

UNIVERSITY OF SOUTHAMPTON

THE ECOLOGY OF THE SLOW-WORM

(*ANGUIS FRAGILIS* L.) IN SOUTHERN ENGLAND.

A Thesis submitted for the Degree of

Master of Philosophy.

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TO JANE

Slow-worm. The blind worm; a large viper, not mortal,  
scarcely venomous.

Dr. Johnson (1785), A  
Dictionary of the English  
Language.

If the adder could hear, and the blindworm see,  
Neither man nor beast would ere go free.

Old rhyme, quoted by Skeat  
(1910), An Etymological  
Dictionary of the English  
Language, 4th Edition.

ALL	Double, double toil and trouble: Fire burn and cauldron bubble.
2nd witch	Fillet of a fenny snake; In the cauldron, boil and bake; Eye of newt, and toe of frog, Wool of bat, and tongue of dog, Adder's fork and blind-worm's sting, Lizard's leg and howlet's wing, For a charm of powerful trouble Like a hell-broth boil and bubble.

Macbeth IV, i 10-19.

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UNIVERSITY OF SOUTHAMPTON

ABSTRACT

FACULTY OF SCIENCE

DEPARTMENT OF BIOLOGY

Master of Philosophy

**THE ECOLOGY OF THE SLOW-WORM (*ANGUIS FRAGILIS* L.)  
IN SOUTHERN ENGLAND**

by Nicholas Dane Smith

The slow-worm, *Anguis fragilis*, is a legless lizard in the family Anguidae. The ecology of the species was studied by weekly visits to two sites on the Isle of Purbeck, Dorset, England from 1981 to 1988. Other sites were visited less often. Animals were found under pieces of corrugated iron sheet that had been placed on the ground. Adults were photographed and identified on recapture by the pattern on the underside of the head. Pregnant females were retained in captivity until the birth of the young.

A total of 3456 slow-worms were found. Capture rates of known individuals were low, often less than once a year. There were differences in rate of captures of four sex and size class over the season. Males predominated in spring, females were found most often in summer and sub-adults and juveniles were commonest in autumn. Rates of movement were low. There was no evidence of territory formation.

Mating was only observed once. Females with sperm in the cloaca were found in May. The litters of 1 to 18 (average 8) were born in late summer. Larger females had larger litters but not larger young. In 1986, litter sizes were small with many of the young deformed. The sex ratios were not equal. The bias was to females at one site and to males at the other.

Cloacal temperatures, low for a temperate reptile, ranged from 9.8 to 33.2 °C, with a median of 24.9 °C. There was little evidence of precise thermoregulation. Cloacal temperatures were highest in summer on sunny days, but varied little with time of day. The distribution in the Iberian peninsula was shown by discriminant function analysis to be correlated with cooler, wetter climates.

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## CHAPTER 1. INTRODUCTION

### 1.1 ANGUIS FRAGILIS AND THE FAMILY ANGUIDAE

The slow-worm, Anguis fragilis L., is the type species of the lizard family Anguidae. The majority of the species in the family (81 of 90) are found in the New World. Many species in the family have elongate bodies and limbs that are often poorly developed or completely absent. There are two genera in the Old World, both limbless. Anguis, with a single living species, is found through much of Europe and western Asia. Ophisaurus Daudin, with twelve species, is found in North Africa, the Balkan Peninsula, Asia and North America. Ophisaurus apodus (Pallas), from south-eastern Europe and Turkey, is the slow-worm's closest living relative and is the only other species in the family found in Europe.

Anguis fragilis was originally classified as a snake by Linnaeus (1758), but it was later recognised as a lizard and placed in the family Zonuridae. Cope (1864) was the first to recognise the Anguidae as a family, including in it most of the presently known genera. The basis of the modern scheme for classifying the higher taxa of lizards was laid by Camp (1923). He placed the Anguidae in the superfamily Anguioidea, which is in turn in the Infraorder Anguinomorpha, along with other small families such as Anniellidae and Lanthonotidae. These groups are based on a long fossil history as well as modern forms (Meszoely 1970; McDowell and Bogert 1954; Rieppel 1980; Estes 1983).

The Anguidae arose in North America in the late Cretaceous. There are three extant sub-families: the Diploglossinae and Gerrhonotinae of the New World, and the Anguinae of both the Old and New Worlds (Meszoely 1970). The Diploglossinae and Gerrhonotinae are visible in the fossil record in the Eocene of North America. The Anguinae have been found in the Eocene of North America and Europe, but it is not known on which continent they arose (Estes 1983).

Anguis has a fossil history dating back to the Lower Miocene of Central Europe, where it arose from Ophisaurus. There are at least two extinct species (Klembara 1981).

There has been some disagreement over the phylogeny of the three subfamilies (Good 1987; Meszoely 1970; Rieppel 1980), but all of these authors agree on the basic scheme of the classification of the family. The three subfamilies, ten genera and ninety species (Pianka 1977; Good 1988) of the family are characterised by the presence of osteoderms, a broad retractile tongue, pleurodont teeth and certain features of the skull (Rieppel 1980).

The Anguidae have long been considered to be one of the prime candidates for the origin of snakes, a view not shared by Rieppel (1980). He argued that the problem of the origin of snakes is far from settled, and that there are no strong reasons for deriving the snakes from any extant lizard family.

#### 1.2 A BRIEF DESCRIPTION OF THE SLOW-WORM

The slow-worm is a medium-sized, elongate, limbless lizard. The head, body and tail are poorly differentiated, so that the general body form is sub-cylindrical. The animal is covered with very smooth overlapping scales which have osteoderms at their centres (Zylberberg and Castenet 1985). The tail when complete terminates in a sharp scale and is a little longer than the head and body together. Tail autotomy is practised fairly readily, but regeneration is very slow and never complete (Bryant and Bellairs 1967). Dely (1981) summarises the scalation of the slow-worm.

The coloration of the slow-worm shows considerable variation between the sexes, and between different size groups. New-born juveniles are gold or greenish-gold dorsally with a sharp change to solid black laterally and ventrally. There may be a thin black dorsal zig-zag line emerging from a dark spot over the pineal eye. As the animal grows the dorsal colour darkens to a shade of brown and the

black lateral regions become lighter. In males this lightening continues through adult life, so that old animals can be almost uniform grey or grey-brown laterally and dorsally, though the venter may be paler grey with some darker spotting. Adult females tend to retain the basic juvenile pattern, but there is a great deal of variation. Some remain very dark and show a prominent mid-dorsal zig-zag, while others become lighter, particularly ventrally. Nearly all females keep the sharp demarcation between the dorsal and lateral coloration typical of juveniles. All individuals over about 100 mm snout-vent length (SVL hereafter) have a pattern of spots on the neck and throat. The body pattern and coloration continues on to the tail, except for the tip of a regenerate which is often uniform black. Some males have a dorsal speckling of blue spots which may be very extensive. The number, shade and size of the spots varies seasonally and with the sloughing cycle (Simms 1970), but their significance is unknown.

There is also sexual dimorphism in head size. The head of a male is noticeably larger than that of a similar sized female. There are no other obvious external sexual differences, such as in the cloacal region, or in relative tail length, that are often found in many other reptile species.

At birth the slow-worm has an SVL of about 45 mm; the tail length (TL hereafter) is very similar. Average-sized adults of both sexes have an SVL of about 160 mm, with a complete tail of about 180 mm. An animal of 200 mm SVL can be considered very large in Britain, but SVLs of up to 290 mm are known from eastern Europe (Dely 1978). The largest recorded British specimen was an animal from Portsmouth of 489 mm total length (TotL hereafter) (Fairfax 1965). The SVL was not recorded, but can be estimated at 230 mm, on the assumption of a complete tail. The above account is based on Smith (1964), Dely (1981) and Simms (1970), as well as personal observations as appropriate.

There are three currently recognised subspecies of the slow-worm. These subspecies and the characters used to define them are due to Wermuth (1950). Anguis fragilis fragilis L. is the typical form found in the western part of the species' range, A. f. colchicus (Nordmann 1840) is the eastern form and A. f. peloponnesiacus Stepanek (1937) is endemic to the Peloponnese peninsula, Greece. The important characters used by Wermuth to distinguish the subspecies are the number of mid-body scale rows, the arrangement of scales in the parietal region of the head and the presence or absence of an ear opening (Wermuth 1950; Dely 1981). The typical subspecies tends to have fewer mid-body scale rows (26 or less; colchicus often has 28 or more), no visible ear opening (frequently present in colchicus) and broad contact between the prefrontal scales in the parietal region (no contact in colchicus). There is also a tendency for A. f. colchicus to be larger than A. f. fragilis (Dely 1972; Cruce 1970), and A. f. peloponnesiacus has a relatively long tail and some differences in pattern.

Unfortunately the situation is not as clear-cut as this brief description implies. The boundary between the eastern and western forms is very unclear in many areas of central Europe (Musters and in den Bosch 1982; Beshkov 1966; Dely 1974). Wermuth (1950) made assumptions about the distributions of the subspecies over large areas when there were no specimens available to him from those areas. He studied 618 specimens housed in German museums (pers. comm.), of which 304 were from German localities and 64 from French ones. There were no specimens from the U.K. or Finland, but nevertheless he included both countries within the range of A. f. fragilis. Voipio (1962) showed that Finnish specimens tended to have the colchicus suite of characters, and thus could not be A. f. fragilis. It is very likely, however, that Wermuth was correct in assigning British populations to A. f. fragilis, since our fauna is derived from northern France, and those populations are

certainly A. f. fragilis (Smith 1964; Wermuth 1950; Yalden 1980). The only British specimen cited in any taxonomic study is one from Guildford in the Leiden Museum (Musters and in den Bosch 1982); it has the fragilis suite of characters.

More recently, Dzukic (1987) studied the taxonomy of the slow-worm in Yugoslavia, clearing up some of the confusion in the region. A. f. fragilis tends to occupy the north, centre and west of the country and A. f. colchicus the east and most of the south. There is a fairly narrow region between the ranges of the two subspecies where animals with intermediate characters are found. This is similar to the situation in Hungary, where the Danube appears to form a natural boundary (Dely 1974).

### 1.3 DISTRIBUTION OF THE SLOW-WORM

The distribution of a species is a reflection of many factors of zoogeography, climate, behaviour, physiology and evolutionary history. Reptiles are ectotherms, so those species living in northern Europe have to compensate physiologically and behaviourally for the relatively low temperatures and sunshine hours in the cool temperate climates of these areas (Spellerberg 1976). In this context it is interesting that the slow-worm has one of the widest distributions of any reptile in the Western Palaearctic region. It is found in every major European country except Eire, (but see McCarthy (1977) and section 1.4), and in parts of south-western Asia.

A number of maps of the total distribution (i.e., range) of the slow-worm have been published in recent years. The best is probably that of Arnold and Burton (1978); the worst is undoubtedly that of Petzold (1971). At the regional level, most of the countries of northern Europe have published surveys which show the distribution, usually based on a Universal Transverse Mercator grid, in some detail, but unfortunately this is not true of southern Europe and south-

west Asia. For these latter areas information is only available from laborious literature and museum record searches. The ex German Democratic Republic, Italy and Poland have no published survey. Relatively uninformative maps or locality lists are available for Albania, Bulgaria, Greece, Iran, Rumania, Spain and Turkey, although Spain has a number of very useful regional surveys. Iceland has no indigenous reptiles. Liechtenstein (where the slow-worm is present; Corbet 1989), Monaco, San Marino and the Vatican City (where it is unknown if the slow-worm is present or not) have no published surveys, but all are too small to be significant at this scale. The reptiles of Gibraltar and Malta are quite well known, but the slow-worm is absent from both (Cortes 1982; Lanza 1973). Since data are lacking for many large areas, defining the distribution on a detailed scale for the whole of its range would be an enormous task, but it is possible to improve on existing maps, using a synthesis of published national and regional surveys along with selective use of other records, such as those from museums.

To arrive at a reasonable statement of the distribution of the slow-worm, all available national surveys and maps cited in Appendix 1 were reviewed. Literature and museum records, as well as regional surveys, were extensively consulted for Iran, Spain and Turkey. The least understood areas are now Italy and parts of the Balkan Peninsula. Figs. 1.1, 1.2 and 1.3, and the notes on page 14 show the result of collating these data.

