1}. h^{-1}) against temperature for *C. austriaca* (males and females in post absorptive condition, n= 17 in all cases except at 5° where n= 14 and at 35° where n= 13). Data collected between May and July 1984 and May and July 1985; converted to Standard Temperature and Pressure (STP)

Temperature coefficients were calculated and are presented in Table 4. These are derived from the equation :

$$Q_{10} = (R_2/R_1)^{10/(t2-t1)}$$

where R_1 and R_2 are the rate of oxygen consumption (ml O_2. g^{-1}. h^{-1}) at the corresponding temperatures t_1 and t_2 (°C).

Table 4 . Temperature coefficient (Q_{10}) values for oxygen consumption rates for *C. austriaca* at different test temperatures (males and females in post absorptive condition, n= 17 in all cases except at 5° where n= 14 and at 35° where n= 13). Data collected between May and July 1984 and May and July 1985; converted to Standard Temperature and Pressure (STP)

Experimental temperatures (°C)	Q_{10} values for mean of oxygen consumption
5 -10°	6.89
10 - 15°	2.62
15 - 20°	1.99
20 - 25°	1.72
25 - 30°	2.23
30 - 35°	2.55
Overall (5 - 35°)	2.66

Q_{10} values were greatest at the two extremes of temperature (5-10° and 30-35°C). A decreasing value for Q_{10} was observed with increasing temperatures from 5-10°, through 10-15° and 15-20°, to 20-25°C where Q_{10} was at a minimum. Progressively higher values for Q_{10} were observed with increasing temperatures thereafter. An overall 'average' Q_{10} for the 5-35°C was calculated as 2.66, which indicates that oxygen consumption almost trebles for each 10°C increase in temperature over that range.
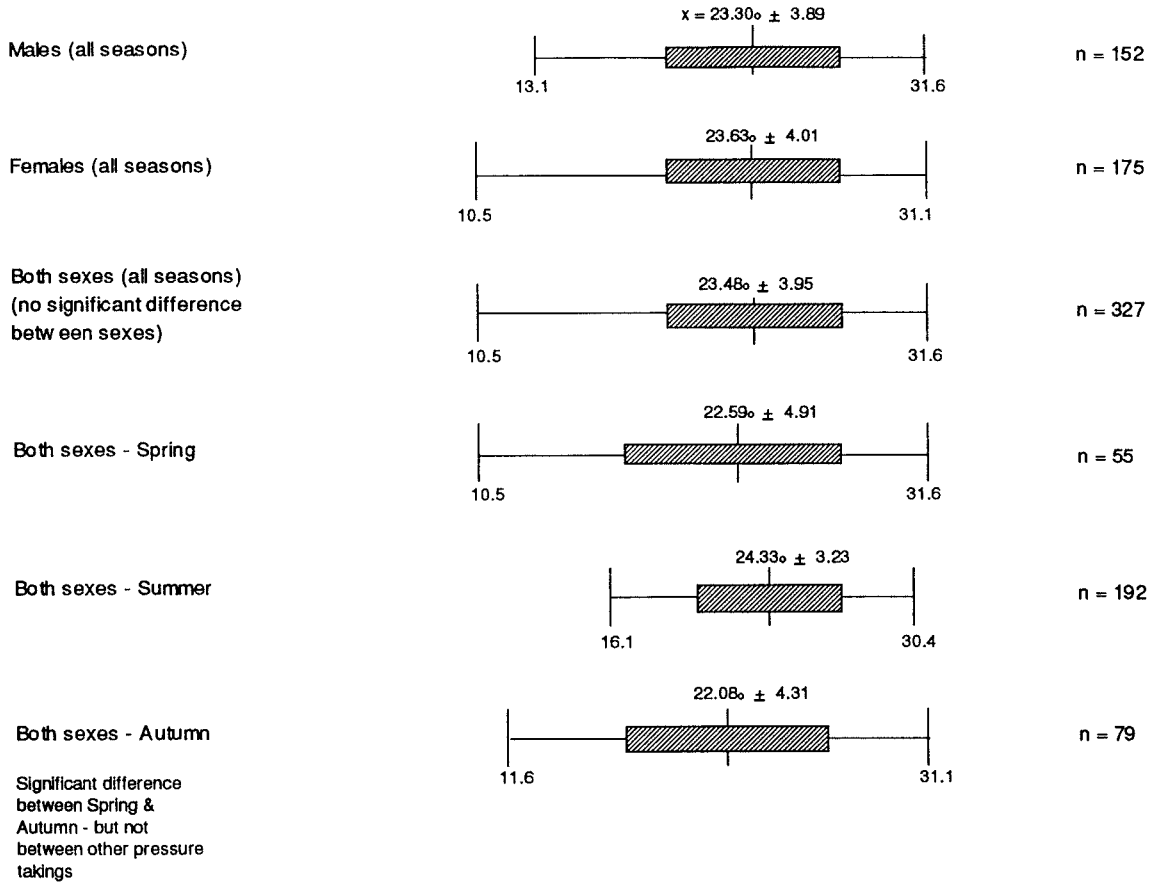
Discussion

a. Body temperatures

The use of cloacal temperature to represent body temperatures has been criticised by some workers. The elongate shape of a snakes body means that different points along the body may show differing temperatures and thus cloacal temperature may not represent a 'true body temperature' of these animals (Bartholomew, 1982; Avery, 1982). This variation may also be significant when comparing results from other studies where other measurements were used (eg stomach temperatures from ingested radio-transmitters (eg Bont *et al* 1986)). Body temperatures may also be affected by handling. These methodological considerations should be borne in mind throughout this discussion.
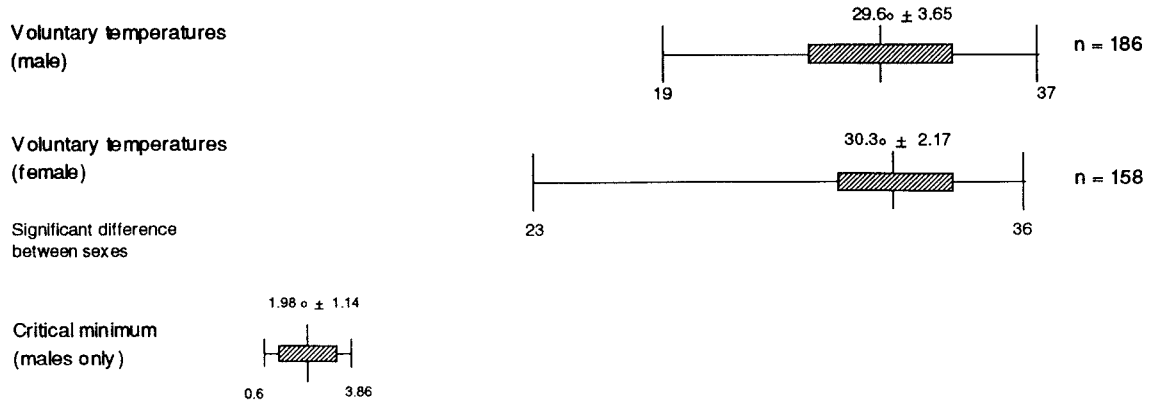
Body temperature data recorded in the field and the laboratory are summarised in Box 1.

Box 1: Summary of thermal data for *Coronella austriaca* from animals studied in the field and in the laboratory (giving mean body temperatures ± standard deviation (shaded bar) and maximum/minimum temperatures recorded; n = sample size)

Field body temperatures

Males (all seasons)
$x = 23.30° \pm 3.89$
13.1   31.6
n = 152

Females (all seasons)
$23.63° \pm 4.01$
10.5   31.1
n = 175

Both sexes (all seasons) (no significant difference between sexes)
$23.48° \pm 3.95$
10.5   31.6
n = 327

Both sexes - Spring
$22.59° \pm 4.91$
10.5   31.6
n = 55

Both sexes - Summer
$24.33° \pm 3.23$
16.1   30.4
n = 192

Both sexes - Autumn
$22.08° \pm 4.31$
11.6   31.1
n = 79

Significant difference between Spring & Autumn - but not between other pressure takings

Laboratory body temperatures

Voluntary temperatures (male)
$29.6° \pm 3.65$
19   37
n = 186

Voluntary temperatures (female)
$30.3° \pm 2.17$
23   36
n = 158

Significant difference between sexes

Critical minimum (males only)
$1.98° \pm 1.14$
0.6   3.86

Smooth snake body temperatures measured in the field varied between 10.5° and 31.6°C. The majority of body temperatures recorded (over 80%) were in the range 19° to 29°C with a mean value of 23.48°C. These are comparable to results from field studies by other workers. Spellerberg and Phelps (1975) reported a mean value of 25.8°C from 88 field measurements of body temperature and Goddard (1981) presented mean values of body temperature of 24.24° and 23.96°C for C. austriaca captured in the open and under cover respectively. Bont et al (1986), in a radio-telemetric study of free ranging C. austriaca, observed that body temperatures were maintained at between 29° and 33°C. Gaywood's (1990) telemetic study of animals in out-door vivaria yielded mean selected temperatures of 30.3°C from 377 observations. These latter two studies, however, used observations of typical 'plateau phase' temperatures attained during the day and excluded lower values when snakes were warming up or cooling down. Inclusion of all records may well have yielded a mean value comparable to that observed during the present study.

Body temperatures were closely related to environmental temperatures and were influenced by the degree of cloud cover. This strong correlation could suggest a tendency towards 'thermoconformity' (sensu Huey and Slatkin, 1976), ie body temperatures following environmental temperatures. The regression equations indicate that body temperatures were typically around 6° above shaded air temperature.

Ground temperature was taken at the site occupied by the animal. Thus this would not only have reflected ambient temperature but would also have been representative of the snakes' behaviour in selecting its thermal habitat. The body temperatures were typically higher than ground temperature (by up to 6°C) at the lower temperature range but both temperatures were typically similar at the higher ranges of temperatures measured in the field. That body temperature did not relate precisely to ground temperature suggests that the mechanism of body temperature regulation in the field was not directly attributable to thigmothermic bask site selection. The influence of cloud upon body temperature further indicates that the species was using direct solar energy by basking to attain its body temperature (ie it is heliothermic).

Observation of the regression relationships between environmental temperatures and body temperatures alone may prove misleading. For both shaded air and ground temperature relationships, body temperature seemed to be relatively higher at lower environmental temperatures. In addition, highest body temperatures (ie those above 29°C) were observed at a range of medium to high environmental temperatures (shaded air temperature between 17° and 28°C and ground temperatures between 22° and 36°).

No snakes were found with a body temperature above 31.6°C in the field. Environmental temperatures were recorded that, based on the regression relationships, would have allowed higher body temperatures to be attained. This is in agreement with other field based studies where maximum values of 31°C were found by Spellerberg and Phelps (1975) and Goddard (1981) and the range 29° to 33°C was observed by Bont et al (1986) and 27.1-35.5°C reported by Gaywood (1990). This may be indicative of the 'preferred' upper-limit body temperature of C. austriaca.

Low ambient temperatures did, however, appear to limit body temperature. In the laboratory a range of temperatures (which ranged from between -2 and 3°C to between 36 and 44°C) was available at all times. Under these conditions body temperatures were much less variable and remained between 19° and 38°C with a

mean value (29.6°C) that was much higher than that observed in the field. Thus it is possible that *C. austriaca* cannot maintain its optimal temperature in southern Britain (where it is at its north-west limit to its range). Another explanation could be that the majority of animals captured in the field were basking and thus were in the process of warming up.

No variation in body temperature was detected throughout the day in the field. Whilst accepting that these data were highly variable, these observations corroborated the conclusions of Goddard (1981), Bont *et al* (1986) and Gaywood (1990) that the species is able to quickly warm up to an operating 'plateau' temperature, which it retains throughout the day. In the laboratory males showed variation in body temperature which reflected the changes in the temperature of the apparatus with fluctuating ambient temperatures. Females, however, retained a consistent body temperature throughout the day. This indicates that females are more precise thermoregulators (*sensu* Gibson and Falls, 1979) than males.