A number of recent maps and faunal lists persist in showing a wide distribution for the slow-worm in Morocco, Algeria and Tunisia (Welch 1982; Petzold 1971). But, nearly a century ago, Boulenger (1891) argued strongly that the slow-worm was not found in these countries. He argued that the original citation by Gervais (1836) was based on a mis-identification of either Ophisaurus koellikeri Gunther (a limbless anguid lizard a little larger than the slow-worm),



or Chalcides chalcides (L.) (A scincid lizard, similar in size and shape to the slow-worm, but with four tiny three-toed limbs). There are no reliable records for this century, even though the herpetology of North Africa has recently been studied in much greater detail. Neither Pasteur and Bons (1960), nor Bons (1972) include the slow-worm in their lists of the Moroccan herpetofauna, although the latter author does not completely rule out the possibility of it occurring high in the Atlas Mountains. It is far more difficult to demonstrate absence than presence in such cases, but it seems improbable on climatic grounds that the slow-worm is found in North Africa today.

Similar considerations apply to the southern half of the Iberian Peninsula. There are a number of old citations for localities such as Sevilla and the Serra de Monchique, Algarve, Portugal (Bosca 1877; Crespo 1972; note 4, Fig. 1.1). These records have led some authors, such as Matz and Weber (1983) and Petzold (1971) to include the whole of the peninsula within the range of the slow-worm. As in North Africa, there are no recent records, and similarly there is the possibility of confusion with Chalcides chalcides which is widespread in the region. It is most unlikely that the slow-worm occurs in these hot and dry mediterranean climates. Chapter 8 discusses these problems in greater detail.

Figs. 1.1, 1.2 and 1.3 show that the slow-worm is found on many islands off the coasts of western and northern Europe. It is mainly absent from those most oceanic and northern in character, such as the Orkneys, Shetlands and Iceland. In the Mediterranean and Adriatic the situation is less clear. The slow-worm is absent from all islands in the western Mediterranean, although there is a single recent record from Sicily (Bruno 1970). There are a few recent records from the northern Adriatic, as far south as Corfu (Bruno 1980; Mertens 1961), and some older ones from the more southerly Ionian islands (Chondropoulos 1986). The

slow-worm is absent from all the more isolated islands of the eastern Mediterranean such as Crete and Cyprus.

The slow-worm has been found at considerable altitudes in a number of countries. Cabela and Tiedemann (1985) give a maximum of 2384 m in Austria. Kramer and Stemmler (1986) give 2100 m as the maximum in Switzerland, and similar altitudes are attained in the spanish Pyrenees (Hopkins pers. comm.).

There has been very little published, apart from general statements, on the preferences or use of habitats by the slow-worm. Most authors, such as Alvarez et al. (1984) agree that it lives in relatively damp, cool habitats, particularly in the south of its range. If this is true it would complement the observation that the slow-worm does not occur in hot, dry Mediterranean climates and tends to be restricted to higher altitudes in the south of its range.

#### 1.4 DISTRIBUTION AND STATUS OF THE SLOW-WORM IN THE BRITISH ISLES

The well-known Biological Records Centre map of the distribution of reptiles and amphibians in the British Isles (Arnold 1973) has been updated by Frazer (1983) and Stafford (1989). These maps are based on the Ordnance Survey 10 X 10 km grid. Additional records have been collected from a variety of sources (mainly personal communications and literature surveys) to produce Fig. 1.4, but it will be seen that the overall picture has not been greatly altered.

It will be noticed that there are a number of areas with a high local density of records that are surrounded by apparently under-recorded areas. It is a truism that maps of this type reflect the density of collectors rather than that of the collected, but it is sometimes difficult to see why some areas of the country are so much better recorded than others. The high density of records around London and the Home Counties is perhaps not surprising, but is there a real lack of naturalists in such parts of eastern and central

England as Cambridgeshire, Lincolnshire and Nottinghamshire or a scarcity of slow-worms? On the other hand, there is a consistency in the relative paucity of records in upland areas such as the Pennines, the mountains of South Wales and central and northern Scotland.

There is only one record of the slow-worm from Ireland (The Burren, County Clare, M3602 (McCarthy 1977)) that can be considered reliable. A single animal was caught, but it was reportedly mating and others were seen, which was taken to indicate a small population. There was nothing to suggest whether this population was indigenous, from escaped pets, or an accidental or deliberate introduction. If the slow-worm is a native species, then it is reasonable to argue that it arrived in Ireland at the same time as the common lizard, Lacerta vivipara Jacquin, Ireland's only native and widespread reptile (Lamhna 1979). This would have been about 9000 years BP, as the Ice Age retreated but before the sea-level rose (Stuart 1982; Atkinson et al. 1987; Yalden 1982). Since the time when Great Britain was isolated from the continent, both the slow-worm and the common lizard have become widespread and have reached northern Scotland. They are frequently found in the same habitats in Britain (pers. obs.). If the slow-worm had reached Ireland before the complete filling of the Irish Sea, as the common lizard presumably did, it is reasonable to argue it would have spread as the latter species, and so would have been as widely recorded. On the continent the two species have similar distributions in the north of their ranges, but the common lizard is found a little further north than the slow-worm in both Sweden and Finland (Gislen and Kauri 1959; Terhivuo 1981), implying that it can tolerate slightly cooler climates. This may be the reason that the common lizard was able to spread north in time to reach Ireland, but the slow-worm was not. The conclusion from this indirect argument is that the Burren population (if such it is) is not a natural one. It is not possible to determine which of

the other possible origins is the true one.

There has been a great deal of interest in the status and conservation of British reptiles in recent years. Most concern has been shown for the smooth snake, Coronella austriaca Laurenti, and the sand lizard, Lacerta agilis L., since they have by far the most restricted distributions and threatened habitats of the six species (Dent and Spellerberg 1988; Goddard 1981; House and Spellerberg 1983; Spellerberg and Phelps 1977). These two species have also generated most interest from the point of view of analysing and explaining their present distributions from the geological history and past climate of the British Isles (Yalden 1980; Beebee 1978; Jackson 1978).

Nevertheless, there has been some attention paid to the "commoner" species, i.e., the common lizard Lacerta vivipara, the adder Vipera berus (L.), the grass snake Natrix natrix L. and the slow-worm. Prestt *et al.* (1974), in their review of the changes in status of all six reptile species, could only provide a single anecdotal case of a reduction in population of the slow-worm due to habitat damage. Cooke and Arnold (1982), using the data from the Biological Records Centre that formed the basis of Arnold's (1973) map, concluded that the slow-worm had declined in status nationally. It was known that the grass snake had declined markedly between the two study periods (pre- and post-1960) and, since it showed a similarly low ratio of pre- to post-1960 10 km square records, so the slow-worm must also have declined.

Cooke and Scorgie (1983) studied the status of the commoner species by an analysis of the answers to a country-wide questionnaire. They found that the slow-worm was common in south-west England (an area that was defined to include Dorset, where the present study took place), widespread but not common in Wales, southern England, East Anglia and south-west Scotland, and sparse or rare elsewhere. Populations had decreased in most regions, usually due to

habitat destruction. This work was dependent on the respondents' subjective answers to the questions, but it is instructive to compare these results with an equally subjective assessment of Fig. 1.4.

### 1.5 LITERATURE AND PREVIOUS WORK ON THE SLOW-WORM

The literature on the slow-worm is enormous, reflecting its familiarity not just to herpetologists, but to naturalists in general. Scanning bibliographical works such as Biological Abstracts and the Zoological Record and the literature lists of relevant papers readily generates well over 1000 references. However, over 75% of them fall into one of two categories: (a) field guides and similar faunal works, frequently popular in character, which often quote earlier authors uncritically, and (b) regional or local species lists, which may include some original data, but are normally useful only for data on distribution.

Morphologically the slow-worm is relatively well-known. There has been a lot of work on many aspects of the soft anatomy, development, histology and osteology. Since the Second World War, however, the emphasis of herpetology has changed generally to physiological, ecological and related areas. This work is discussed, as it relates to the slow-worm, in the following chapters. Despite this change of emphasis, there has been no long-term study of the ecology of slow-worm populations, in contrast to many other British and European reptiles.

At the popular level, the natural history of the slow-worm is well known. The following account is distilled from well-known works such as Rollinat (1934), Simms (1970) and Smith (1964). The slow-worm emerges from hibernation in March and mates in April or May. The males are said to fight over females. From three to over twenty young are born (i.e., the slow-worm is viviparous) in August or September. A wide variety of invertebrates is eaten, but slugs and earthworms are preferred. The slow-worm is preyed upon by

many species, such as some of the smaller raptors, thrushes and snakes. It has been suggested that, to avoid predation by birds, slow-worms, particularly females, mimic the adder's dorsal pattern (Smith 1974 (no relation); Avery 1974). The slow-worm lives in a variety of habitats, including heath and woodland edges, and is relatively tolerant of man. They can often be found in suburban gardens and are seen as the gardener's friend because they eat so many slugs. Slow-worms rarely bask in the sun as other lizards do, and are slow and rather snake-like in their movement; indeed that is how they got their English name. They are often killed from a mistaken belief that they are venomous, or just because they superficially resemble snakes. The slow-worm is noted for its longevity, as it is the world's longest-lived lizard, with a claimed maximum age in captivity of 54 years (McFarlan 1988).

#### 1.6 AIMS OF THE PRESENT STUDY

Autecological studies on reptile species were the first to try to understand the ecology of these animals. They provide basic data on a wide variety of aspects of the biology of a species. The majority of the earlier studies were done in America, where Fitch was probably the best known worker in the 1950's and 1960's. He studied a variety of Middle American lizard and snake species in some detail. Probably his best known work was on the copperhead, Agkistrodon contortrix, a widespread relative of the rattlesnakes, Crotalus (Fitch 1960).

This type of study has been the starting point for more searching work into community ecology, life history strategies, thermoregulatory behaviour and a host of other areas. Autecological studies have tended to raise more questions than they answer, though they are obviously still necessary for many reptile species as basic information on their biology is lacking. Autecological studies are very often the start of an understanding of the ways that

reptiles and other species adapt to their environments.

Because of its familiarity to many European naturalists, laymen and professionals, and the large literature on it, there seems to have been an assumption by many ecologically inclined herpetologists that a lot is known about the slow-worm. It has been indicated that this is not so. There are very few papers in the journals that deal with any aspect of the ecology of the slow-worm, and the large number of popular works often uncritically copy their predecessors without citing any basic data.

The aim of the present study is thus to find out something of the ecology of the slow-worm. Data were collected on population density and structure, movements, thermal relations, growth rates and reproduction. Questions such as: do they thermoregulate? and: do they form and hold territories? are addressed. These data are compared with previous work.

Notes to Figs. 1.1, 1.2, 1.3 and 1.4.

Fig. 1.1 Distribution of the slow-worm in western and northern Europe.

Fig. 1.2 Distribution of the slow-worm in eastern Europe and the Soviet Union.

Fig. 1.3 Distribution of the slow-worm in south-eastern Europe and south-west Asia.

Arrows indicate islands where the slow-worm is known to be present. The numbers on the maps refer to the notes below:

- 1 The only reliable Irish record (McCarthy 1977).
- 2 Present in West Berlin (Muller 1976); included as found in all East Germany although no survey.
- 3 Confirmed in Serra de Sintra (Malkmus 1979).
- 4 Old probably false records (Bosca 1877; Crespo 1972).
- 5 Fragilis/colchicus boundary in Hungary (Dely 1974) and Yugoslavia (Dzukic 1987).
- 6 Only reliable record for Sicily (Bruno 1970).
- 7 Old record, probably erroneous (Dolmen 1978).
- 8 Records of unknown validity (Gislen and Kauri 1959).
- 9 Unlikely to be found (Gislen and Kauri 1959).
- 10 Old records from larger Ionian islands (Chondropoulos 1986), but recent information lacking.
- 11 Presumed present, at least at higher altitudes.
- 12 Old and unreliable records, Euboea and Thaxos.
- 13 The Peloponnese Peninsula; A. f. peloponnesiacus found mainly at higher altitudes (Bringsoe 1986).
- 14 Very little data for northern and eastern Greece.
- 15 Populations from northern Iran are disjunct from those in Turkey and the Caucasus, which are disjunct from those in western Russia and eastern Europe.

Fig. 1.4 Distribution of the slow-worm in the British Isles. There are 216 10 km square records additional to Arnold (1973), shown by crosses, of which 73 are from Frazer (1983) and 44 from Stafford (1989). The rest were from personal sitings, the literature and local Biological Record Centres.



Fig. 1.1 Distribution of the slow-worm in western and central Europe.

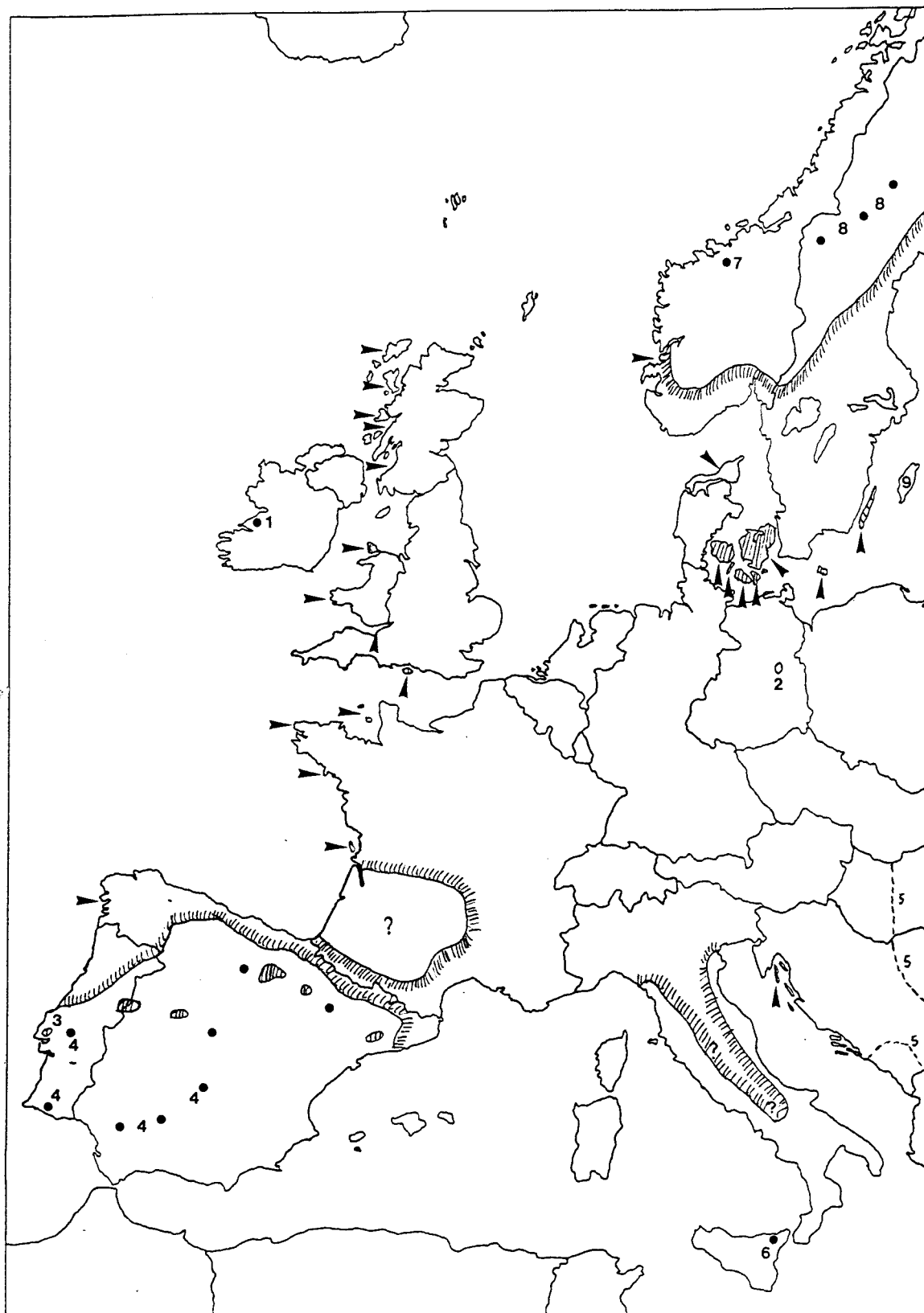


Fig. 1.2 Distribution of the slow-worm in eastern Europe and the Soviet Union.

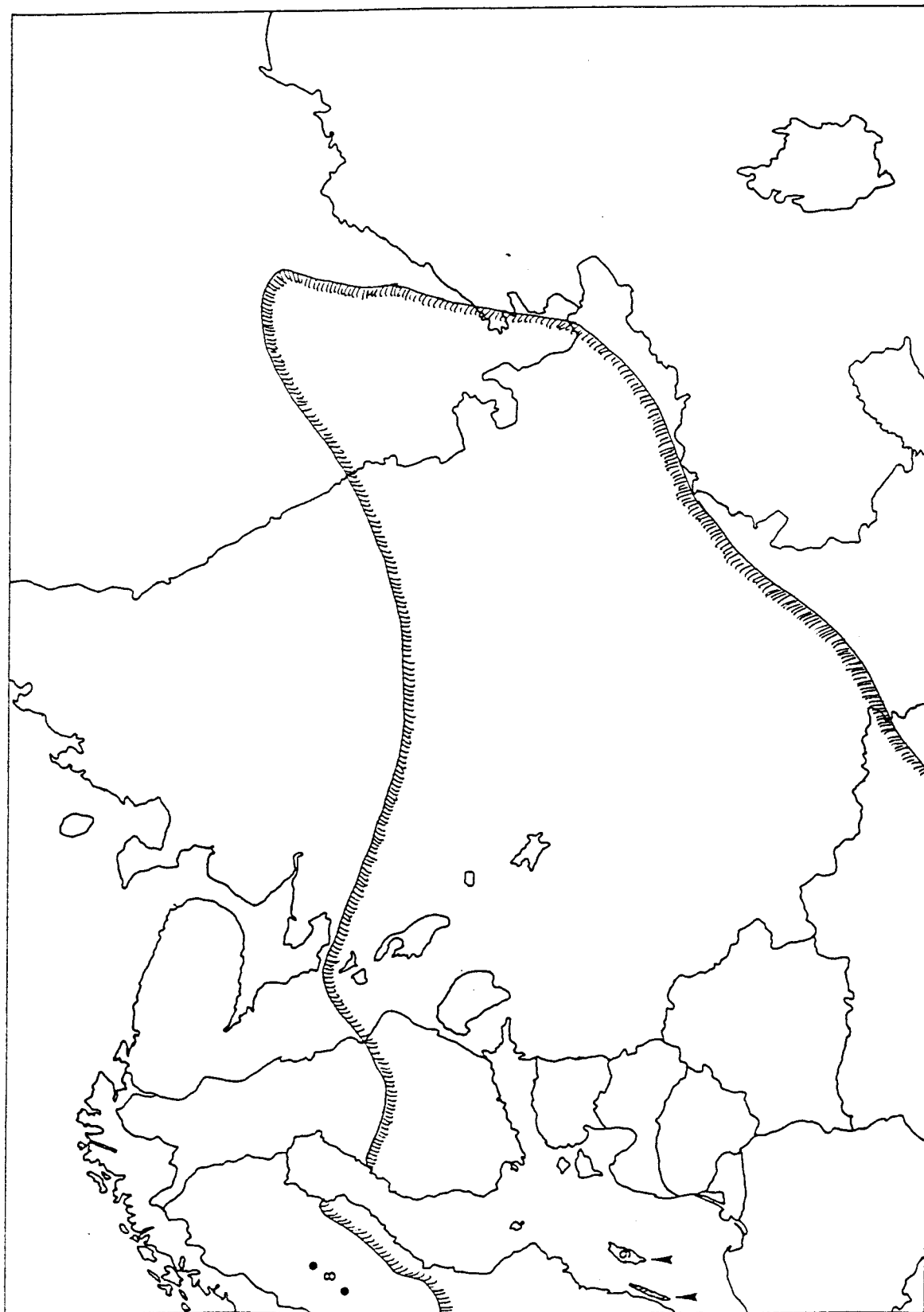


Fig. 1.3 Distribution of the slow-worm in south-eastern Europe and south-western Asia.

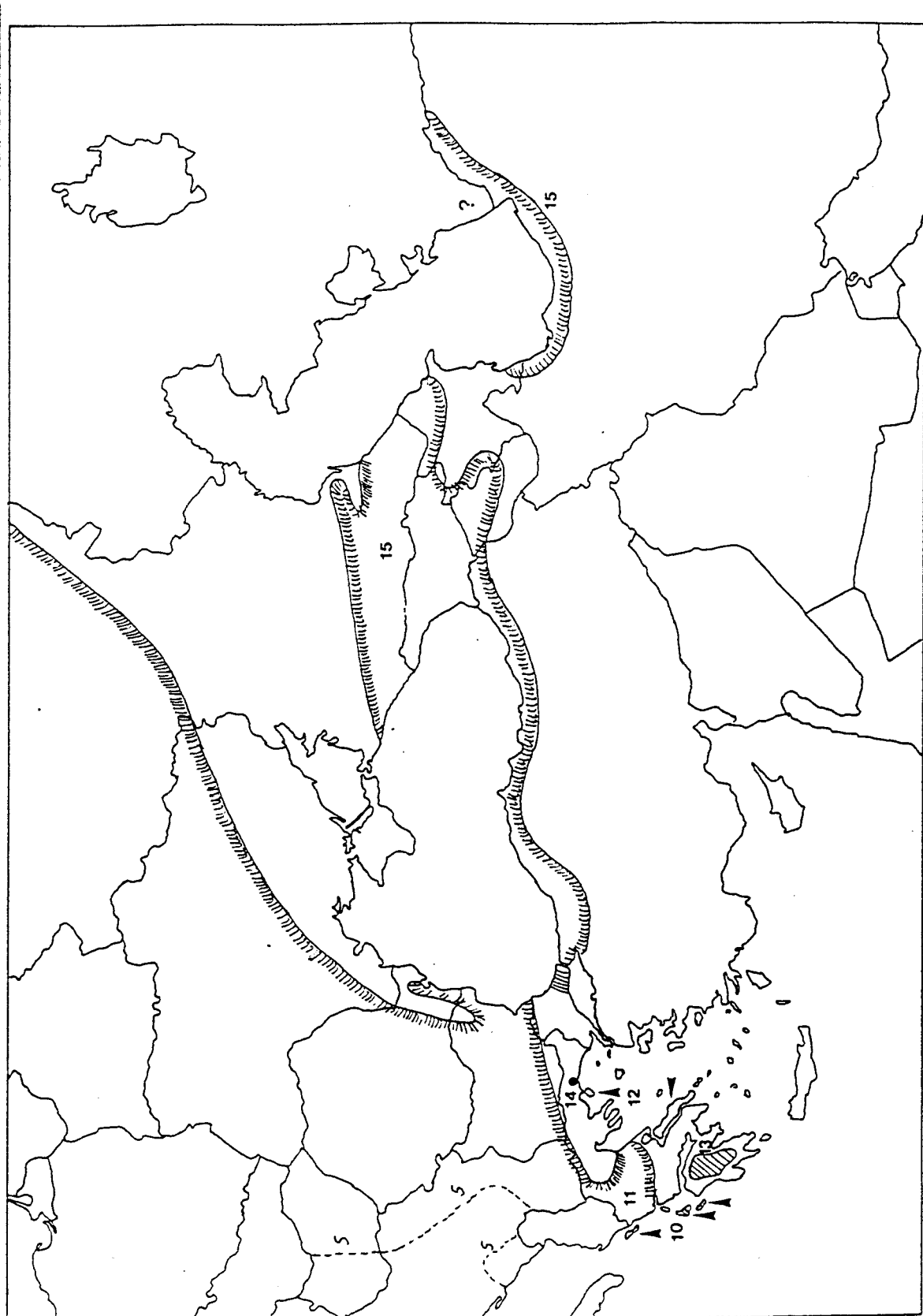
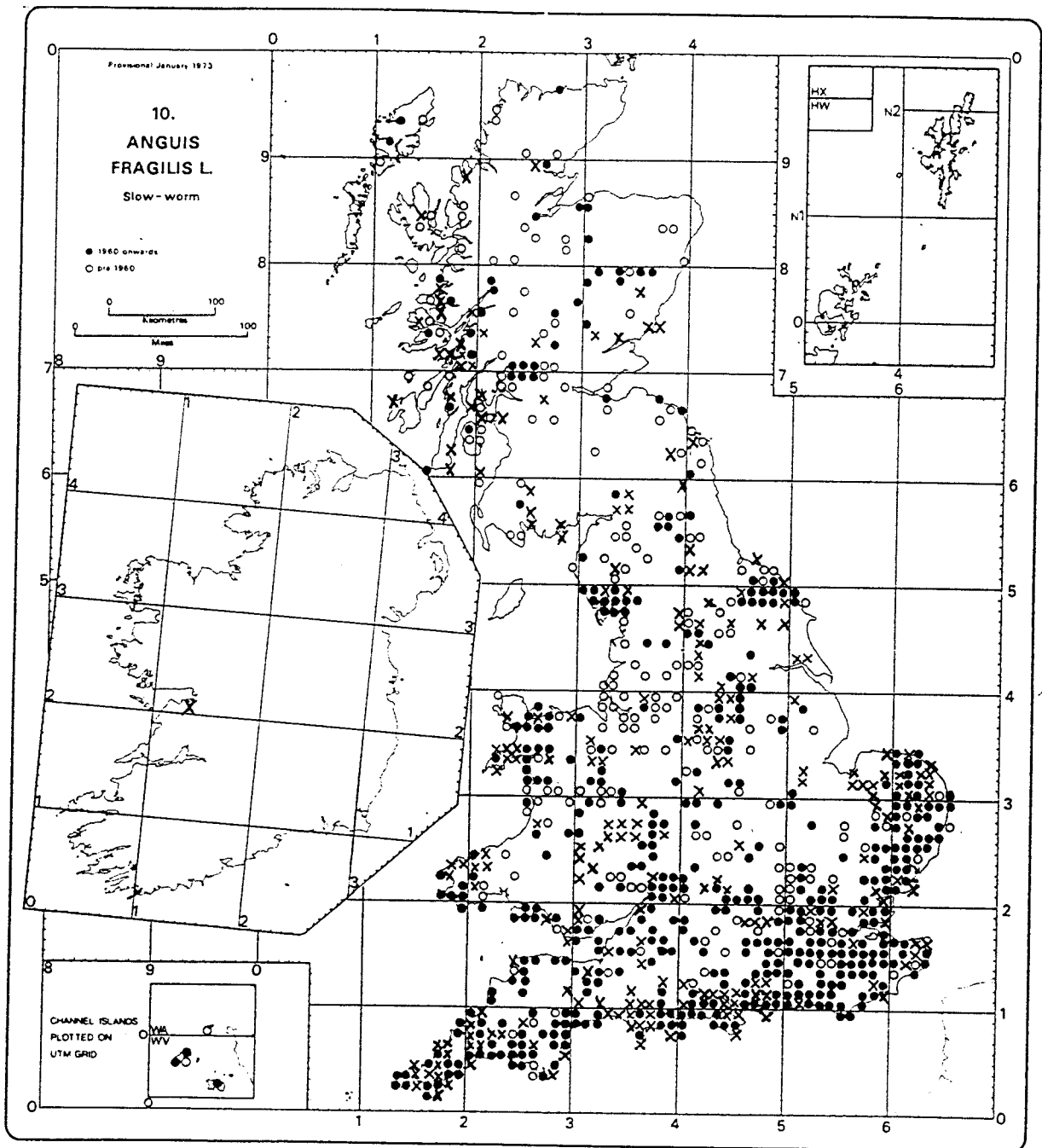