It is likely that other behavioural considerations will affect the precision of body temperature maintenance and consequently smooth snakes may not be able to exploit potential heat sources with maximum efficiency (the role of various biotic and abiotic factors in affecting maintenance of body temperature has been reviewed by Huey (1982)). Notably *C. austriaca* is cryptically coloured and apparently relies on concealment for defence and possibly as part of its foraging strategy. Smooth snakes are known to 'mosaic bask', that is bask while partially or even totally concealed by vegetation. Thus thermoregulation may represent a trade-off between conflicting behavioural needs; namely the need to bask and the need to be concealed. The term 'cryptic heliotherm' has been used to describe this behaviour (S. Hardes, *pers. comm.*). Consequently periods of basking in the open may be ended prior to achieving optimal body temperatures and the habitat of basking partially concealed (sometimes at the base of vegetation) may also mean that these higher body temperatures cannot easily be achieved.

It is worth noting that the laboratory experiment allowed the animals to select temperatures and remain under cover at all times. Thus there was no need for the trade off between temperature regulation and selecting cover.

b.   **Critical minimum**

The critical minimum temperature is effectively an 'ecologically lethal' temperature. When body temperatures reach this value the animals lose their powers of locomotion (see Spellerberg 1976). A mean value of 1.98°C was calculated for this study (range 0.6 to 3.86oC); however the limitations of small sample size and use of only male snakes should be borne in mind. A previous estimate of critical minimum temperature was given by Spellerberg (1976) as 3.5°C.

This value is of largely theoretical significance. While it defines the absolute lower thermal limit for smooth snakes, it is unlikely that animals in the wild will often encounter such temperatures - usually they will retreat as temperatures fall well before this value is reached. However, there have been exceptional occasions where rapid cooling of the environment, as observed below the sheeting, can 'catch' animals out before they reach cover (Spellerberg *pers. obs.*).

The value calculated in this study is for animals taken directly from the field (acclimatised to field conditions in April to July). Snakes can be acclimated to lower

temperatures resulting in a lower critical minimum temperature. Consequently the 'ecologically legal' lower temperatures are likely to be lower early and late in the year.

c. **Metabolic rate and temperature**

The metabolic rate of C. *austriaca*, as shown by rate of oxygen consumption, increased with increasing temperature. The overall Q_{10} over the range 5° to 35°C was 2.55, indicating an almost exponential relationship between rate and temperature. However, a general overview of the whole curve is too simplistic and overlooks differences that occur at different portions of the curve. The most noticeable feature of the semi-logarithmic plot of oxygen consumption against temperature is the diminished rate of increase between 15° and 25°C. The Q_{10} values associated with the two five degree intervals are both less than 2. This temperature range encompasses those body temperatures most frequently encountered in the field. As such, this 'slight levelling of the curve' may be indicative of a degree of metabolic homeostasis over 'normal' body temperatures in the field.

Maintenance of 'precise' body temperatures in the field seems difficult for C. *austriaca* which demonstrates a wide variation around the mean value. Metabolic homeostasis could provide a compensatory mechanism which could decrease potential disruptive physiological effects resulting from changes in body temperature within the activity range. In addition, such physiological adjustment might preclude the need for behavioural thermoregulation in order to sustain a consistent, and perhaps in some way optimal, level of metabolism (Davies and Bennett 1981). Thus this will be useful in decreasing the need for energetically expensive locomotory behaviours. C. *austriaca* is known to demonstrate only small movement rates (Gent & Spellerberg, 1993).

Between 15° to 25° there was a displacement of the metabolic rate temperature curve to the right. Thus a reduction in temperature below a certain threshold caused an instantaneous relative increase in oxygen consumption (and conversely an increase above this threshold caused a relative decrease in oxygen consumption). This displacement may indicate an adaptation to cool climates as it permits efficient metabolism throughout the activity range. Such metabolic shifts have been reported for other reptiles; eg the garter snake *Thamnophis sirtalis* (Aleksiuk, 1971) and the common lizard *Lacerta vivipara* (Tromp and Avery 1977).

As temperature progressively increased or decreased from this intermediate range, this control over metabolic rate was lost. Between 10° and 15°C and between 25° and 35°C the values for Q_{10} were between 2.0 and 3.0. At the higher temperature level, benefits of enhanced physiological processes, such as digestion and assimilation, muscular activity and development of ova, will be offset by more rapid energy expenditure. With decreasing temperature below 15° the converse is true; and the marked reduction in energy expenditure would result in impeded physiological functions. The much larger Q_{10} below 10° may relate to a rapid onset of torpor, thus reducing energy expenditure at sub-activity temperatures but allowing a rapid return to suitably high metabolic rates once adequate temperatures for activity are reached. Thus such a system would act as a temperature dependent metabolic 'switch' changing between active and subsistence metabolic rates. These temperatures coincide with the likely minimum emergence temperatures for C. *austriaca* observed by Bont *et al* (1986) and during the present study.

d. Implications for survey and monitoring

Field surveyors need to understand the relationship between their study animals and the weather, especially for ectothermic species. This can allow better planning of survey effort (eg such that conditions are selected to maximise the chance of finding animals) or may serve to allow more precise interpretation of the data collected on the basis of prevailing weather conditions.

Smooth snakes are ectothermic and their emergence and subsequent activity are affected by weather. Many factors will contribute to prevailing weather conditions, eg air temperature, brightness, wind, humidity, rain, etc. Indeed even preceding weather conditions will affect behaviour. Knowing how these affect body temperatures (or intuitively inferring how this happens) will help the observer determine whether smooth snakes are likely to be active or not. The species can not show precise control over body temperature in conditions that are 'thermally limiting', and is likely to be active only when conditions allow body temperatures between 10 and 33°C. In fact, approximately 80% of observations made where of animals with body temperatures between 19 and 29°.

The ability to record smooth snakes is not the same as smooth snake activity. By relating laboratory determined 'preferred temperatures' to field observations, it appears that the majority of animals caught in the field were 'warming up' and had not yet reached their 'preferred temperature' (approximately 30°C). Once at this temperature it is likely that the animals would become more difficult to find. Indeed it is probable that the animals become more secretive as their body temperature approaches this temperature; the need to raise temperature becomes lessened and so the benefits of being concealed will start to outweigh the benefits of basking in the open. At lower environmental temperatures smooth snakes demonstrate a wide range of body temperatures. This shows that even on cool days high body temperatures can be achieved. Implicit in this, though, is the fact that snakes will need to bask for longer in cooler weather to achieve these body temperatures.

Consequently ideal conditions for survey are those during which a wide range of body temperatures are observed as these may yield the greatest numbers of basking animals. This is typically when shade air temperatures are between 15 and 22°C.

Observers also need to be aware of how the temperatures on different parts of any site vary with regard to both the extent of change and the rate of warming. Figure 5 shows an example of variation on a small site as a consequence of vegetation height and substratum. Smooth snakes respond to these microclimatic differences, both in choice of bask site and in activity period. While aiming to select a site that allows a body temperature of about 30° by choice, smooth snakes will also balance how long they remain in that site with other equally imperative (and often conflicting) needs such as finding food, mates or predator avoidance. Data collected during this study indicate that temperatures of occupied 'basking sites' rarely exceed 30° and are more usually likely to be between 18 and 28°C.

The effect of cloud cover on depressing body temperature should be borne in mind when undertaking survey. This has the effect of increasing survey periods on otherwise warm days, but also preventing or delaying emergence on cooler days. Consequently warm days with some cloud or cooler cloudless days tend to provide best conditions for seeing snakes. These allow snakes to be active but not to be able to warm to achieve their thermal optimum too quickly.

Key:
1. O-O-O   shade air

2. △-△-△   Open ground

3. ●-●-●   Below thin vegetation

4. ▼-▼-▼   Below thick vegetation (*Calluna*)

5. ◇-◇-◇   Below ground (10cm depth)
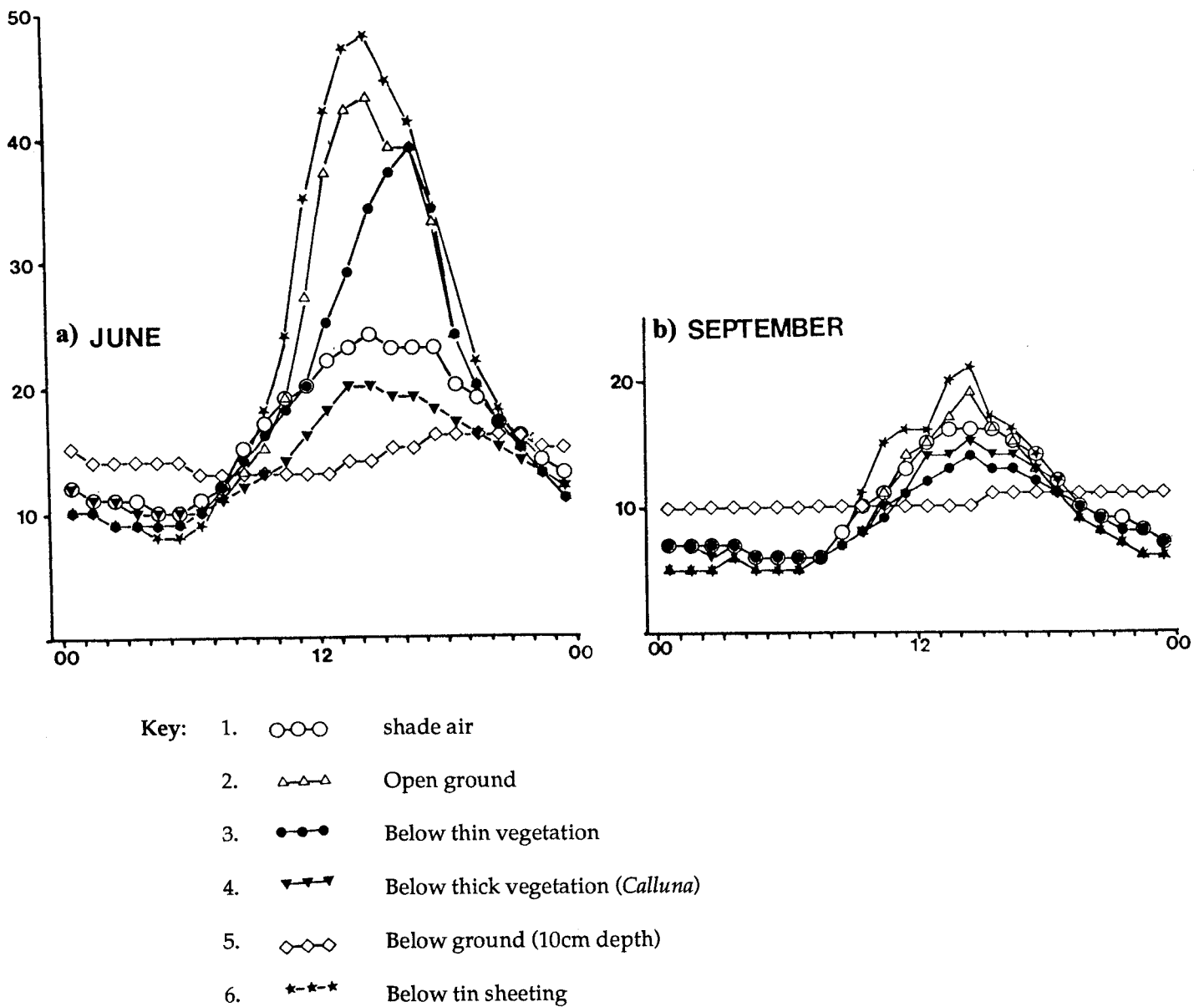
6. ★-★-★   Below tin sheeting

Fig. 5: Mean temperatures (°C) recorded at hourly intervals for six locations (see key) in the environment (samples of 5 to 8 days duration) during a. June and b. September 1986.