Fig. 1.4 Distribution of the slow-worm in the British Isles.



## CHAPTER 2. GENERAL METHODS

### 2.1 INTRODUCTION

In recent years the range of techniques available for studying the ecology of reptiles has increased considerably. Many advances have been concerned with tracking individual animals over considerable times and distances (Kenward 1987). All such methods must obviously be tailored to the attributes of the species as well as the needs of the researcher.

The slow-worm has a number of attributes which make most of the standard field methods, as well as many of the modern techniques, difficult or impossible to use. Under most weather conditions it is very reluctant to bask openly, making it very difficult to find and observe (but see Stumpel (1985)). The elongate, smooth body means that it is not feasible to attach any of the presently available radio-tracking transmitters or other tracking devices, such as Cobalt-Samarium magnets (Lloyd, pers. comm.), that have been used to follow fossorial and semi-fossorial animals. The slow-worm is far too small a species to envisage using any known implanted radio transmitter. Its scales are much too fine and closely aligned to the body for clipping, and of course there are no digits to permit toe-clipping.

It was possible to overcome some of these problems, at the expense of some compromises. These methods, and their problems and compromises, are discussed below and in later chapters.

### 2.2 STUDY SITES

After some initial investigation, two main sites came to provide the bulk of the data used in this study. Both are on the Isle of Purbeck, an area of lowland heath, farmland and chalk grassland in south-east Dorset. Gregory (1976) categorized the climate of southern Dorset as AMw, i.e.,

with a growing season of at least nine months, annual rainfall neither reliably nor frequently low, but with a winter maximum.

The first, which is hereafter called DA, was the overgrown garden of an uninhabited cottage 3 km south of Wareham. The vegetation was composed mainly of a variety of thick grasses, along with bracken (Pteridium aquilinum (L.)) and bramble (Rubus L. spp.). There were also stands of hawthorn (Crataegus monogyna Jacquin) and garden escapes and ornamentals such as Rhododendron L., apple (Malvus pumila Mill.) and lupins Lupinus L. The useful area of the site was 0.1 ha. It was bounded by a railway embankment, a large arable field and an area of impenetrable scrub.

The second main site, here called DC, was a stretch of the disused Wareham to Swanage railway line at Corfe Castle. The railway was opened in 1885 and closed and dismantled beyond Furzebrook in 1972 (Reeve and Hawkins 1980). Most of the line had been allowed to become derelict and overgrown since closure. The vegetation consisted of adventitious species. Extensive areas of the track bed had become overgrown with bramble and ivy (Hedera helix L.). There were also quite large stands of Valerian (Valeriana officianalis L.) and Horsetails (Equisetum L. sp.). The site extended from the end of the platform on the down side of the station to a point 150 m to the south of it. A stretch of 50 m on the east side of the track bed was also used. It was only feasible to use a narrow strip of the track bed for finding slow-worms, mainly the area covered by Hedera and Rubus. Beyond this strip the embankment fell away sharply and was covered with an impenetrable layer of Rubus. On the other side of the strip was the bare ballast of the old track bed. The useable strip was thus estimated to be 3 m wide. The site an estimated area of 0.1 ha.

A number of other sites were visited less regularly than DA and DC, and these are listed below with their codes.

DB; A short stretch of the Wareham to Swanage line mid-

way between DA and DC.

DE; A small area immediately adjacent to Wareham station.

GA; The island of Steep Holm in the Bristol Channel, 6 km west of Weston-super-Mare, Avon. The island is a limestone outcrop of the Mendip Hills, with an area of 20.1 ha and a maximum altitude of 78 m. Alexanders (Smyrnum olusatrum L.) covered most of the centre of the island. Bramble, elder (Sambucus nigra L.), nettle (Urtica sp. L.) and Sycamore (Acer pseudoplatanus L.) were also common.

HA; A section of Roydon Woods, a Hampshire and Isle of White Naturalists Trust nature reserve. A strip of heath at the edge of the wood was used.

SB; A small area at the edge of the campus of the University of Southampton. This site was open woodland with a ground covering of Hedera, Rubus and grasses.

In addition, there were a number of other sites that were visited irregularly, and colleagues and members of the public also provided information. In the chapters that follow, the majority of the analysis and discussion is concerned with the two major sites DA and DC, but data from the other sites will be used and discussed where appropriate.

Meteorological data were obtained for the Dorset sites from the Meteorological Office publication "Monthly Weather Report", using the data for Swanage and Winfrith.

## 2.3 FIELD METHODS

### 2.3.1 Searching and captures

It was not possible at any site to use standard capture methods, such as pitfall trapping or drift fencing, which have been employed in population studies of reptiles. No site could be visited frequently enough and the potential for environmental damage was considerable. At DC these methods would have been physically impossible because of the track-bed ballast.

It has often been observed that many reptile species, including the slow-worm, can often be found under stones, planks of wood, metal sheets and other discarded objects. Such artifacts have previously been used in studies of reptile ecology that involve species that are difficult to find by standard methods (e.g. Goddard (1981) on Coronella austriaca). These artifacts are not traps; their usefulness to the investigator depends on the animal finding them and remaining under them long enough for there to be a reasonable chance of capturing them. If these artifacts are used, it is possible to visit a site at any time that is convenient, which is certainly not so with a trapping technique. On the other hand the factors that influence the use of the artifacts by the animals are unknown.

At all sites pieces of corrugated galvanised iron sheeting were used. These sheets measured 1.2 X 0.6 m and are colloquially known as "tins", and will hereafter be referred to as such. At DA 75 tins were placed in an approximate 5 X 5 m grid. At DC 30 tins were placed at 5 m intervals on the west side of the line. On the east side there was a small 5 X 5 m grid in an area of grass and umbellifers, and a partial 5 m interval line as the station buildings permitted. At both sites tins that had previously been discarded were left in place and used. Fig. 2.1 shows a plan of site DA.

### 2.3.2 Site visits

The study season normally lasted from March to October. Slow-worms appeared out of hibernation earlier, or entered it later, only in very exceptional years. The two main sites were visited on one or two days per week during the season and once or twice each on those days, as weather, time and other conditions allowed. Frequent visits to DA began in 1981 and to DC in 1982, and lasted until 1987, with occasional visits being made in 1988. Table 2.1 shows the numbers of visits to the most important sites for each year



of the study. At each visit, all tins were turned over and all vertebrates were recorded. General weather conditions, such as air temperature, cloud cover and approximate wind strength were noted.

### 2.3.3 Data from finds of slow-worms

Slow-worms found under a tin, and the occasional individual seen basking, were caught by hand. A few individuals escaped, but the capture rate was high at 93% over all sites. The usual reasons for failing to capture an animal were (a) more than one animal under a tin, allowing one to escape as the other was caught, and (b) the quickness of very active individuals on hot days in the dense (and often thorny) vegetation under the tin.

Upon the capture of an animal the following were recorded as appropriate: date, time (always recorded as BST), tin number, identity of animal, sex or age category, SVL, TL, whether tail complete or regenerated, weight, body temperature, any distinguishing marks, reproductive state, stage in sloughing cycle, and any noteworthy behaviour. The identity of any other vertebrate under the tin was also noted. The definitions of these data categories are amplified below.

The identification of individuals is discussed below (2.4). After some initial work, all animals were classified into one of four sex and size categories. Adult males and females were distinguished by the criteria given in section 1.2. A SVL of 130 mm was taken as the minimum size for an adult, based on the minimum size of reproductive females and the development of adult-type coloration and pattern in males. Non-adults were divided into two classes. Animals that were similar in size and coloration to new-born young were classified as first-year juveniles. Second-year and older animals could normally be identified by their size (over 70 mm SVL in spring, compared with 45 to 50 mm for first-year animals), and their coloration that was similar,

but somewhat darker, to that of first-year juveniles. These categories and their validity are further discussed in Chapter 3.

The snout-vent length (SVL) was measured from the tip of the snout to the posterior edge of the scale row covering the cloacal opening.

The tail length (TL) was measured from the posterior edge of the scale row covering the cloacal opening to the tail tip, including the pointed terminal scale in a complete tail. Taking these last two measurements was not always straightforward. There was always some potential error because of the slow-worm's smooth scales, frequent struggling and liability to autotomy. This error was reduced with practice.

The completeness or otherwise of a tail was easily determined from a combination of its length, the presence of the sharp terminal tail in a complete tail or the presence of a regenerated portion in a previously autotomised organ.

The weight of an animal was measured by placing it in a small plastic bag of known weight and suspending it from a "Pesola" letter balance of either 10 g or 50 g capacity. With care it was possible to weigh all animals accurately to 0.1 g, except in windy conditions.

The body temperature was measured with a "Schultheiss" narrow-bulb thermometer calibrated to 0.1 C. inserted gently in to the cloaca. Care had to be taken to avoid injuring the animal and to ensure that useful data were obtained. Cloacal temperatures were not taken from animals of less than 130 mm SVL or from heavily pregnant females. Readings taken more than 15 seconds after capture or from animals that struggled vigorously were not counted because of the possibility of heat transfer to or from the animals' body.

The methods used in the study of reproduction are discussed in section 2.5.

Animals that were about to slough had a distinctive

blue-grey tinge to the ventral scales. Immediately before sloughing the skin felt loose and pieces would sometimes come away in the hand. It was not possible to determine any other stage in the sloughing cycle.

If an animal evaded capture all possible data, such as tin number, age or sex category and time were still recorded. All animals were released at the point of capture in the minimum possible time.

## 2.4 IDENTIFICATION OF INDIVIDUALS

### 2.4.1 Introduction

It is of great benefit to the study of the populations of a species if the animals in that population can be individually identified. Ferner (1979) reviewed the methods for marking reptiles and discussed the criteria which should determine their use. It has already been noted that the slow-worm has a number of attributes that make the standard scale- or toe-clipping techniques impossible to use (Section 2.1). Branding, whether hot or cold, was considered too invasive, since it was possible that it could have caused causing unnecessary harm and led to unpredictable changes in the behaviour or survivorship of individuals. Stumpel (1985) obtained very few recaptures using hot-wire branding in a study of the slow-worm in the Netherlands. A non-invasive method which, as Dunham et al. (1988) indicate, has been little used in population studies of reptiles is photography. For this method it is necessary that the species has a pattern which is unique to an individual (a "fingerprint"), and that it can be photographed readily and assigned to the correct animal on recapture. This method has been used with success in studies of Lacerta agilis, where the dorsal pattern was recorded (Dent 1986), and in the Great Crested Newt, Triturus cristatus, using the bold ventral pattern (Hagstrom 1973). In both these cases the pattern is complex (especially in L. agilis) and does not lend itself to scoring or other objective method, such as

that used by Hailey and Davies (1985) on the Viperine Snake, Natrix maura L. in Spain. These authors described the "information content" of the bold and easily scored pattern on the ventral scales. It was suggested some years ago by Carlstrom and Edelstam (1946) that identification by photographs was possible in the slow-worm (as an aside in a discussion of its use in the grass snake) so it was decided to see if the method was appropriate to the present study.

#### 2.4.2 The photographic method

The most suitable pattern on the slow-worm which can be used for photographic identification, i.e., the one which could possibly be unique to each individual and was easy to photograph, is the spots and lines on the underside of the head and neck. To photograph this area, the fore-part of the animal was held gently but firmly between a block of foam, into which a groove had been cut, and a clear perspex sheet. The foam and perspex measured 12 X 10 cm. The fore-parts of the animal were manipulated carefully into the groove so that the underside was visible through the perspex. The groove was cut off-centre so that a small piece of paper with the animal's basic details (number, sex, date and measurements) on it could be placed next to the head to be included in the photograph. The camera was a Canon A1 35 mm SLR with a Tamron 90 mm SP lens set at its minimum focusing distance of 39 cm. This combination produced an image of half life-size on the negative. The camera could easily be held in one hand and the animal in the block in the other. The free part of the animal's body was supported by allowing it to twine naturally around the fingers. Two or three photographs were taken of each animal at different exposures on standard 125 ASA black and white film. Contact prints were made from each negative, and the best contact from each individual was sorted into its sex and size class and stapled to 8 X 5 inch cards, 20 to a card.

The pattern of a captured animal was compared to the

contact prints using a X10 hand magnifier. It normally took from one to ten minutes to identify an animal or show it to be a new capture, depending on the number of photographs to be searched and their quality. If the animal was a new capture it was given an identification consisting of the two letter site code and the next vacant number starting at 1.

#### 2.4.3 Advantages and disadvantages of photography

It is very useful if an identification method immediately allows the animal to be classified as new or a recapture. This is obviously not possible with the photographic method since the animal is not permanently marked. The success of the method also depends on the quality of the photographs; poor quality can easily result in non- or mis-identifications. The sex and measurements can be used as a check, but not as positive identification. The method is potentially time consuming and involves the use of fairly delicate equipment in the field. There is a lot of variation in the neck patterns between animals; it was much easier to identify those with a strongly contrasting pattern.

A potentially serious problem is raised by the question of whether the pattern is constant over time. It became obvious as the study progressed that the pattern changed as the animal matured (Section 1.2). Very young juveniles lacked a useful pattern, as the throat was nearly uniform black with a few very small paler spots. It became of the adult type at about 100 mm SVL. The lack of pattern, the small size of the animals, the large numbers of the smaller size classes caught and the changes in the pattern inevitably led to confusion and misidentification. It was thus decided to restrict the photography to animals larger than about 100 mm SVL. Information on growth rates, numbers and other population parameters thus had to be found by less direct means (Chapters 5 and 6).

A related question concerned the constancy of the

pattern once it had become of the adult type. If there had been a gradual change in the adult pattern over the period of this study, then there would always have been the possibility of misidentification. A considerable number of animals were kept in captivity during this study, often for quite long periods and through several sloughing cycles. In all cases the pattern stayed constant, so that there was never any doubt about the identity of the individual. A number of animals were followed in the field for five years or more, but it was always possible to identify them on recapture, even when successive captures were made up to two years apart. Furthermore, there was never any indication that the patterns of two animals were so similar so as to cause confusion.

There were several advantages to the photographic method over other possible methods. There is a minimum of disturbance, it involves no injury to the animal, it is usually fairly quick and the cost is low once a suitable camera and lens are available. If there is doubt about an identification, another photograph can be taken for later detailed comparison with others. But, in a species such as the slow-worm, as this discussion should indicate, there are few alternatives once branding is discounted. Newer technology, such as the electronic tagging advocated for domestic dogs and also used with trout (Penman pers. comm.), may be an alternative to photographic identification, but at the time of writing the detection equipment is very expensive.

## 2.5 THE STUDY OF REPRODUCTION

To obtain data on aspects of the reproduction of the slow-worm it was necessary to keep pregnant females in captivity until the birth of the young. Pregnant females could be identified from their plump appearance and the presence of small scars on the neck, which resulted from the strong grip of the male's jaws during copulation. These

scars disappeared after copulation, so their presence indicated recent mating. It was also sometimes possible to find motile sperm in the cloacal fluid of a recently mated female. Mating was only observed once in the field, so it was necessary to use the less direct data given above to infer the date of mating and the gestation period.

All obviously pregnant females were kept until the birth of the young in individual containers 30 X 30 cm in the natural light cycle at a temperature of approximately 22 deg. C (range 20-24). They were fed on slugs and worms. Water was provided ad libitum.

When the young were born, their SVLs, TLs (both to 0.5 mm) and weights (to 0.01 gm) were taken. The female was re-weighed and measured. All dead fetuses, obvious deformities and unfertilized eggs were noted. Dunham et al. (1988) argued that the "tertiary" clutch size, i.e., the number of fertile embryos in a clutch of eggs, is the only reasonable count to use in the analysis of reptilian populations. This is the definition used here, but for the analysis of the relationships between the size and weight of the young themselves, only those that were alive and without obvious deformity were considered. All females and viable young were released at the point of last capture of the mother within two days of the birth.

The sexual activity of males could sometimes be shown by the presence of motile sperm in the cloacal fluid. There was also a marked tendency for them to evert the hemipenes upon capture during the presumed mating season.

## 2.6 STATISTICAL ANALYSIS

Many statistical tests require that the data are normally distributed. If a parametric test is carried out without testing for the assumptions, then the results will be suspect. The probability of a false result will depend on how far the data depart from normality and the sensitivity of the test being used. Non-parametric tests,

normally based on an analysis by ranks, are available as substitutes for the majority of parametric tests.

In the chapters that follow, all data were tested for its normality before any further analysis was carried out. If there was significant deviation from normality a non-parametric test was used. Tests were carried out using the methods of Sokal and Rolf (1981) and the STATGRAPHICS Statistical Graphics System (STSC Inc.). A probability of 0.05 (5 %), two-tailed, is taken as the maximum for statistical significance, and degrees of freedom (d.f.) are normally given.



Fig. 2.1 Plan of site DA.

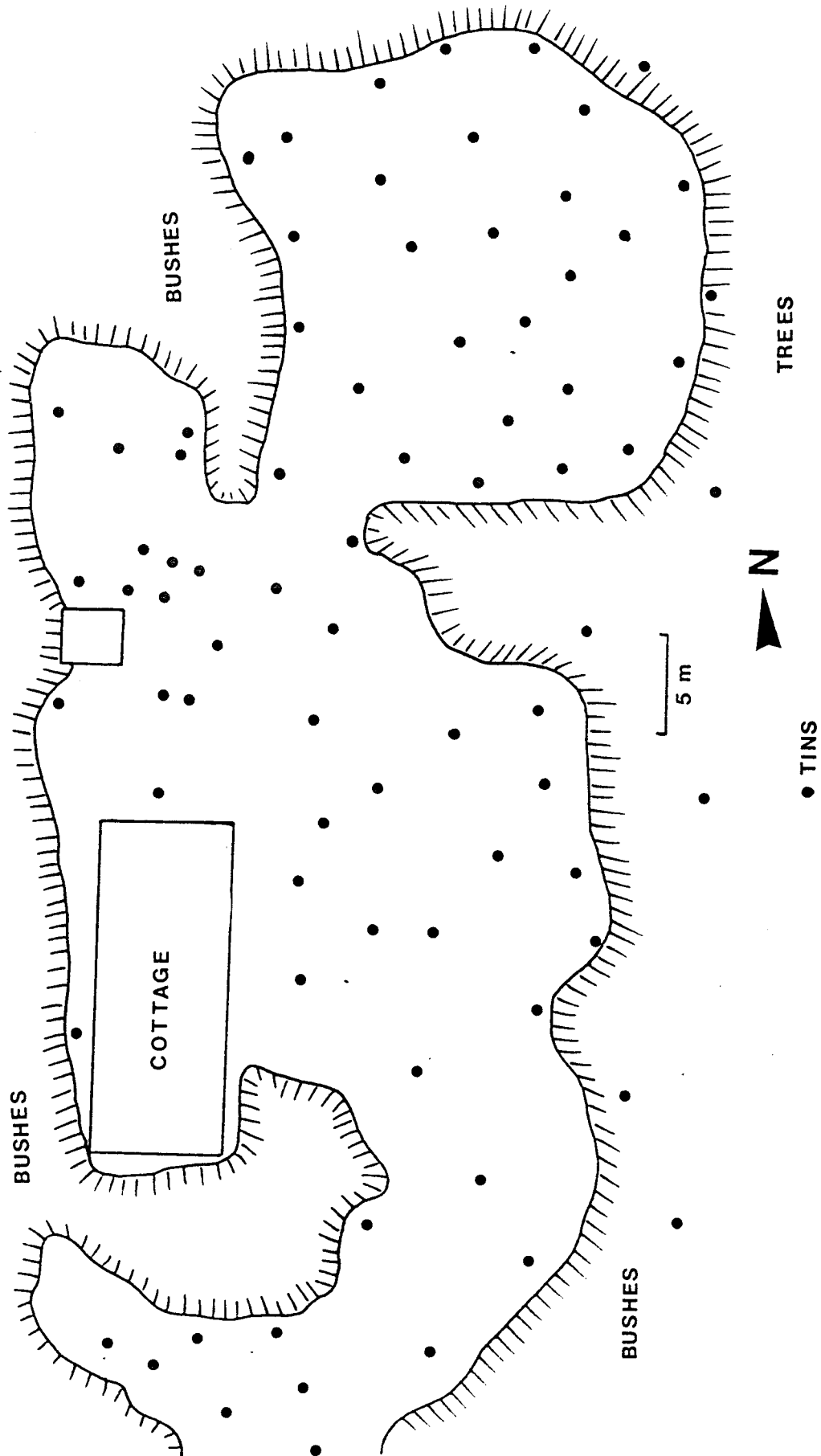


Table 2.1 Numbers of visits to main and secondary sites for each year of the study.

SITE	YEAR								TOTAL
	1981	1982	1983	1984	1985	1986	1987	1988	
=====	=====	=====	=====	=====	=====	=====	=====	=====	=====
DA	10	66	60	61	59	47	24	5	332
DB		18	2	7	13	1			41
DC		34	52	50	67	42	19	6	270
DE			3	7	13	5			28
SB	1	7	16	27	2	1	1		55
GA			2	6	2			1	11
HA			10	7					17

## CHAPTER 3. CAPTURES AND MOVEMENTS

### 3.1 INTRODUCTION

This chapter presents the results of the numbers of slow-worms found at the two main sites. The variation in the numbers of each sex and size category is related to the month and the weather conditions at the time of the visit to the site. The rate of captures of identified individuals is analysed, and some data on movements and ranges are presented. Sightings of other reptile species are discussed.

There has been almost no work on the numbers of slow-worms found and the environmental factors that may affect behaviour. One or two studies have found differences between months in the number of animals caught. One of these was autecological (Stumpel 1985), the others were studies of reptilian communities (mainly in the Iberian peninsula) such as those of Bas López (1984) and Bea (1980). The methods used make it very difficult to compare the data with the present study and the number of animals found was often small. Tins have not been used very often. Stumpel (1985), for instance, relied on sightings of the animals while they were basking, with the result that his samples were strongly biased towards finding females and away from finding juveniles. There was little analysis of the possible differences between the behaviour of animals that may have explained these results. Goddard (1981) used tins in his study on the smooth snake, but found too few slow-worms for a detailed comparison with the present study.

The data presented here are intended to describe the seasonal behaviour as accurately as possible. The times of entering and leaving hibernation are described. Other seasonal behaviours, such as mating and birth, will be discussed in the next chapter. Care must be taken, however, when the results of the seasonal and sexual

variations in the numbers of animals found (either as a gross figure or as the numbers found per visit) are considered. There is no known relation between the numbers of slow-worms found and the population size or density. The following sections will show that there are considerable differences in capture frequencies between individual animals and between sex and size classes. This underlines the importance of individually identified animals, since only by using the data from them is it possible to relate behaviour and weather conditions to the known population.