Time of day was shown not to be a reliable indicator of body temperature, since during the study a wide variety of weather conditions were observed at different times of day. This allowed some high body temperatures to be recorded at either end of the day while, conversely, some low body temperatures were recorded during the middle of the day. However it is possible to select times of day when the weather is more likely to yield optimum searching conditions. In general, earlier in the day is preferable during the Summer.

The lower recorded body temperatures during Spring and Autumn, compared to Summer, indicate that these two seasons are the preferred seasons for study since snakes are likely to be basking for longer.

The observations during this study also show the importance of standardising survey effort for monitoring populations and the difficulty in doing so. While time of day, season and even weather conditions can be standardised to some degree, there is still a large amount of variation in observed body temperatures and consequently in observed behaviour. Consequently as well as trying to set conditions for survey, it is important to recognise that several visits need to be made during any survey to allow the collection of data that can be used for comparisons between successive years for monitoring purposes.

e.   **Implications for management for conservation**

A knowledge of the thermal ecology of the smooth snake is important for guiding conservation work since it allows an understanding of the way in which the species uses its habitat. It therefore helps identify management requirements and guide captive breeding programmes.

In the field smooth snakes need to be able to regulate their body temperatures, and aim to achieve a value of around 30°. During the course of any activity season (typically April to early October in Britain) a wide range of weather conditions prevail. Smooth snakes are active in air temperatures between 10 and 30°. Different microclimates within a site are very important for smooth snakes. These allow different parts of sites to be selected as conditions vary. Although the species does not seem to need to thermoregulate precisely and will accommodate a range of body temperatures, it is likely that this represents a trade-off between conflicting behavioural requirements within the constraints of the climate.

Managing a site to ensure that the area is warm and generally unshaded by large trees is important since it is likely that the smooth snake in Britain is restricted to its southerly range largely due to the unsuitable climate elsewhere. However it is equally important to ensure that there is a heterogeneous thermal environment at ground level where the snakes are found. Consequently a diverse structure should be maintained in the shrub layer vegetation. Smooth snakes are known to be fairly sedentary (Gent and Spellerberg 1993) and consequently this structural diversity, ranging from thick bushes (typically heathers *Erica* spp. and *Calluna vulgaris*, but possibly bramble *Rubus fruticosus*) to open ground (bare or with leaf litter, short lichen or short grass) should be provided in a close mosaic. Although smooth snakes can show behavioural adaptations to uniform vegetation, eg climbing up in bushes, selecting different vegetation structures and basking beneath then at ground level seems a preferred strategy and also one that suits 'sit and wait' hunting.

By looking at laboratory and field observations of the species' thermal ecology, some issues can be identified that have implications for animal husbandry when keeping the animals in captivity, perhaps for breeding programmes. While, given a choice, smooth snakes may select a body temperature of about 30°, their physiology seems to be adapted to a wide range of body temperatures. Indeed it appears that there is an adaptation to a temperature lower than the 'preferred body temperature', perhaps relating to the body temperature most often encountered in the wild. Behaviourally snakes may aim to maximise their body temperatures, given that at the same time in the wild other behavioural traits, such as the need to select cover, would be operating

at the same time. If temperatures are kept too high in captivity, or where these other traits are not being demonstrated (perhaps cover is provided throughout the vivarium or food is provided nearby so hunting is not necessary) it is possible that the snakes will consistently select temperatures that are too high. Therefore, in captive situations, it is important to try to mimic natural weather cycles to maintain a healthy population of animals; for these reasons open air 'semi-natural' vivaria should be used where possible.

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Acknowledgements

Discussion following the talk by Tony Gent on outline of reptile thermal ecology and its relevance to survey methods

Henry Arnold: If adders need higher temperatures than smooth snakes or grass snakes, why do they live further north?

[*]**Tony Gent:** I think that's probably due to behavioural adaptation. The information I have from Martin Gaywood suggests that adders are much better at adapting behaviourally to sub-optimal conditions. The higher temperature is their *preferred* body temperature but they seem to be able to cope better at sub-optimal temperatures than the other two species.

[1]**Henry Arnold:** So, body colouration, for example, might be a significant factor. Black animals could be at an advantage in terms of achieving a high body temperature.

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[*][Note added by Martin Gaywood at editing stage:

Adders attain higher body temperatures than the other two species even when operative temperatures (T_e) are the same.

Behavioural thermoregulation is believed to be a major mechanism through which reptiles compensate for geographical variation in the thermal environment.

[1]Thermoregulation benefits from black coloration are likely to be offset by risks such as increased predation]

Discussion: The conservation objectives and scientific basis of reptile survey

Keith Corbett: A living reptile is able to utilise its physiology by, for example, dilating and contracting the blood system to take up heat more efficiently. It can also utilise its behaviour. Reptile temperature regulation is much more efficient than an inanimate object. In your talk you were comparing these two systems. Can you do this realistically?

Tony Gent: We probably need a better model to describe what is happening in the wild.

Henry Arnold: I thought the point of using a 'snake model' was that it takes out those physiological and behavioural abilities from the equation to give a measure of the environmental conditions.

Tony Gent: That is right. While accepting its limitations, the idea is that the model provides a better idea of the environmental conditions than just, for example, shade air temperatures. The difficulty is then working out how to use that value, especially where we do have animals that 'break the rules'. What that might mean in terms of practical reptile monitoring is that you may have a much wider window of temperatures to work in than with your simplified snake model. You can then say that, under this wider range of temperatures, it may be likely to see snakes because they do have the capacity to be active.

Keith Corbett: Do you know if these measurements were taken on animals which were basking or those which were active? Active animals, for example those out foraging or searching for mates, tend to be at temperatures which are at the higher end of the ranges which you've described. It's difficult for basking animals because you don't know how long they've been out basking.

Tony Gent: I know that these measurements, which were taken by Martin Gaywood, were conducted in outdoor vivaria and he did conduct spot checks to keep track of what the animals were doing. All of these measurements would have been taken during the active phase - but this may include both basking and 'more active' behaviours.

Bill Whitaker: Does anybody know at what body temperatures grass snakes have when they are swimming or at what environmental temperatures they can swim at?

Tony Gent: Adrian Harley and Peter Davies have done some work looking at various natricine snakes, in particular looking at the body temperatures during different activities such as swimming and hunting. This information is published.

Bill Whitaker: I ask because I remember seeing grass snakes hunting for great crested newts at about 11 o'clock at night.

Tom Langton: I have seen the same kind of thing at 2 o'clock in the morning.

Keith Corbett: I have seen grass snakes actively hunting in the spring when the temperatures must have been fairly low, much lower than 15° which was one of the temperatures someone mentioned before.

Jan Clemons: I saw grass snakes in March of this year in ponds while I was looking for toads and the temperature must have been around 5°C.

Jim Alexander: While the snakes are hunting, they will presumably be creating their own body heat through the action of muscle.

Tony Gent: I'm not actually sure how significant that is. Certainly movement does increase metabolism considerably - but probably doesn't generate much in the way of body heat.

Howard Inns: Did Martin Gaywood come up with a practical proposition for a simple 'reptile thermometer', that you could build at home?

**Tony Gent: In fact he was quite cautious about that idea. Although it is attractive, there do seem to be a lot of practical problems. For example, even if we were to decide that simply a piece of copper tubing with a thermometer inside would be useful, we would then have to decide exactly where place it for readings. These practical problems seem to preclude its value for use in the field. An easier way round the problem would be to set parameters on the basis of air temperature but one of Martin's conclusions was that air temperature is a very poor predictor of body temperature.

Henry Arnold: We have to be sure about exactly what we want to know from these data. For example, do we really want to be looking for reptiles while they are basking? It may in fact be easier to see them when they are in fact slightly sluggish.

Tony Gent: That might well be the case. Perhaps we need to work out when the temperatures are such that it's warm enough to tempt the animals out but not so that they are so active that they are then difficult to find.

Henry Arnold: Consequently we need to look more at the behaviour of the individual species and target our observations to periods when the animals are most easily observed.

** [Note added by Martin Gaywood at editing stage:

There may be some value in further developing the idea of a 'snake thermometer' in certain circumstances, eg at long term monitoring sites or studies at important sites to assist develop some form of standardisation]

Monitoring slow-worms and common lizards, with special reference to refugia materials, refugia occupancy and individual identification

Anne Riddell
Durrell Institute of Conservation and Ecology, University of Kent, Canterbury CT2 7NX

Introduction

Slow-worms *Anguis fragilis* Linnaeus and common lizards *Lacerta vivipara* Jacquin are both regarded as widespread lizard species, but are known to have been declining in Britain in recent years. This study set out to discover their use of different habitats within the same Canterbury nature reserve, with the aim of pinpointing optimal habitat and identifying the most successful refugia materials, and involved devising an individual recognition system for use in the field. The study period included a sustained summer drought, which appeared to cause a slow-worm population crash.

Background

Intensive monitoring of slow-worms and common lizards took place at Canterbury Environmental Education Centre from 3 April to 30 October 1995. A further three months' monitoring will follow in March to May 1996. As a National Grid-owned nature reserve, managed as a partnership project in conjunction with Kent County Council, it is used by Kent schools but has no other authorised public access. An electricity sub-station is situated at the eastern end. Historically, it was grazing marsh, which was later gravelled in the 1930s. It stands 6 m above sea level and is screened from view by a series of man-made bunds of London clay. These vary in height but on average stand 4-6 m above ground level. Most lizards are found on or near these bunds. The reserve is bounded to the north-west by a major arterial route into Canterbury, to the south-east by the Great Stour River and on the remaining sides by light industrial development and housing.

About 25 years ago the bunds were heavily planted with trees to create a woodland screen. However, many of them have not survived, leaving small areas of light woodland and grassy slopes which have been managed for wild flowers and insects.

The lack of public disturbance made it extremely attractive for a reptile study. No previous monitoring had been carried out but grass snakes, slow-worms and common lizards had been seen occasionally.

Sites, materials and methods

Initially, in October 1994, four sites were chosen on the bunds facing the compass points, based on the most recent lizard sightings, for a preliminary survey in April 1995. These were all on managed slopes mown to encourage wild flowers. But they were quite unsuccessful and despite the closed nature of the reserve, were highly visible from the nature trails and were vandalised and disturbed.

Well-hidden sites with the new criteria of assessing reptile use of less intensively managed, different habitats were then chosen on more secluded parts of the bunds and this data covers these sites from 1 May to 19 October - the last sightings for 1995.

Site A, facing north-west, was part of the surviving woodland and the tree cover and aspect of the site meant it was the coolest of the three. On the opposite side of the same bund and only 2 m away over the crown was Site B, a south-easterly flower meadow of mainly ox-eye daisy grading into grassland, with woodland at the crown of the slope and common reed beds at its foot. This was the most sheltered and varied of the three sites. The most open and warmest was Site C, 160 m away, a rough grassland slope, also facing south-east, which was subject to minimal management to reduce Hawthorn colonisation.

In the absence of a standard reptile survey method, techniques were devised as required. A survey site 10 m x 15 m was marked out on each of the three chosen habitats and a variety of materials placed upon it to attract reptiles (11 refuges per site), sampling approximately 4.5% of each site (Figure 1a, b and c). With an extremely limited budget and the proximity of a scrap metal dealer's, travellers' caravan site and housing estate on the reserve boundaries, tins were not considered a viable proposition. Therefore a variety of materials were used in an experiment to identify successful survey refugia - including tins - but also corrugated asbestos, carpet, roofing felt, hardboard and logs. The refuges (at least two of each material per site) were not placed randomly but strategically, with reference to the target reptiles' behaviour, as the purpose was to obtain maximum encounters. Accordingly, they were placed to offer a range of sunshine and shade conditions at different times of the day and of the year and to make the maximum use of the open areas and topography. The choice of which material was placed on a 'hot spot' was random.