## 3.2 ANALYSIS

### 3.2.1 The sex and size categories

Chapters 1 and 2 have described the criteria used to distinguish males and females readily. In the early part of the study, an attempt was made to differentiate three categories of non-adult animal, based essentially on size (i.e., SVL): juveniles up to one year old, juveniles between one and two years (second-year juveniles) and those over two years but not yet adult (sub-adults). It soon became obvious that the first category was clear enough for further analysis, but the second and third were in practice indistinguishable. Growth rates after the first year were so variable that it was impossible to classify a given animal into one of the two categories of second-year juvenile or sub-adult. This point is discussed further in Chapter 6, and Figure 6.1 shows it clearly. There were thus four clearly defined categories used in the following analyses. Refinement of this system in future will depend largely on the ability to individually identify smaller (i.e., less than 100 mm SVL) juveniles.

### 3.2.2 Finds of slow-worms at each visit to a site

Once the problem of sex and size categories was resolved as well as possible, it was easy to count the numbers of each found at a visit to a site. The numbers of tins remained constant at DA and DC over the study period, so a visit was regarded as one sampling effort. It was unusual at DA to find slow-worms under more than 10% of the tins, but DC this proportion was higher, up to about 20%. Because of the (usually) low rates of captures of slow-worms and the variability of the numbers captured, it was more feasible to analyse the incidence of capture of the sex and size categories over periods of a month. Sites, categories, months and years were compared by Kruskal-Wallis tests.

### 3.2.3 The dates of entering and leaving hibernation

There is no generally accepted method of producing a single measure of the dates of entering and leaving hibernation from the point of view of the population. There is often considerable variability between individuals within a season (Prestt 1971) and the method used will be determined by several factors, not least of which is the time available to the researcher (van Nuland and Strijbosch 1981). These authors used a method which may be applicable to some other studies, but cannot be used for comparing their data with the present work. They visited their sites every day, counting the date of emergence or retreat as the "decade", or ten day period, in which they observed the fifth (or fifth last) animal. The species studied were Lacerta vivipara and Lacerta agilis, and males, females and juveniles were considered separately. It is of interest to compare this work to the present study, but this cannot be done directly, since the slow-worm sites could not be visited as frequently.

It has been shown for many temperate reptile species that males emerge from hibernation before females or juveniles, although this is by no means the universal pattern (Gregory 1982). Whether or not this was so was analysed for the slow-worm by using ranks. The first 10 (or last 10) captures in a season were ranked by the order of capture and the ranks of the sex and size classes compared by Kruskal-Wallis tests. Comparisons were also made between years and sites. A fairly small sample size was used to ensure that the captures did not extend too far into the season, as this may possibly have led to the captures being a long time after the emergence or before the entry they should have represented. Animals found on the same day were given the same rank; the order of capture on a given day was ignored. The same procedure was applied to the dates of retreat into hibernation.

Environmental temperatures are frequently considered as influences on emergence and retreat (Gregory 1982). In this study the number of years with sufficient data was too small for correlations to be made.

#### 3.2.4 Relationship of weather conditions to finds of slow-worms

The behaviour of reptiles in temperate areas is known to be affected by weather conditions. Slow-worms cannot be observed directly in the field under most circumstances, so the only way to find out what possible effects the weather may have is by an analysis of the numbers captured. This is a poor substitute for continuous observation, such as by radio-tracking, but at the moment there is no alternative in the field. The relationship (if any) between the numbers found and the activity of the animals is unknown.

The variables that were available for this analysis were air temperature, cloud cover and wind. One-way parametric anovas were carried out on the number of each

sex and size category for air temperature. Cloud cover and wind speed were recoded into four categories for analysis by Kruskal-Wallis tests.

#### 3.2.5 Analysis of the frequency of capture of individuals

The use of photographs meant that there could be some analysis of the time intervals between captures and the movements of animals over time. It has already been indicated that the time between successive captures of an individual was frequently very long; intervals of a year or more were not unusual. This tended to restrict the data available for estimating growth rates, movements and so on. The time period in days between successive captures was compared between sites and sexes using Kruskal-Wallis tests.

#### 3.2.6 Analysis of movements and ranges

The tins at DA were mapped, related to an arbitrary origin and the distances between them were calculated by Pythagoras. Movements were assumed to be in a straight line. The number of days between successive captures was calculated and the speed of movement was then estimated as meters per day. If the two captures were in different years, then the intervening winter was ignored, and the number of days calculated by assuming an active year of 200 days, i.e., emergence on the 1st April and retreat on 18th October. At both sites the number and placement of the tins were fixed. The dimensions of the grid of tins defined the limit to the maximum distance over which an animal could be recaptured. This resulted in a considerable underestimate of the speed of movement when the time between successive captures was long. Most analysis of distance and speed of movement used only those captures less than 32 days (i.e., a month) apart to make allowance for this possible bias. The distribution of

frequencies distance and speed were both highly non-normal, and so all analyses of these variables in relation to other variables were done using non-parametric tests such as Kruskal-Wallis one way anova by ranks and Spearman rank correlation coefficients. The two sites were compared in the same way, but, as discussed below, they were very different and the comparisons should be treated with caution. The comparisons are most valid when the distances moved are small and apparently unrestricted by the boundaries of the area of the site that it was possible to use.

The analysis of territories, home range and movements has been a fruitful area of research into reptilian ecology, but there are few data on the slow-worm. Stumpel's (1985) fairly sparse data indicated that the slow-worm tends to move rather small distances between successive captures, with no known seasonal migrations. There was little evidence of a relation between the number of days between captures and distance moved. There are no data on the home ranges of slow-worms, nor is there any on territoriality. It is not known if there are social interactions between animals, although "fights" have been reported occasionally (Smettan 1983).

There have been many definitions of the home range of an animal. Rose (1982) stated it to be "the entire area within which an individual moves", while Barbour et al. (1969) defined it as the area traversed in normal activity, such as feeding and reproduction. Anderson (1982) favoured a probabilistic approach, since the area is not used uniformly, but certain parts, such as a good food source, are favoured. Some of the problems over what is considered a home range stem from the time period used to calculate it and also from the use of the word "home", which has connotations that may not be justified by the data or behaviour of the species.



The analysis of home range has become considerably more sophisticated as the availability of suitable software has increased. Despite this the classic method of the convex polygon is still used frequently, since it is very easy to determine, is accurate if the sample size is large enough and allows results to be compared with older work (Southwood 1978); Rose (1982) recommended its use for these very reasons.

In the present study the rate of recapture was far too low for the area delimited by the points of capture to be considered as the home range. Home ranges can change with time; a range defined by captures made over a six-year period cannot be a home range. Therefore these areas, although calculated by the convex polygon method, will not be termed home ranges, but total ranges and areas. The total area is the convex polygon estimate of the area covered by the animal over the time it was recaptured, and the total range is the distance between the furthest two points in the area.

The minimum number of captures necessary for an estimate of the total range was taken as 5; these captures must have been under at least 5 different tins. At DA the range was then estimated by convex polygons. Since DC was effectively a site with a single dimension, the range was taken as the distance between the two tins farthest apart. This unfortunately meant that it was not possible to compare the sites since the ranges were measured in quite different ways. At DA it was also possible to find the distance between the tins used by an animal that were farthest apart, but this cannot be compared to DC because of the difference in the sites. DA was a "closed" site; there was a limited area over which tins could be placed, while DC was "open" in that the track bed extended for a much greater distance than was actually used.

It was possible to compare animals within a site. The ranges (and at DA the areas) were compared between the

sexes for SVL (taken as the average over the captures), the number of years that the animal was captured over, the number of times it was captured and the number of tins used by it. These variables were compared by Kruskal-Wallis tests and rank correlation.

### 3.2.7 Finds of other vertebrate species

All six British reptiles and a number of species of mammals and amphibians were found during this study. All were recorded, but the incidence of most of them was low, making an analysis of their incidence impossible. Two species, the adder and the common lizard, were common enough to make some conclusions about their yearly cycles at the two sites.

## 3.3 RESULTS

### 3.3.1 Numbers of slow-worms found

Tables 3.1, 3.3 and 3.5 show the numbers of slow-worms caught at the two main sites, and the number of slow-worms at the subsidiary sites. The highest numbers of captures were often in May and June, with the fewest in March and October. The numbers caught tended to be higher at DC than at DA. These points are considered in more detail below.

### 3.3.2 Emergence from and retreat into hibernation

The earliest date on which slow-worms were observed was 24th February 1975, when three males were found basking on a small grassy bank at a site in Southampton. Another early observation was of a male, also basking, at a site in Southampton on 27th February 1977. The earliest find during the present study was of a female on 26th February 1982 at DA. The animal appeared to have been dead for some time and may not represent a natural emergence.

The normal pattern in spring was for emergence to occur in March, although few animals were found per visit

in that month. At DA there was no difference in the order of emergence when the sex and size classes were compared ( $H = 4.096$ ,  $p > 0.25$ , 61 d.f.), while at DC there was a small difference, with first-year juveniles and sub-adults emerging earlier than adults ( $H = 8.917$ ,  $p < 0.05$ , 50 d.f.). However, there were considerable differences in the numbers of each category seen at both sites, with males predominating.

There were marked differences in dates of emergence between years at both sites. At DA the dates were early in 1982, 1983, and 1985, and late in 1984 and 1986 ( $H = 24.643$ ,  $p < 0.0001$ ). The situation was similar at DC ( $H = 37.313$ ,  $p < 0.0001$ ), with the same years being late or early.

The sites were compared by sex and size category and year. There was no difference in the order of dates between the sites for males ( $H = 0.443$ ,  $p > 0.5$ ), females ( $H = 0.054$ ,  $p > 0.8$ ) or sub-adults ( $H = 1.016$ ,  $p > 0.3$ ), but there was a difference in first-year juveniles ( $H = 7.614$ ,  $p < 0.01$ ), those at DA coming out earlier than at DC.

Four years were compared between the sites. There was no difference in 1983 ( $H = 3.425$ ,  $p > 0.05$ ) but there were differences in 1984 ( $H = 5.728$ ,  $p < 0.02$ ), 1985 ( $H = 5.563$ ,  $p < 0.02$ ) and 1986 ( $H = 9.126$ ,  $p < 0.005$ ). There was no consistent difference between the sites, as animals emerged at DA earlier than DC in two years and at DC earlier than DA in the other two. Sample sizes were too small to compare sex and size categories within years.

The latest observations in the year were in the exceptionally warm autumn of 1984, when a sub-adult was found at DA and a sub-adult and a first-year juvenile were found at DC on 2nd November.

In most years there were few captures after the middle of October. There was no difference between the sex and size categories in the order of retreat into hibernation

at DA ( $H = 5.561$ ,  $p > 0.1$ , 62 d.f.), but there was a difference at DC, where females and first-year juveniles were found later than males or sub-adults ( $H = 24.401$ ,  $p < 0.0001$ , 54 d.f.).

As was shown for emergence, there were differences in dates of retreat between years. The differences were highly significant at DA ( $H = 23.892$ ,  $p < 0.0001$ ) and DC ( $H = 39.005$ ,  $p < 0.0001$ ). At DA this difference was caused by the retreat being very early in 1983. If that year is ignored, there were no differences between the remaining years ( $H = 3.731$ ,  $p > 0.25$ ). At DC both 1983 and 1986 were early.

### 3.3.3 Monthly variation in the numbers of slow-worms found per visit

Figs. 3.1 and 3.2 indicate the average numbers of slow-worms found per visit by month for each year at the two main sites. It is obvious that there are differences between sites, years, sex and size categories and months. The factors that may influence these differing rates of capture are considered below.

Kruskal-Wallis tests of the number of animals of each sex and size category captured per visit against the month at DA showed that there were significant differences for males ( $H = 60.27$ ,  $p < 0.0001$ ), females ( $H = 41.03$ ,  $p < 0.0001$ ), sub-adults ( $H = 30.43$ ,  $p < 0.0001$ ) but not for first-year juveniles ( $H = 11.41$ ,  $p > 0.1$ ). At DC the pattern was similar, except that there was significant variation of the numbers of first-year juveniles caught by month (males,  $H = 45.21$ ,  $p < 0.0001$ ; females,  $H = 22.15$ ,  $p < 0.005$ ; sub-adults,  $H = 57.95$ ,  $p < 0.0001$ ; first-year juveniles,  $H = 44.46$ ,  $p < 0.0001$ ).

It can be seen from Fig. 3.1 and 3.2 that males formed the majority of captures in March. The numbers found per visit tended to decline over the year to autumn. Female numbers were low in spring, rising to about a quarter of

all captures in summer. Few sub-adults were found in spring, but the number rose steadily as the year progressed, until by autumn they were about half of all captures. First-year juveniles tended to be found in low numbers throughout the year, rising slightly in the autumn as that year's neonates appeared. The total number of first-year juveniles found, and the average number found per visit, both correlated well with the average number of viable young in the litters born the year before ( $r = 0.883$ ,  $p < 0.001$  for the total,  $r = 0.828$ ,  $p < 0.01$  for the average, 9 d.f. for both; data for the numbers of viable young are given in the following chapter). The pattern of captures of all categories was similar at the two main sites.