The sites were visited on average three to four days a week (up to six in May and June - the peak period) and if sightings were high then each site would be visited up to three times in one day to record maximum encounters. To preserve the vegetation on these small survey sites, a track was walked between refuges and the habitat in sequence between scanned for reptiles. These were caught by hand, weighed, measured and released. Good fieldcraft skills were required to monitor the whole of each site and not just the refugia.

Identification

For the purposes of this study (to consider population size, growth, dispersal and home ranges), it was essential to identify individuals in the field and initially a marking scheme was attempted. But slow-worms proved a challenge. Tippex, nail varnish and permanent marker were all tried and rejected. Field trials of the first two in May gave less than 24 hours' recognisable marks and a trial in an outdoor reptiliary with captive slow-worms in less abrasive grassy conditions gave only 48 hours. The permanent marker was better but was dependent on finding the same individual at regular intervals - a trial of captive juveniles produced a maximum of 12 days' markings in one juvenile, but others had to be re-marked one, two or three times during that period, especially in the days immediately after sloughing when the skin seemed exceptionally absorbant and the marks faded rapidly. Juveniles were the greatest problem to identify as they were so similar in size and appearance.

Other marking materials such as enamel paints were rejected on the grounds of potential toxicity or visibility to predators. Toe clipping of common lizards was excluded as unacceptable interference. The use of pit tags was inappropriate for either species on the grounds of scale design and body size and it appeared an intimate knowledge of individuals based on each's characteristics was required.

Slow-worm chin spots were rejected as too complicated a pattern to memorise in the field if dealing with large numbers of animals. Also the chin markings fade dramatically as the slow-worm prepares to slough.
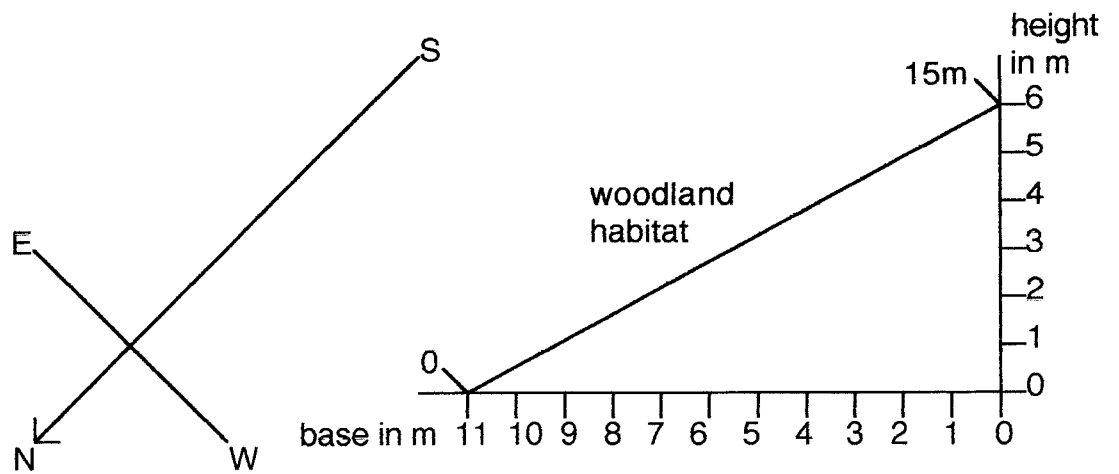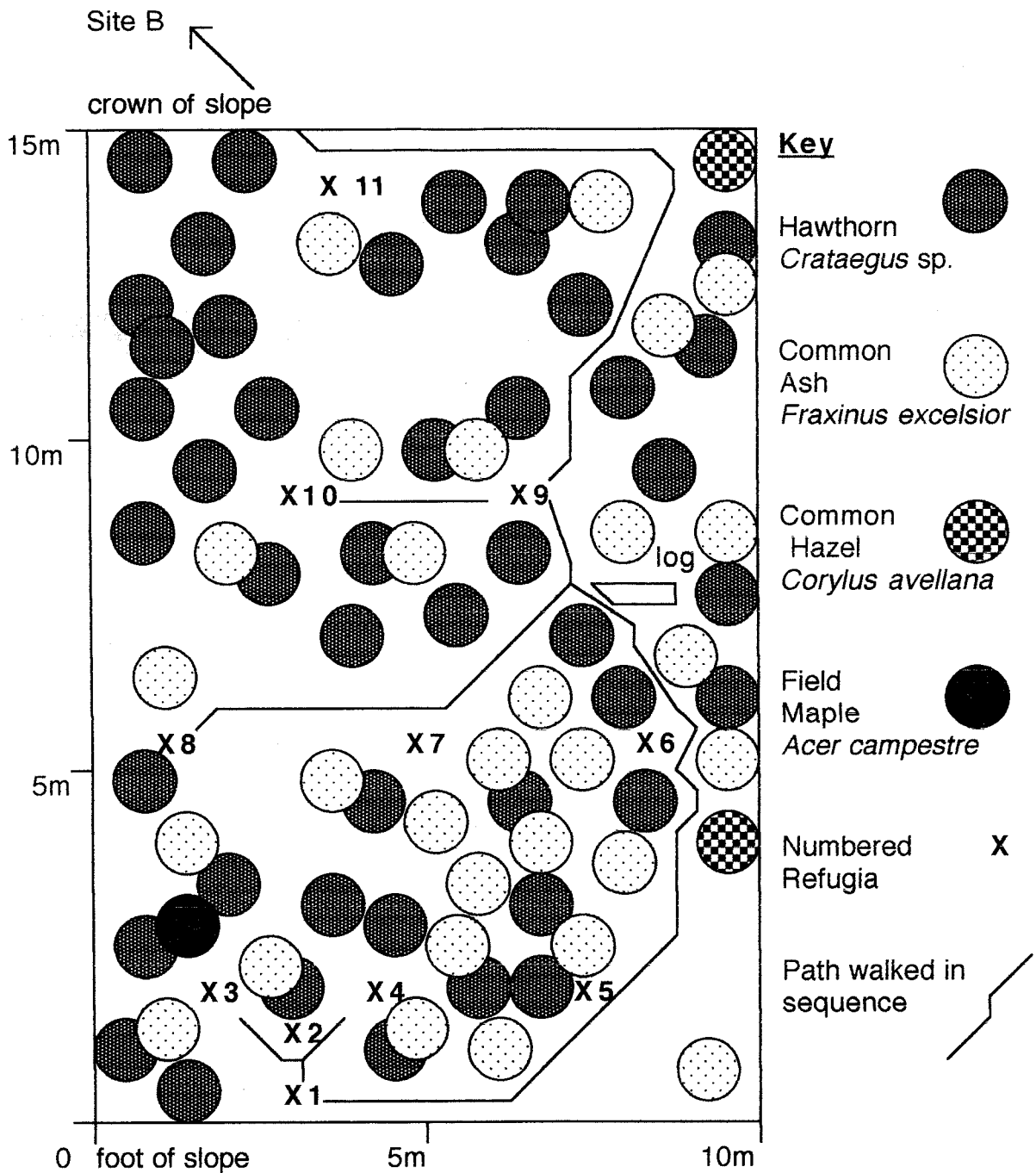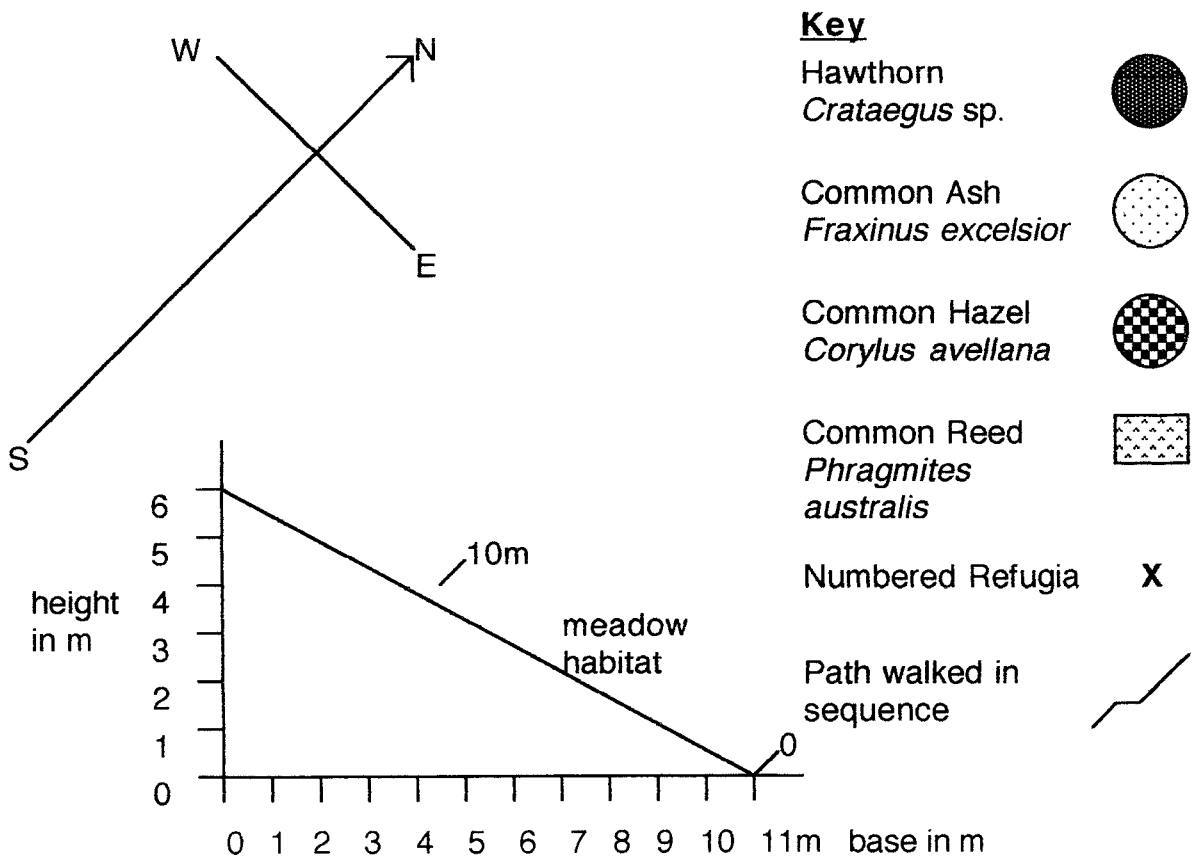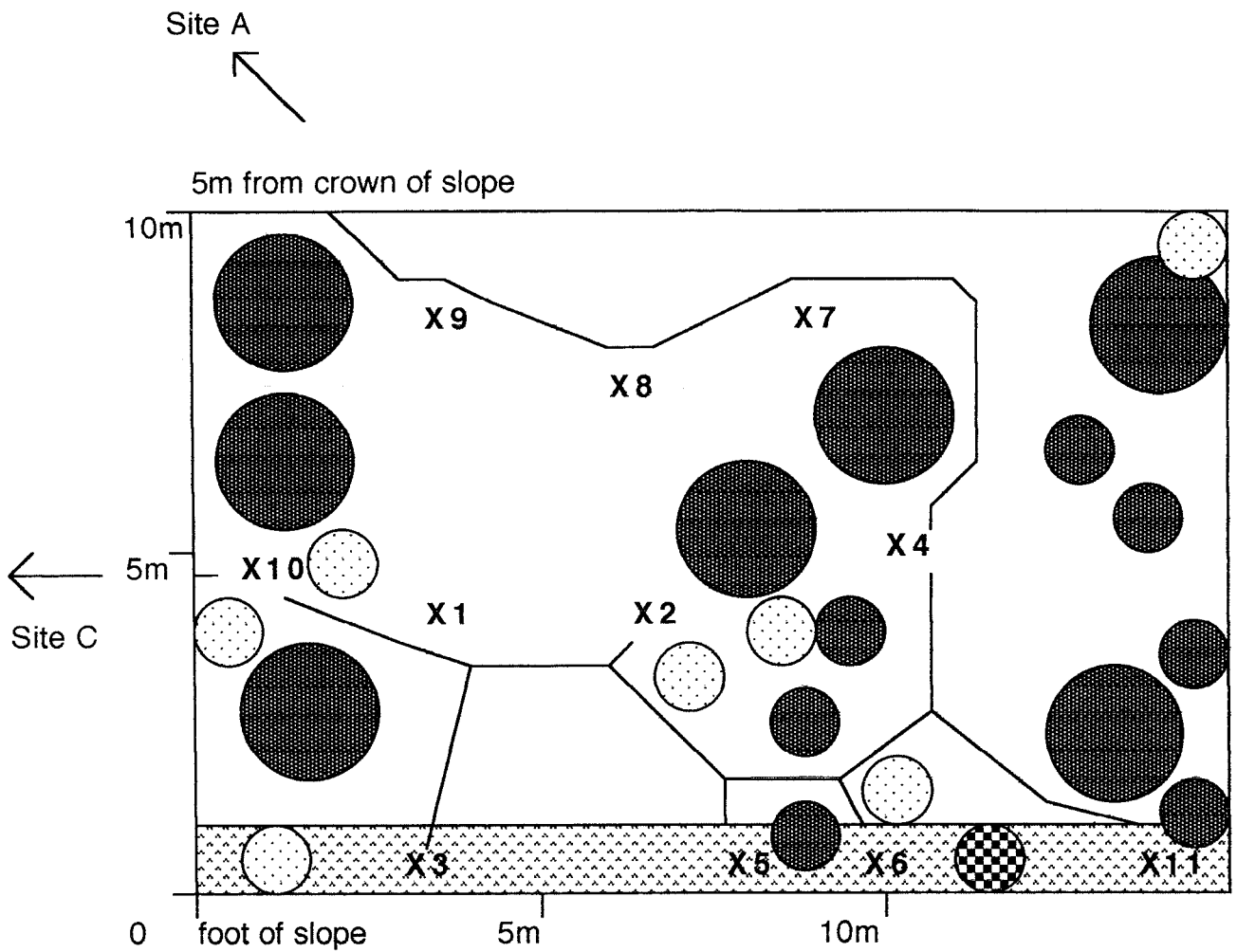
Figure 1a. Site A - woodland habitat