#### 3.3.4 Relationship of weather conditions to finds of slow-worms

There were significant differences in the numbers caught per visit and the four recoded levels of cloud cover for all categories of animal except males at DA (males,  $H = 5.742$ ,  $p > 0.1$ ; females,  $H = 8.805$ ,  $p < 0.05$ ; sub-adults,  $H = 14.022$ ,  $p < 0.005$ ; first-year juveniles,  $H = 11.844$ ,  $p < 0.01$ ). At DC there were no differences in the numbers caught and cloud cover ( $p$  for all  $> 0.2$ , Kruskal-Wallis tests).

There was no difference in the number of any sex or size category with wind speed, which was recoded into four groups, at either site ( $p$  for all  $> 0.25$ , Kruskal-Wallis tests).

The variation in the numbers caught per visit with air temperature was analysed by one-way parametric anova, using the number of animals caught as the classifying factor. Since the number of times that three or four or more of a sex or size category were caught was small, all such samples were grouped. At DA there were no significant differences between the numbers caught and air temperature

for males ( $F = 2.237$ ,  $p > 0.05$ , 188,4 d.f.), sub-adults ( $F = 0.874$ ,  $p > 0.45$ , 189,3 d.f.) or first-year juveniles ( $F = 0.493$ ,  $p > 0.65$ , 189,3 d.f.). There was a slight tendency for fewer captures at higher temperatures. However there was a difference for females ( $F = 3.023$ ,  $p < 0.05$ , 189,3 d.f.). More females were found at higher temperatures, reflecting the tendency for them to be found in summer.

The situation was not quite the same at DC. There were no differences in the number of males, females or first-year juveniles with air temperature ( $p$  for all  $> 0.05$ ), but a significant difference for sub-adults ( $F = 2.485$ ,  $p < 0.05$ , 122,6 d.f.).

### 3.3.5 Frequencies of capture of individuals

Table 3.6 shows the frequency of captures by year of several representative individuals from both DA and DC to show the irregularity and unpredictability of those captures. These data are summarised in Fig. 3.3, which shows the frequencies of capture of all adult photographed individuals at DA (of which there were 132, plus 28 sub-adults) and DC (of which there were 204). At DA, there were fewer males photographed than females (50 to 82; see Chapter 5 for a discussion of sex ratios). Only two animals, (DA2, female and DA19, male) were found in every year from 1981 to 1987. A further four (two of each sex) were found in six of the seven years. The most frequently caught animal was DA19, which was found 34 times. Two other males were found over 20 times. The most frequently caught females were DA46 (17 times) and DA2 (16 times). The animal found most times in a single year was DA20, a male found 14 times in 1982.

At DC there were more males photographed than females (115 to 89, plus 58 sub-adults) At DC only one animal was found in every year from 1982 to 1987, DC18, a female. Two, one of each sex, were found in five of the six years.

DC18 was also the most frequently caught animal at 19 times. A female was caught 15 times and two females and a male 14 each. The animal found most times in a single year was DC98, a female found 11 times in 1985.

It was quite common for an animal to "miss" a year, so that there was a gap of a year or more between two consecutive captures. At DA this was the case for 22 of the 160 individuals that were photographed (13.75 %), or 23.9 % of the 92 animals that were found in more than one year, and at DC 25 of the 260 (9.6 %), or 25.0 % of the 100 animals that were found in more than one year. The longest gap between consecutive captures at DA was four years for a female, from 25th June 1983 to 29th May 1987. At DC the gap was even longer at five years, also for a female, from 20th July 1982 to 9th September 1987. There was no doubt of the identity of these animals using the photographic method.

Kruskal-Wallis tests showed that there were marked differences between the sexes and the sites. At DA, individual males were found more times than females ( $H = 19.228$ ,  $p < 0.0001$ , 144 d.f.); the same was true at DC ( $H = 9.220$ ,  $p < 0.005$ , 261 d.f.). When the sexes were compared between sites, it was found that individual males at DA were found more frequently than at DC ( $H = 15.749$ ,  $p < 0.0001$ , 162 d.f.), but there was no difference in females ( $H = 1.895$ ,  $p > 0.15$ , 161 d.f.). These tests were carried out on captures made over the same period of years at both sites. Captures at DA before 1982 were ignored.

### 3.3.6 Movements

Fig. 3.4 shows the movements over time of a male and a female at DA. The areas of movement are shown to be mutually exclusive because they were chosen for clarity, not because they may represent territories. Both animals illustrate the unpredictability of the frequency of capture of individuals. DA16 was found twice in a week (11

and 18 June 1983), but also with a gap of nearly a year (30 June 1984 to 8 June 1985). DA38 is the same; there were gaps of less than a week (23rd to 29th April 1983 and 5th to 6th May 1985) and nearly a year (21 May 1983 to 11 May 1984). There is no obvious relationship of time between captures and straight-line distance moved. Note also that both animals were found under the same tins more than once.

Fig. 3.5 shows the frequency distribution of distances moved for males and females at DA, for all recaptures and for those 31 days or less apart. The maximum distance, 69 m, can be compared with 71 m for the distance apart of the two most widely separated tins.

The speed of movement, in m/day, is shown in Fig. 3.6, again for males and females, and for all captures and those 31 days or less apart. There were few rates of more than 4 m/day in males, and even fewer in females.

There was a significant difference in the distance moved between successive captures when the sexes were compared at DA ( $H = 8.452$ ,  $p < 0.005$ , 387 d.f.). Females moved greater distances than males. When only those captures less than 32 days apart were considered, the difference disappeared ( $H = 0.019$ ,  $p > 0.85$ , 175 d.f.). There was no difference between the sexes in the rate of movement (for all movements,  $H = 0.044$ ,  $p > 0.8$ ; for captures less than 32 days apart,  $H = 0.113$ ,  $p > 0.7$ ). Males tended to move less between captures than females (an average of 10.4 m, compared to 12.9 m for females), but their rate of capture for individuals was higher (i.e., the number of days between captures was lower) leading to the conclusion that there was no difference in the rates of movements. The means, medians and interquartile ranges of distance and rate by sex are shown in Table 3.7.

The situation at DC was fairly similar. Males moved greater distances than females ( $H = 5.164$ ,  $p < 0.05$ , 255



d.f.) but this difference disappeared when only those captures less than 32 days apart were considered ( $H = 2.376$ ,  $p > 0.1$ , 126 d.f.). There was no difference between the sexes in rate of movement ( $H = 1.332$ ,  $p > 0.2$  for all records;  $H = 1.580$ ,  $p > 0.2$  for records less than 32 days apart). Table 3.7 gives the basic data.

At both sites there were a small number of records for sub-adults. The sample sizes were too small for comparison with adults, but the data were frequently close to that of females.

The distance moved between successive captures at DA did not vary with month (males;  $H = 15.485$ ,  $p > 0.15$ , 129 d.f.; females;  $H = 3.097$ ,  $p > 0.7$ , 35 d.f.), neither did the rate of movement (males;  $H = 5.378$ ,  $p > 0.4$ ; females;  $H = 2.160$ ,  $p > 0.9$ ). These tests were done using captures less than 32 days apart.

At DC there was a significant difference in distance moved with month for males ( $H = 22.019$ ,  $p < 0.002$ ), but not for females ( $H = 6.648$ ,  $p > 0.45$ ). This probably reflects the reduced rate of recapture in the summer months. There was no difference in the rate of movement for either sex (males,  $H = 9.213$ ,  $p > 0.15$ ; females,  $H = 4.844$ ,  $p > 0.65$ ).

The Kruskal-Wallis tests comparing DA and DC are given in Table 3.7. There are significant differences in three of the measures for males but none for females. The means, but not necessarily the medians, for distances moved and rates of movement were higher at DC than DA for both sexes, although this was not always confirmed by statistical significance. These differences are probably a reflection of the different lay-outs of the sites rather than a real difference in behaviour in the populations.

### 3.3.7 Areas and ranges of movement

The basic data for the areas and ranges of movement are given in Tables 3.8 (DA) and 3.9 (DC).

Twenty-six adults, fourteen males and twelve females, had sufficient numbers captures from at least the minimum number of tins for an analysis of the area covered and the range. Male covered the larger areas, but the difference was not significant ( $H = 2.074$ ,  $p > 0.1$ , 25 d.f.). The greatest area covered was 798.0 m<sup>2</sup> by a male, DA91. This can be compared with the area of the site of 1000 m<sup>2</sup>, or 0.1 ha. Males also had larger ranges. The difference was just significant (1 way ANOVA,  $F = 4.483$ ,  $p = 0.045$ , 1,23 d.f.).

Spearman rank correlations showed that for males there was a significant positive correlation between range size and the number of tins used ( $r_s = 0.660$ ,  $p < 0.02$ ), but none for the number of captures or SVL ( $p$  of both  $> 0.05$ ). There was no correlation of range size with any of these variables in females ( $p$  for all  $> 0.5$ ). The area covered by males was significantly positively correlated with all three variables (number of captures,  $r_s = 0.756$ ,  $p < 0.01$ ; number of tins  $r_s = 0.908$ ,  $p < 0.002$ ; SVL,  $r_s = 0.547$ ,  $p < 0.05$ ). For females only the number of captures was just significant  $r_s = 0.594$ ,  $p = 0.049$ ; tins and captures  $p > 0.05$ ).

All animals overlapped extensively with many or all of the others in space and time. There was no evidence of territory formation by any sex or size group.

At DC there were ten males and nine females with sufficient data for analysis. There was a significant difference between the sexes in the range of movements ( $H = 4.507$ ,  $p < 0.05$ , 18 d.f.). There was no correlation between the size of the range and the SVL, the number of times the animal was captured or the number of different tins it under which it was found (Spearman rank correlation, sexes separate,  $p > 0.4$  for all cases). Larger sample sizes may show correlations with some of these factors.

The complete length of the site was used by these 19 animals. There was considerable overlap between the ranges. All of them were found under the tins between 66 and 92 m from the end of the station platform. Fourteen overlapped at one point, 66 m from the end of the platform. All but one also overlapped in time with all the others. There was no evidence of a length of the site being exclusive to any group of animals. Eight of the ten males were found around 88 m. The females had smaller ranges and overlapped less, but 5 of the 9 were still found at the 66 m point. There was no evidence for territory formation.

### 3.3.8 Finds of other vertebrate species

All six of Britain's reptile species were found at DA, while at DC five were found. The numbers found per visit to the two main sites is shown in Tables 3.2 and 3.4.

The common lizard, Lacerta vivipara, was found quite frequently at DA and were seen basking on top of tins as well as under them. They emerged from hibernation at a similar time to the slow-worm. The greatest numbers were seen in spring and in late summer after the young were born. The population was resident. There were far fewer sightings of Lacerta vivipara at DC, although the seasonal pattern was the same.

The sand lizard, Lacerta agilis, was seen infrequently at DA. Most sightings were in May, and were of individuals that had presumably come from the small population that lived on the heath to the north of the site. Occasionally a single animal would stay on the site for a week or two and so was recorded several times. Sand lizards were never seen at DC as the nearest population was some distance away.

The adder, Vipera berus, was by far the commonest snake at either site. Animals were nearly always found under tins. At DA the numbers seen were low until late

spring or early summer. There was a peak of sightings in July, then a rapid decline in August and September. More adders than slow-worm were found on some visits in the summer. This pattern of sightings was similar at DC, although, like the common lizard, fewer were seen. There was a higher rate of sightings in spring at DC.

These data correspond to the known seasonal behaviour of the adder (Prestt 1971; Viitaanen 1967). Hibernation is communal, and males emerge before females. After sloughing, male combat and mating in the vicinity of the hibernaculum, the adults disperse to summer feeding areas in April and May. They return to the hibernaculum in late summer, prior to entering hibernation in October. This pattern fits well with the observed frequency of sightings during the year if DA and DC are be regarded as feeding areas.

The grass snake, Natrix, and the smooth snake, Coronella austriaca, showed a similar pattern of occurrence at both sites. Sightings of both species were concentrated in late spring and summer. Both species are known to move considerable distances (Madsen 1984; Goddard 1981) and so it is likely that the individuals were moving through the sites.

Two amphibian species, the common toad, Bufo bufo, and the common newt, Triturus vulgaris, were occasionally found under tins at DA and DC. Most finds were in early spring or late autumn.

Field voles, Microtus agrestis, were common at DA where the ground vegetation was largely grass. Runs and nests were found under tins in spring, becoming much less frequent later in the season due to the disturbance of turning the tins over. Wood mice, Apodemus sylvaticus, were also seen occasionally at this site. Shrews, Sorex sp., were found at DA and DC, where they were the only mammals.