Figure 1b. Site B - Flower meadow

crown of slope

10m

X 5

X 2 **X 1**

X 3

5m

X 11

X 8

log

X 7

X 6

X 9

X 4

X 10

0   5m from foot of slope   5m   10m   15m
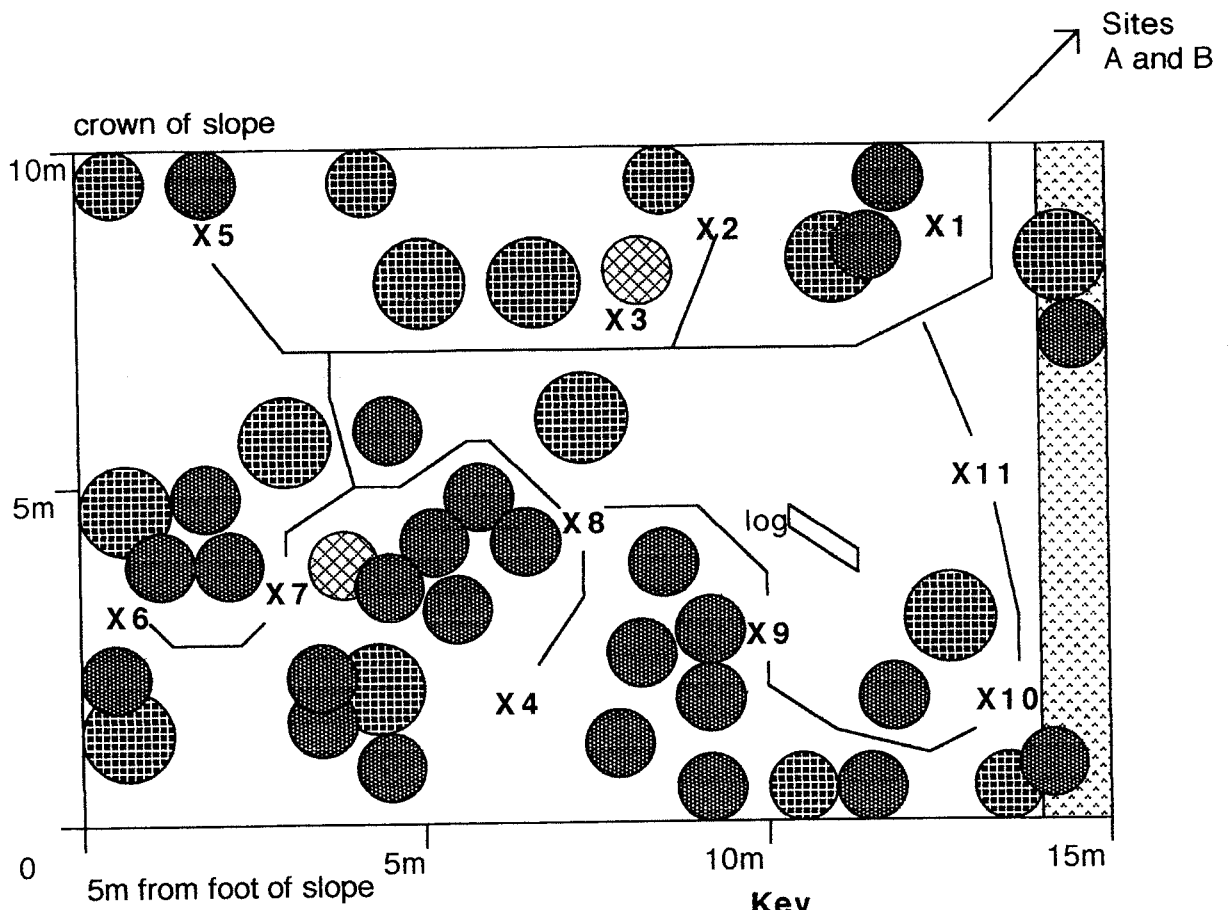
Sites
A and B

Key

Norway Maple
Acer platanoides

Hawthorn
Crataegus sp.

Common Oak
Quercus robur

Common Reed
*Phragmites
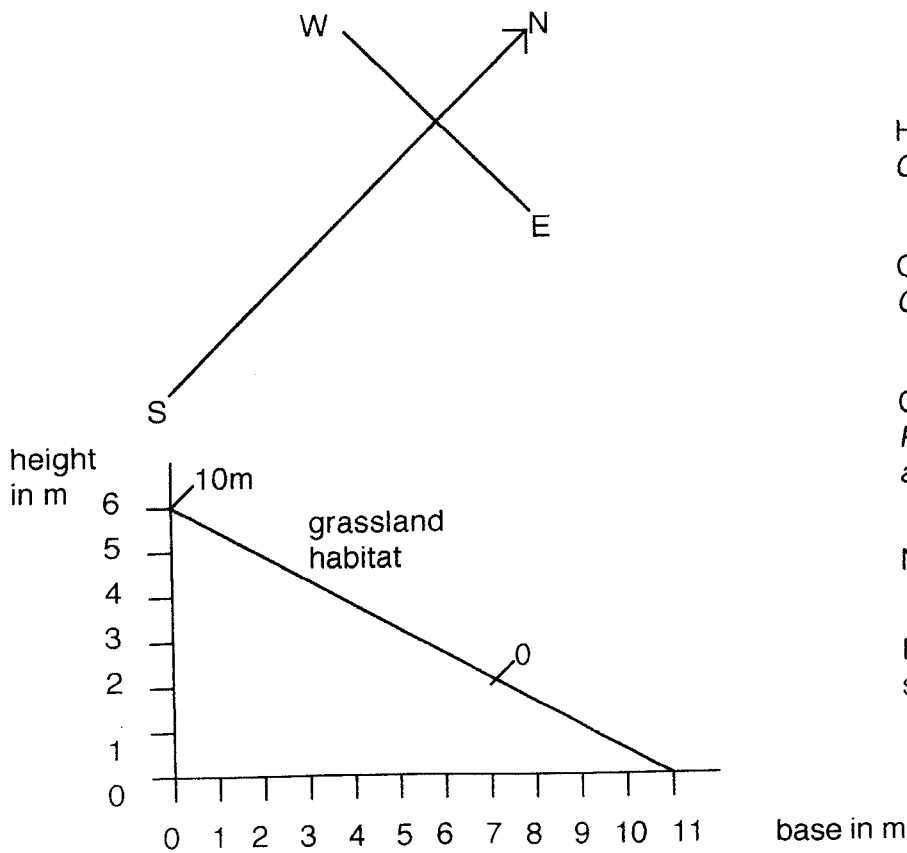australis*

Numbered Refugia   **X**

Path walked in
sequence

W   N

S   E

height
in m

10m

grassland
habitat

0

6
5
4
3
2
1
0

0 1 2 3 4 5 6 7 8 9 10 11   base in m

Figure 1c. Site C - rough grassland

However, the head markings (Figure 2 - AF is *Anguis fragilis*; LV where it appears later is *Lacerta vivipara*) proved easy to recognise and an identification system using this technique, which may not have been attempted previously for this species but have proved successful in adders *Vipera berus* and smooth snakes *Coronella austriaca*, was devised.

The vertebral stripe ends on the head in different patterns which appear to be individual to each reptile. There are similarities of shape - generally a pincer-style design with a dark dot between the two forks and often a separate patterning towards the snout - but they are dissimilar enough to identify individuals on successive occasions. These patterns were drawn in a field notebook, as well as photographed. In addition, details of each slow-worm's measurements, tail condition, colour, scarring and any other clues to its identity were noted.

Even in males this head pattern is retained when the juvenile stripe has gone. As the season progressed, the head marks alone proved to be sufficient, leading to 105 identifiable individuals in the survey. Patterns were also seen in hatchlings. Further work would be required to find if these marks change with age. A successful individual field identification technique would assist greatly in learning more about this secretive reptile's behaviour.

Common lizard males were identified by the pattern on their anal scale (Figure 3) which was extremely distinctive. Females were not always so obliging. A large number did have spotting on this scale, but occasionally the belly pattern had to be used instead. Hatchlings were unidentifiable initially but by September belly spots were showing. Preliminary patterns were taken in an attempt to match them to individuals the following spring. By the end of the first season there were 30 identifiable adults and subadults in the study.

With a well-equipped Kent County Council field studies centre on site, its technology was tested to record individual markings. A hand-held scanner which produced a digital image to be stored on a computer database seems an exciting prospect for identification records in the future. A further development has been the use of a Canon ion digitising camera for image storage on computer.

Results

Out of 202 slow-worm encounters, 178 or 88.2% of animals seen were caught and identified. More reliance could be placed on slow-worm data than that for lizards - where only 23.9% were caught from 155 encounters.

The overall slow-worm population structure on the reserve was as expected with smaller numbers of adults and larger numbers of young. But the population structure per site was variable, with only small numbers of juveniles on the wooded and flower slopes while Site C, the unmanaged grassland, had large numbers. This habitat provided far more ground cover for both juveniles and their invertebrate prey in spring and early summer. However, the largest number of adults and subadults were found on the flower slope with its mosaic of microhabitats, indicating the importance of the interfaces between habitats to this species. Seasonal migration between the woodland and flower meadow was observed.

Turning to the slow-worm encounter rate (Figure 4), the large percentage of juveniles on the grassland was reflected in the encounter rate for that site in May, although it tailed off dramatically during the year. The second of the two charts shows how many of those encounters were with identifiable individuals. Encounter levels were high in early summer, then declined steeply as temperatures rose during July. There were no sightings at all from 19 July until 6 September, and few encounters in September and October, leading to concerns about the population's survival.
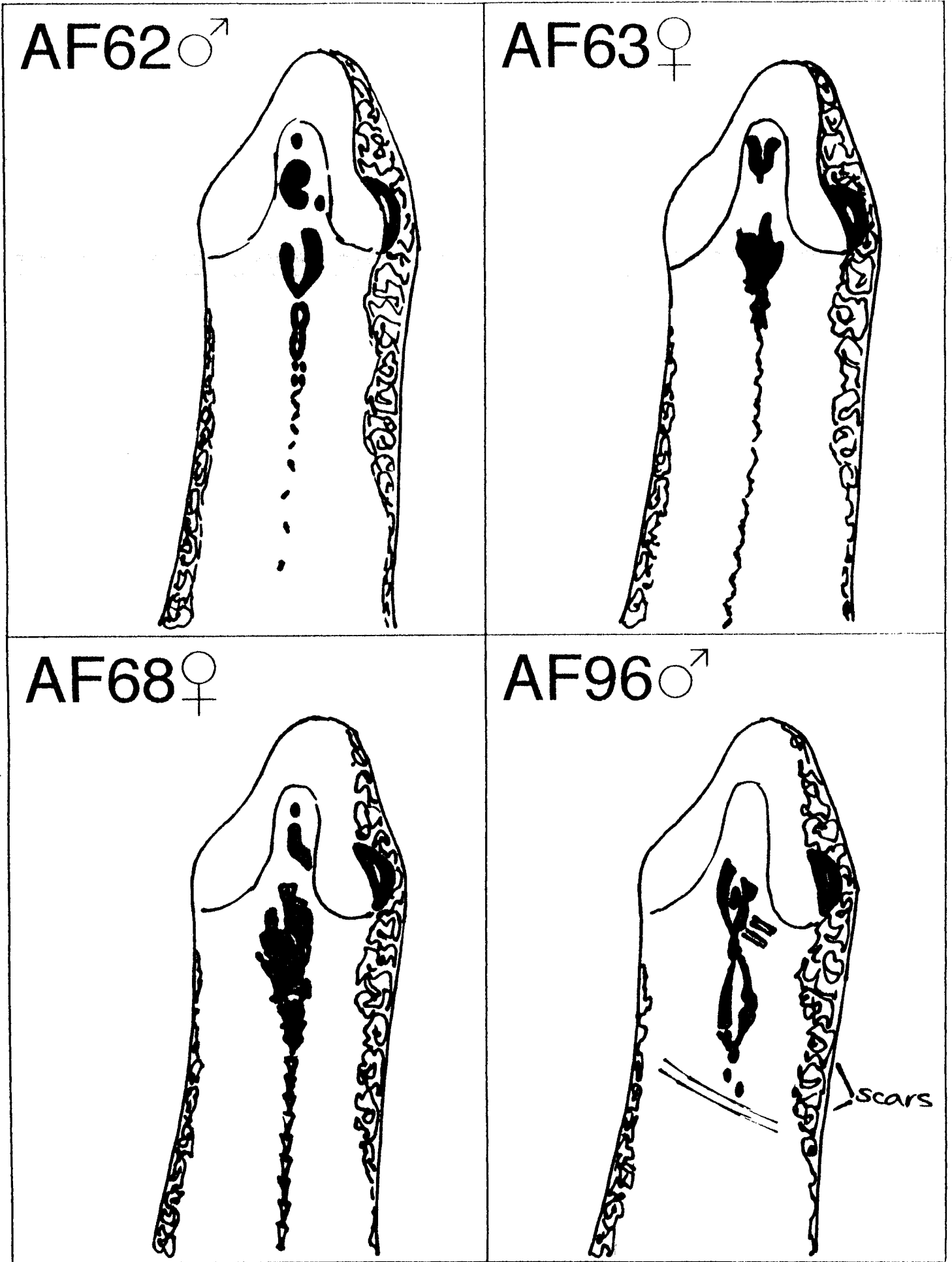

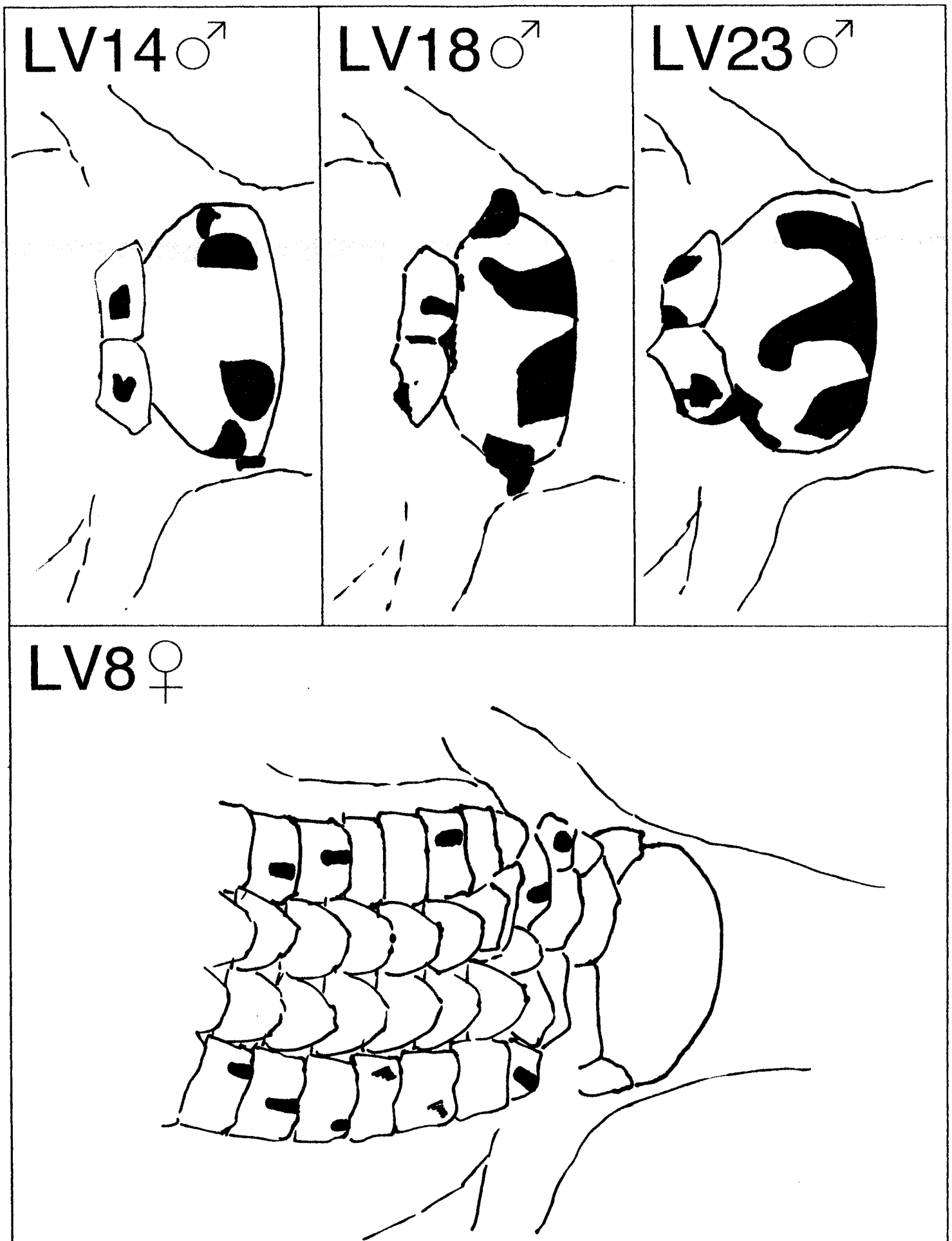Figure 2. Identification of individual slow-worms

Figure 3. Identification of individual common lizards

AF Encounters per Site
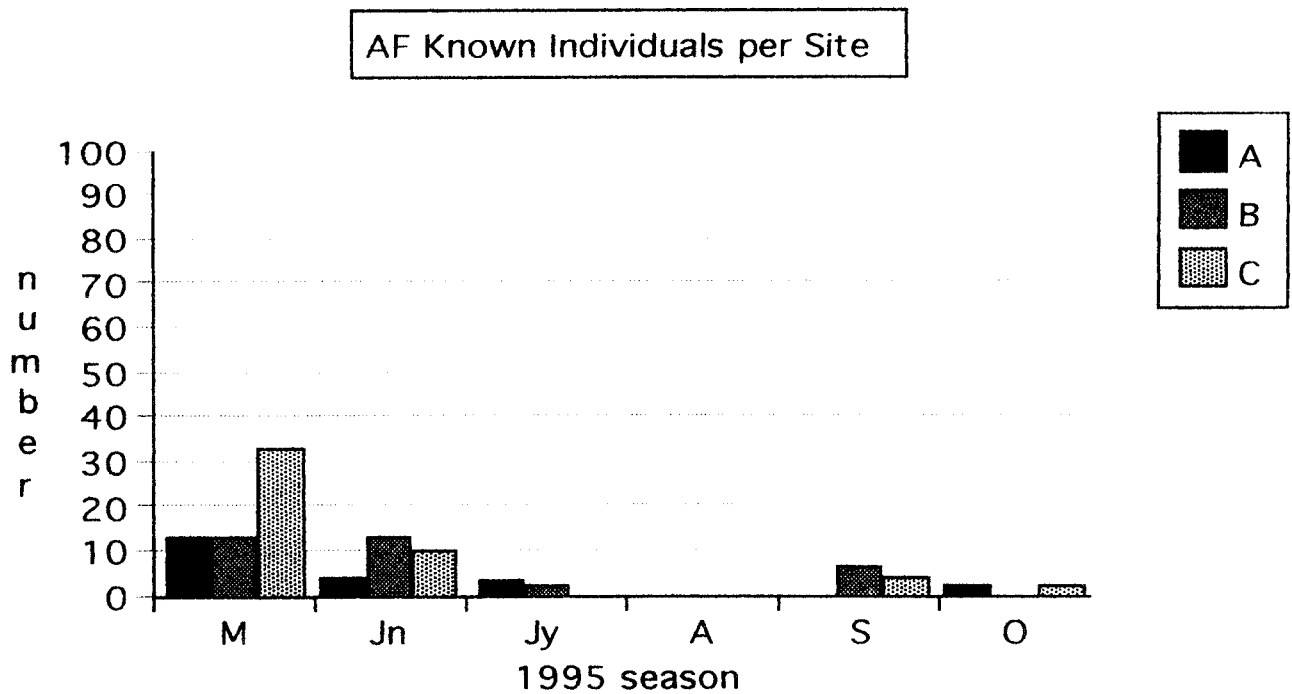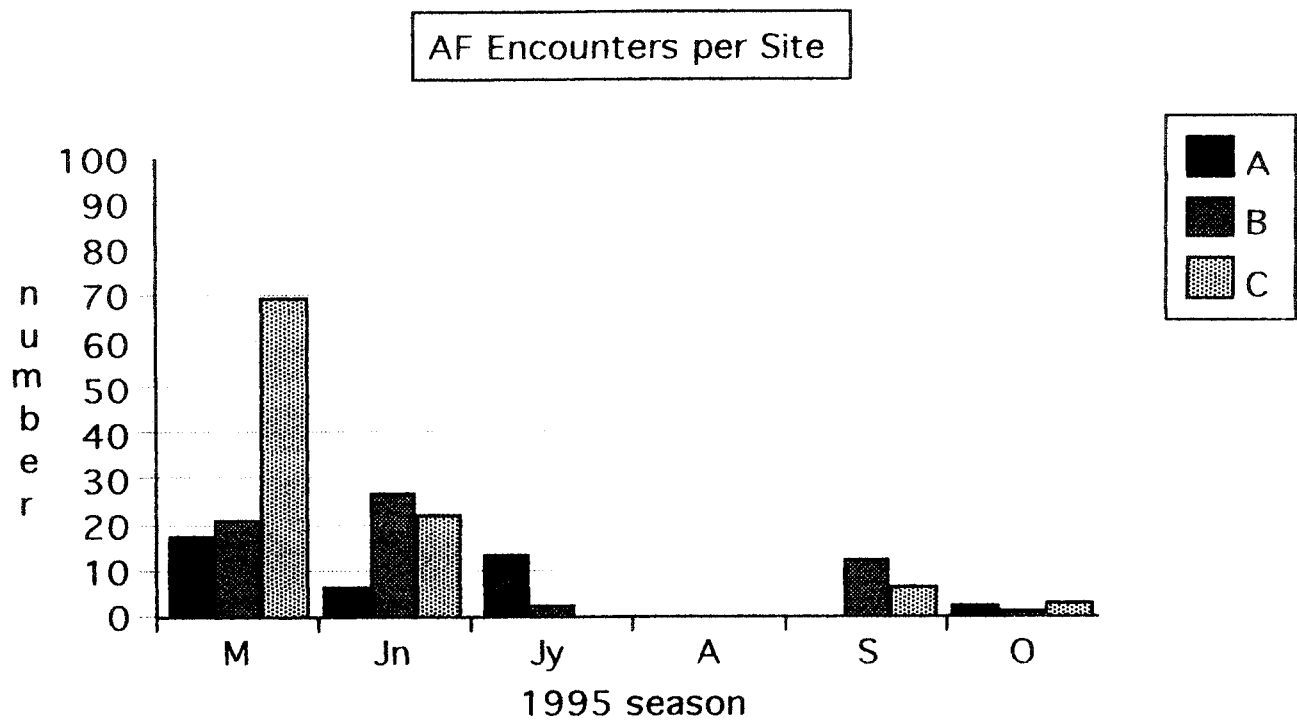
AF Known Individuals per Site

Figure 4. Encounters of, and use of sites by, slow-worms 1995 season: 1 May-19 October

The common lizard population, in contrast, consisted mainly of adults. Very few subadults and no 1994 juveniles were found during the 1995 season. Again, the rough grassland was by far the best for lizard encounters - 45 here during May compared with just one on the flower slope. Encounter rates on Site B remained in single figures throughout the year and lizards were seen in the wood only on very hot days in July.

The vast majority of identified individual slow-worms were found just once but those that were found repeatedly were usually associated with a time of change, such as sloughing, going into or coming out of aestivation/hibernation over a two or three week period. Once the change was complete, they were not seen again. Lizards were quite different and known individuals caught several times were often under different refuges but always on the same site.

The times and temperatures at which slow-worms were encountered (Figure 5) varied during the year. The first part of the morning was the most successful - from 10-11 am in May and June - but there seemed to be a 'second sitting' from 1-3 pm.

On the temperature front, slow-worms were seen above ground between 8° and 22°C but 11-17°C seemed to be the preferred window.

Lizards operated at generally higher temperatures - 11-24°C on average with very few encounters below 10°C - with a morning peak of activity in May between 9 and 10 am. Although there were few time periods in the day when no lizards were found, in September and October there were again two 'sittings', mid-morning and early afternoon.
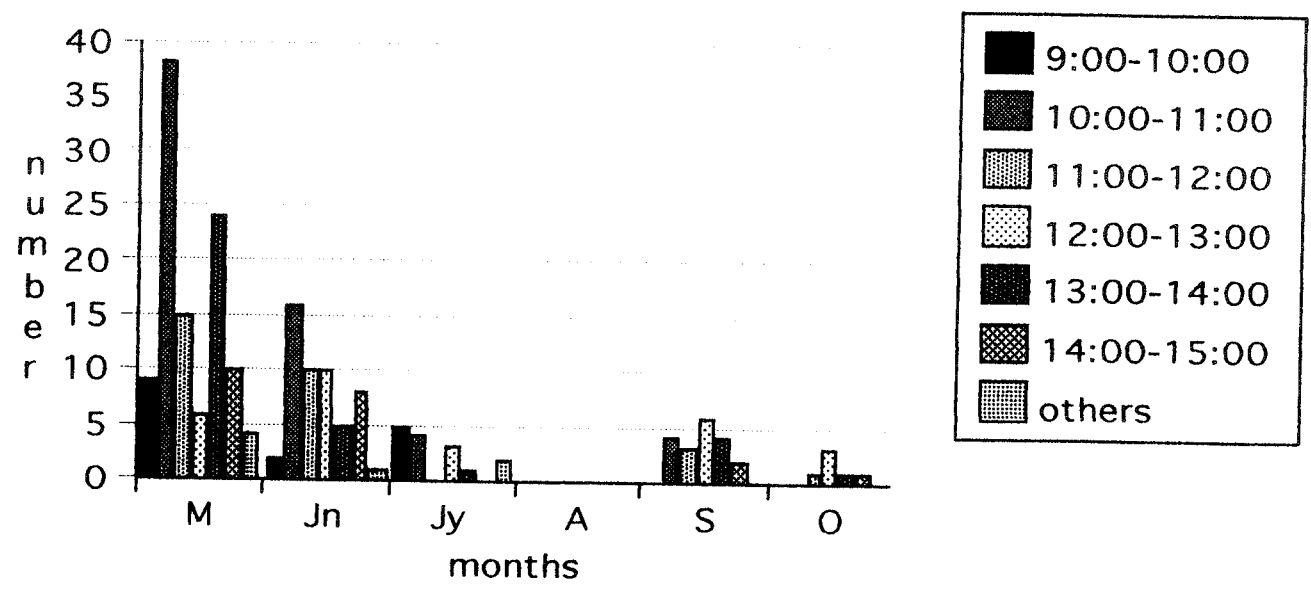
Refugia

The 1995 season's hot weather made temperatures under tins in mid-summer soar to over 50°C and still in the low 40s at 7 pm. While tin certainly attracted slow-worms in May and early June, in this exceptional summer it quickly became too hot for them and was outstripped in encounter rates by roofing felt throughout the year, with corrugated asbestos and carpet also scoring highly (Figure 6). Hardboard was also reasonably successful and all of these materials warmed up more slowly and retained their heat longer than tin. Temperatures beneath these refuges, even in high summer, were nothing like as extreme as those under tins, varying perhaps 2-8° higher than the soil beside the refuge, compared with perhaps 25° higher under a tin.

Lizards too preferred roofing felt as both a basking site and a refuge, although the high number of lizard encounters in the grass around the refuges indicated their alertness to intrusion.

Drought

Slow-worm encounters following one of the hottest and driest summers on record (many August days were more than 5°C above normal with a local maximum of 31.5°C and no significant rain between 14 June and 2 September) were depressing (Figure 7). They dropped as anticipated during the hot weather but numbers were expected to rally in September and early October, boosted by the year's hatchlings. This did not happen. Only 14 slow-worms were found from the end of the drought to the final sighting of the year (2 September-19 October) and only five of those were hatchlings. Most of the survivors were on the flower slope. Lizards, on the other hand, appeared to recover well.

AF Encounters per Time of Day

Legend:
- 9:00-10:00
- 10:00-11:00
- 11:00-12:00
- 12:00-13:00
- 13:00-14:00
- 14:00-15:00
- others

AF Encounters v Temperature

Legend:
- 0-5
- 5-10
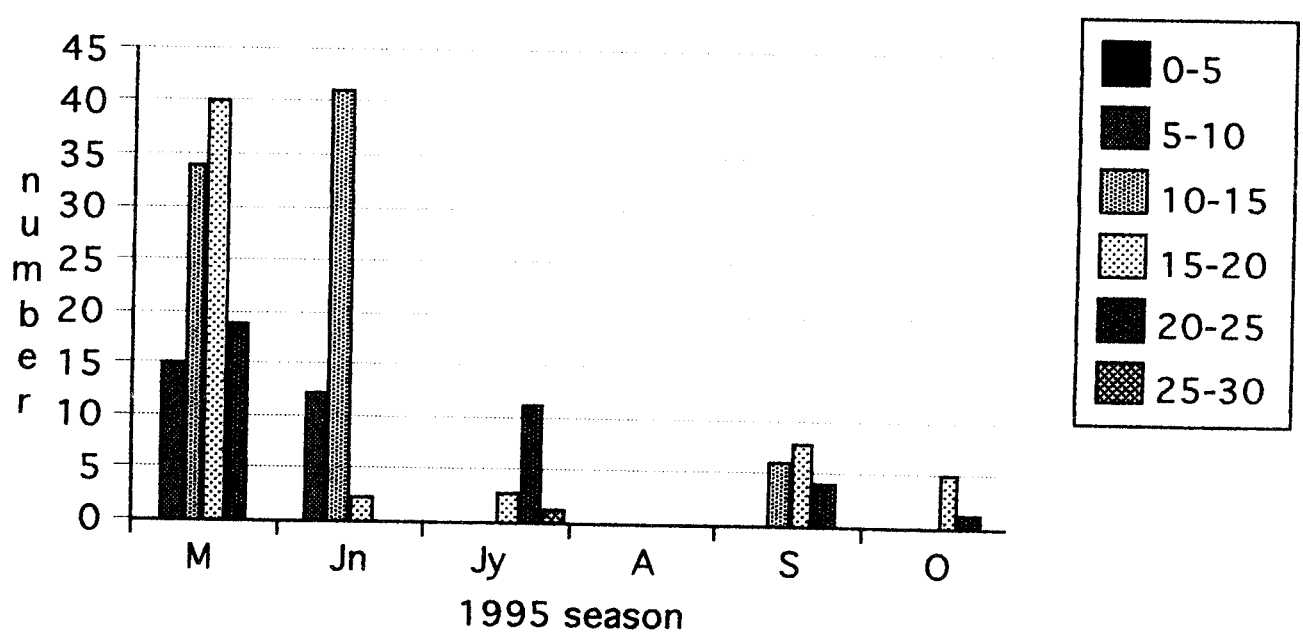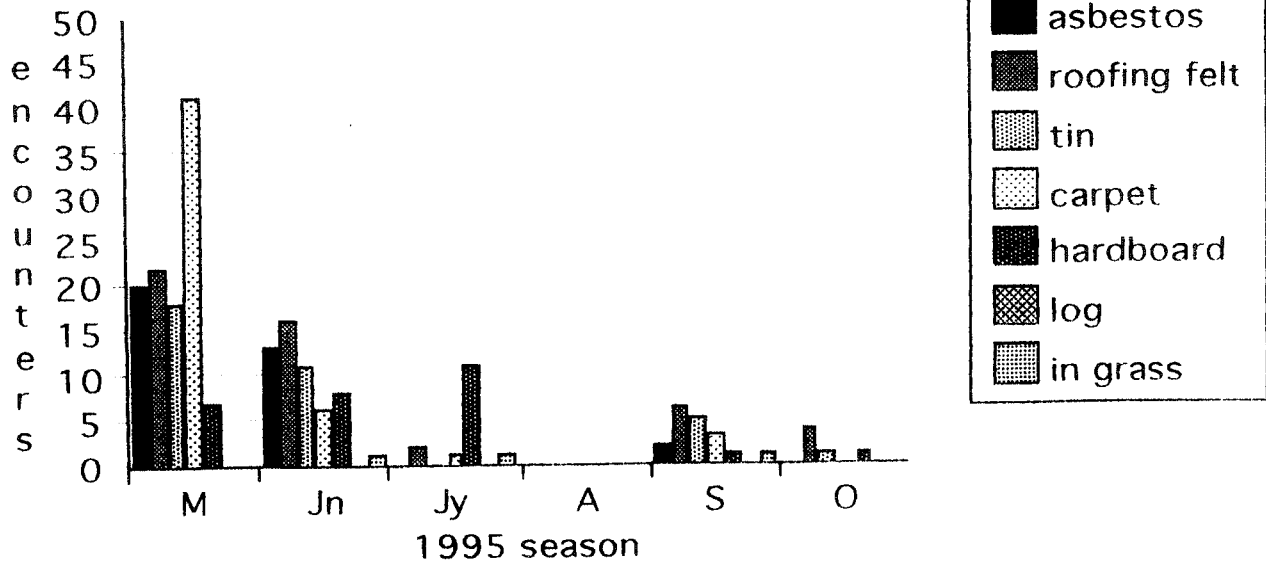- 10-15
- 15-20
- 20-25
- 25-30

Figure 5. Encounters of slow-worms - time of day and temperature, 1995 season: 1 May-19 October

a) Slow-worms

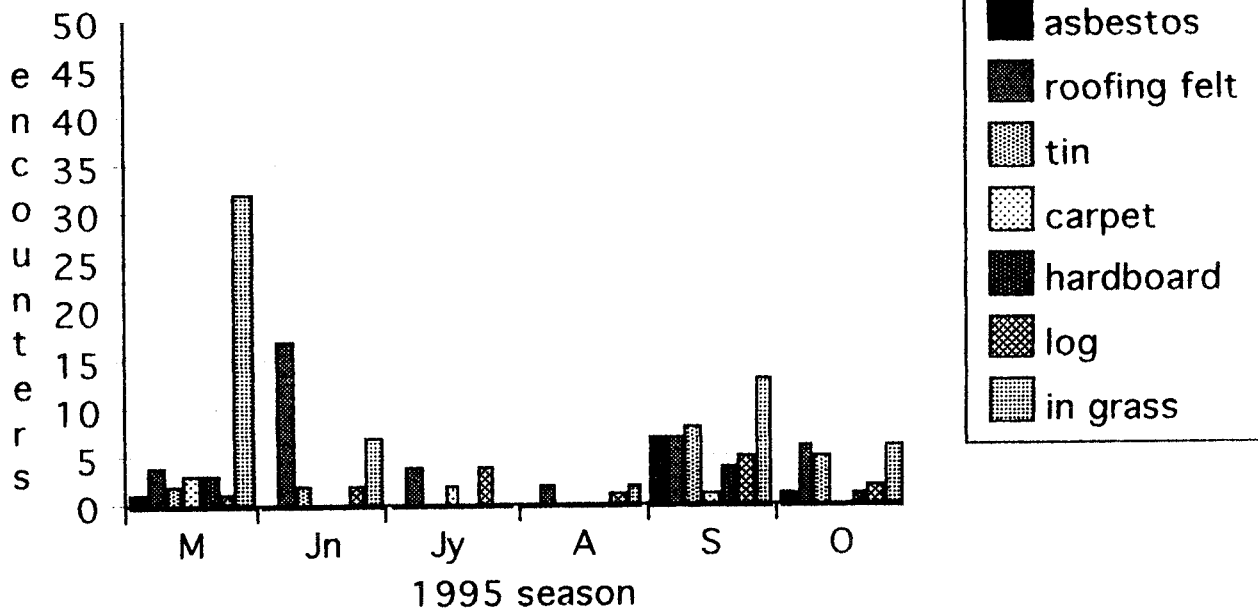AF Use of Materials 1995

b) Common lizards

LV Use of Materials 1995

Figure 6. Refugia - use of materials by slow-worms and common lizards, 1995 season: 1 May-19 October

a) Slow-worms AF Encounters per Site

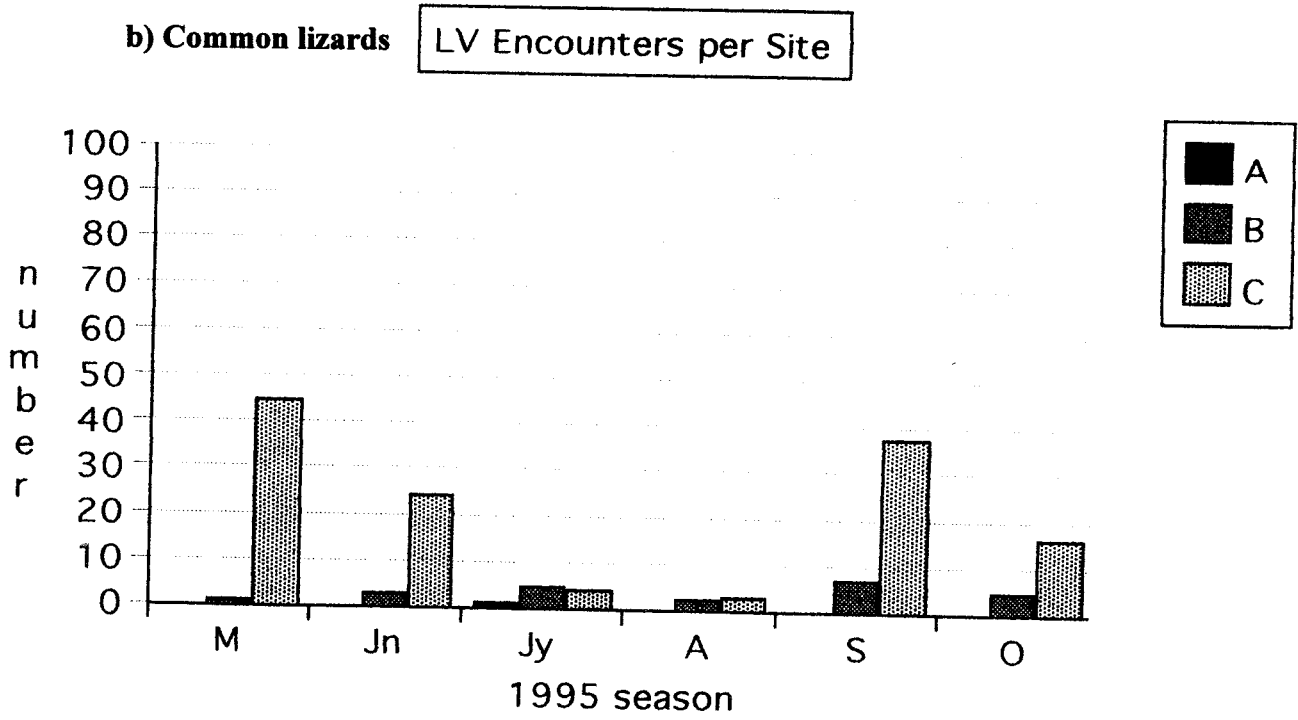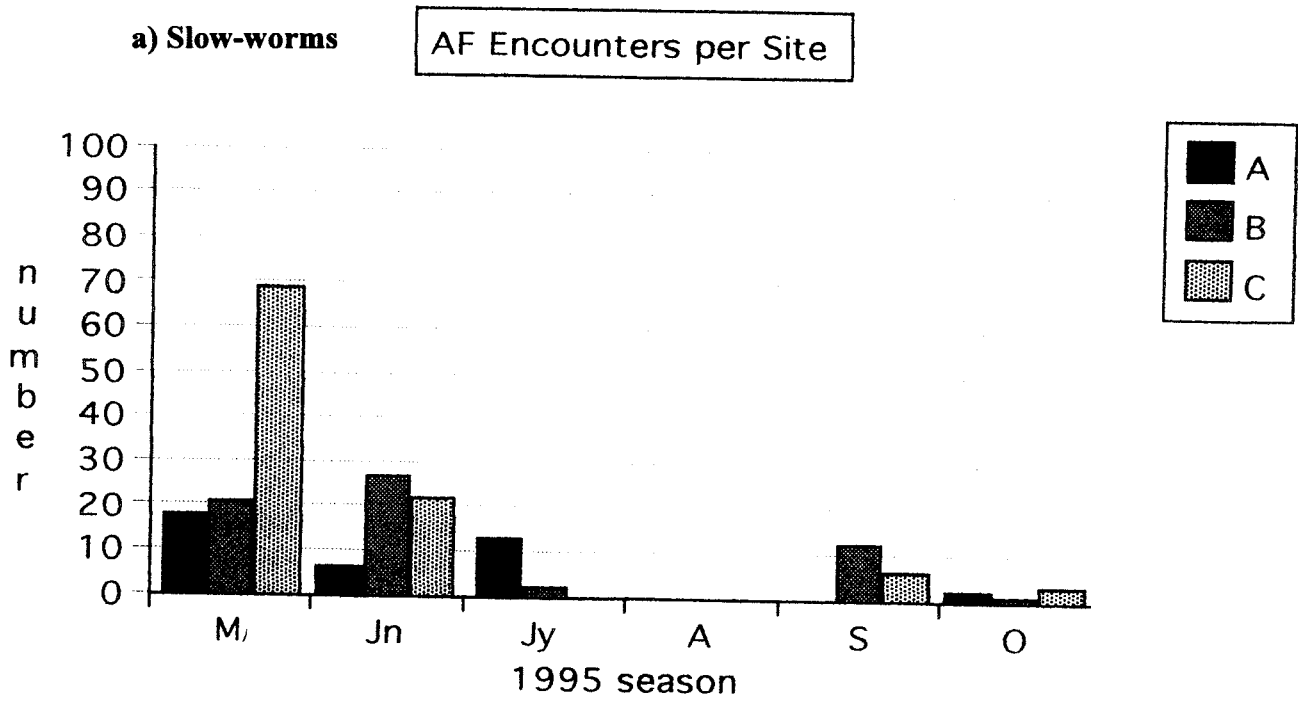**b) Common lizards** LV Encounters per Site

Figure 7. Encounters of slow-worms and common lizards, 1995 season: 1 May-19 October

One of the autumn slow-worms was a female last caught in June 1995, and was the only one to have been caught previously. Despite the intervening 12 weeks, she showed no growth or weight gain and was in extremely poor condition. Others bore old injuries which had not healed, had breathing difficulties or were also in poor condition. One, caught at 12:30 on 19 October, a sunny day of nearly 20°C, bore all the signs of having just emerged from a long period underground. Although the refuge - roofing felt - had been in the full sun for several hours and was dry and warm (16°C underneath the felt) the slow-worm was wasted and covered in condensation, extremely lethargic and had that sickly, shrunken look of slow-worms newly emerged in spring.

Concerns that the slow-worm population on this reserve crashed as a result of the extended drought and exceptional aestivation period cannot be confirmed until further monitoring takes place during the 1996 season. The following possibilities were considered:

❑ Had the slow-worms moved off the slopes until conditions improved? The reserve was searched but no more animals were found.

❑ Did predation suddenly increase? Most known bird and mammal predators occur on the reserve, but fox dropping analysis revealed no recognisable reptile predation.

❑ Was starvation a factor? Soft-bodied invertebrate prey disappeared for several weeks.

❑ Had they slipped from aestivation to hibernation? September's rain rapidly gave way to unseasonably cold temperatures and night frosts, despite the later Indian summer. Even then, no reptiles were seen.

❑ Was the period of aestivation too long and only those with greater reserves survived? No 1994 juveniles were found in autumn 1995, and the majority of encounters were with adult females. Were they perhaps pregnant but reabsorbed their young and survived that way?

❑ Had the population peaked? What this a cyclical crash?

Or was it possible that on this particular artificial site, where the clay was compressed when it was brought by lorry and tipped on to the land to form the bunds, there is a direct association between the compacted clay drying out through the long hot summer of 1995 and the small re-emergence rate the following autumn? If a JCB was taken to the bunds, would the slow-worms be revealed, shrivelled and dessicated in the clay?

Conclusion

Preliminary findings indicate that rough grassland plays an essential role in providing shelter and invertebrate prey for both lizard species in spring and early summer before vegetation has grown up. It remains the optimal habitat for the more philopatric common lizards. However, slow-worms appear to require a greater mosaic of microhabitats. Both species make use of a variety of refugia but roofing felt and other materials which heat up more slowly and retain their heat longer appear to be more successful survey methods than traditional tinning for reptiles.

The long summer drought of 1995 may have been catastrophic for slow-worms, at least on this reserve where they inhabit man-made London bunds. Dessication cannot be proved. But while the largely terrestrial common lizard with its broader diet appeared to rally after the hot, dry summer, the stark decline in autumn encounters for the fossorial slow-worm,

dependent on soft-bodied prey, is difficult to explain if the drought was not a factor. This will not be resolved until intensive monitoring resumes in spring 1996.