### 3.4 DISCUSSION

#### 3.4.1 Numbers of slow-worm found per visit and weather

It is possible to draw few conclusions from the analysis of the numbers of animals found and the weather conditions. Air temperature and cloud cover are crude indicators of the slow-worms' microhabitat, but unfortunately it was not possible to investigate further. The slow-worm is a particularly difficult animal to study in the field in this respect.

Although there were considerable differences in the numbers of the sex and size categories found between the months, it was difficult to relate this to any weather factor. The problem is that the factors that influence whether or not a slow-worm moves underneath a tin are unknown. Some of these influences may be guessed at: temperature may be important, as may security. Stumpel (1985) found most animals by sight and without using tins in high summer. He found 118 of the total of 170 animals in July and August. Females were 124 of all captures, 102 were found in July and August; many of them were basking and pregnant. In the present study females were commonest in summer, but there was certainly not the dominance of captures that Stumpel (1985) found. There are clear indications of differences in behaviour between males and females, with the suggestion that pregnant females bask more, or at least more openly, than non-pregnant. This should be a fruitful area for laboratory studies.

#### 3.4.2 Hibernation in the slow-worm

Hibernation in reptiles is usually thought of as a period of winter dormancy brought about by the "thermal unsuitability" of the environment (Gregory 1982). Some authors have argued that the term "hibernation" should not be used for reptiles, because the physiological processes involved in adapting to the low temperatures of winter are

not the same as those in mammals. Gregory (1982), however, points out that the mammalian adaptations are paralleled by those in reptiles and that the word can be used reasonably when discussing reptiles.

All British reptiles hibernate. At least one species, the common lizard, has been shown to be an obligate hibernator, at least in the female (Gavaud 1983). Some reptiles with wide latitudinal distributions are known to be facultative hibernators in the cooler parts of their distributions and active all year in the warmer areas (Gregory 1982). The climate of Europe is too temperate for year-round activity in reptiles, except perhaps at the southern extremities, where some small species may be active on warm days. There have been reports of adders emerging on unusually warm days in December and January, but this is not part of the species yearly cycle (Gaywood pers.comm.; Smith 1964).

Both exogenous and endogenous factors are known to be related to the times of entering and leaving hibernation. By far the most commonly studied exogenous factors are ground and air temperatures and light period. Endogenous factors have been very little studied and in most cases the evidence is circumstantial. It is possible that in at least some species a complex of factors operates. Van Nuland and Strijbosch (1981), studying Lacerta vivipara and Lacerta agilis in the Netherlands, found that the variability in the dates of entering and leaving hibernation was less than would be suggested by the variability, over 5 years, between the seasons, and they concluded that an endogenous rhythm was operating in addition to the exogenous factors.

Van Nuland and Strijbosch (1981) were able to visit their sites every day, which was impossible in the present study. Even so, some clear differences emerged. There were some clear differences between the years for both retreat and emergence, although it is not known what environmental

factors influenced these differences. Similarly, there are too few data to discuss the factors that are related to the difference between the sites. The problem was the infrequency of visits to the sites in spring and autumn.

#### 3.4.4 Movements, areas and ranges

The only previous data on movements in the slow-worm are from Stumpel (1985). He measured 60 movements, of which only three were of more than 32 m and forty-three were less than 8 m. The largest distance moved was 130 m and the greatest rate 80 m in seven days. These data are comparable to the data given here, although it is interesting to note that Stumpel was using a much larger area (500 ha) and the animals were not "restricted" by the use of tins. All available data indicate that the slow-worm moves over small areas, does not form territories at any time, and does not make seasonal movements.

Avery (1976) argued that lacertid lizards from cooler temperate climates, such as Lacerta vivipara, have to spend more of their time thermoregulating than those from warmer climates (such as Podarcis sicula from Italy). Consequently they have less time for "social" activities such as holding territories. Lacerta vivipara maintains a relatively high and stable body temperature, weather permitting. The body temperatures of the slow-worm are discussed in Chapter 7. It is sufficient to say here that the slow-worm has low body temperatures compared to other temperate lizards and does not thermoregulate with precision. Although the slow-worm is from a completely different family to the two species studied by Avery (1976), it seems to fit the model of a cool temperate lizard devoting little or no resources to territory formation. The difference, of course, is that it does not maintain high body temperatures either.

Information on the Anguidae as a whole is very meagre. Stamps (1977), in an extensive review of social behaviour

and spacing patterns in lizards, could find no evidence of territories being held, and no work has been produced since that date. The slow-worm is frequently kept in captivity, but the only interactions noted by any observer, including the present one, have been the occasional lick when two animals meet (Simms 1970). Stamps (1977) considers that this lack of social behaviours may be correlated with secretive habits. Presumably it is hard to hold a territory if one cannot be seen by a rival; the slow-worm has no known scent glands that would enable it to mark an area.



Fig. 3.1 Numbers of each sex and size category found per visit by month at DA.  
Each year is shown, thicker line is average for all years.

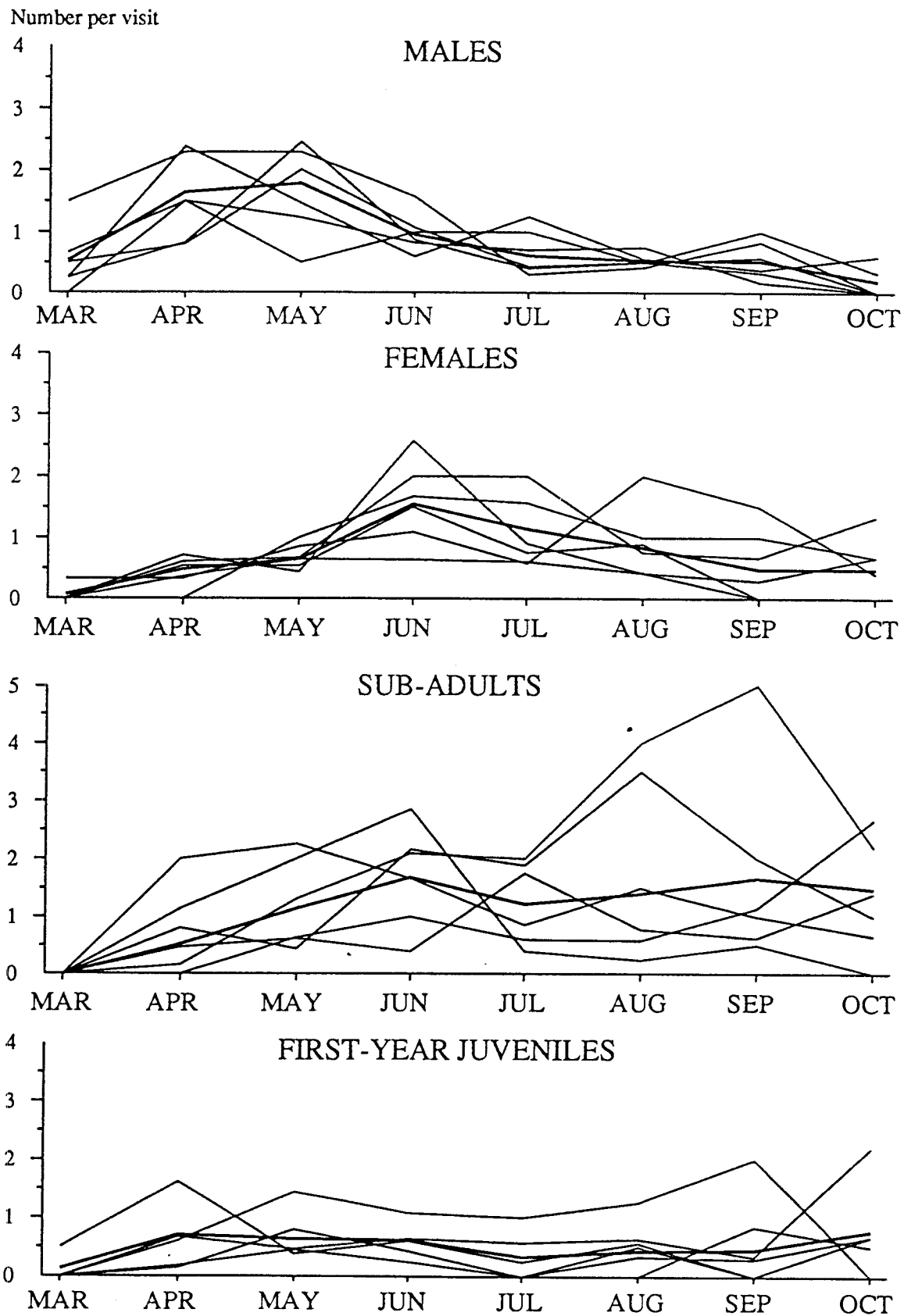


Fig. 3.2 Number of each sex and size category found per visit by month at DC.  
Each year is shown, thicker line is average for all years.

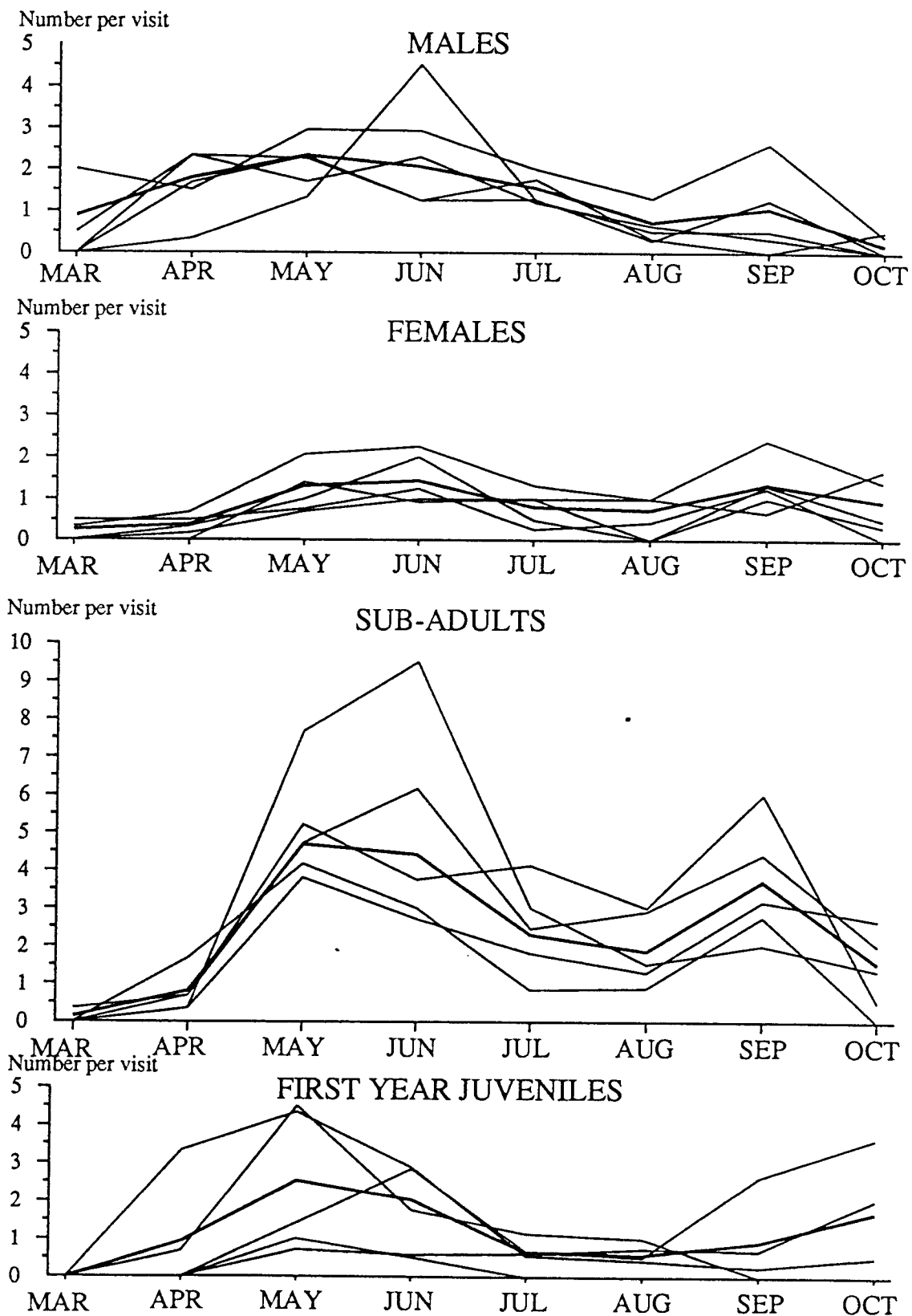


Fig. 3.3 Frequency of captures at DA and DC of individually identified animals.

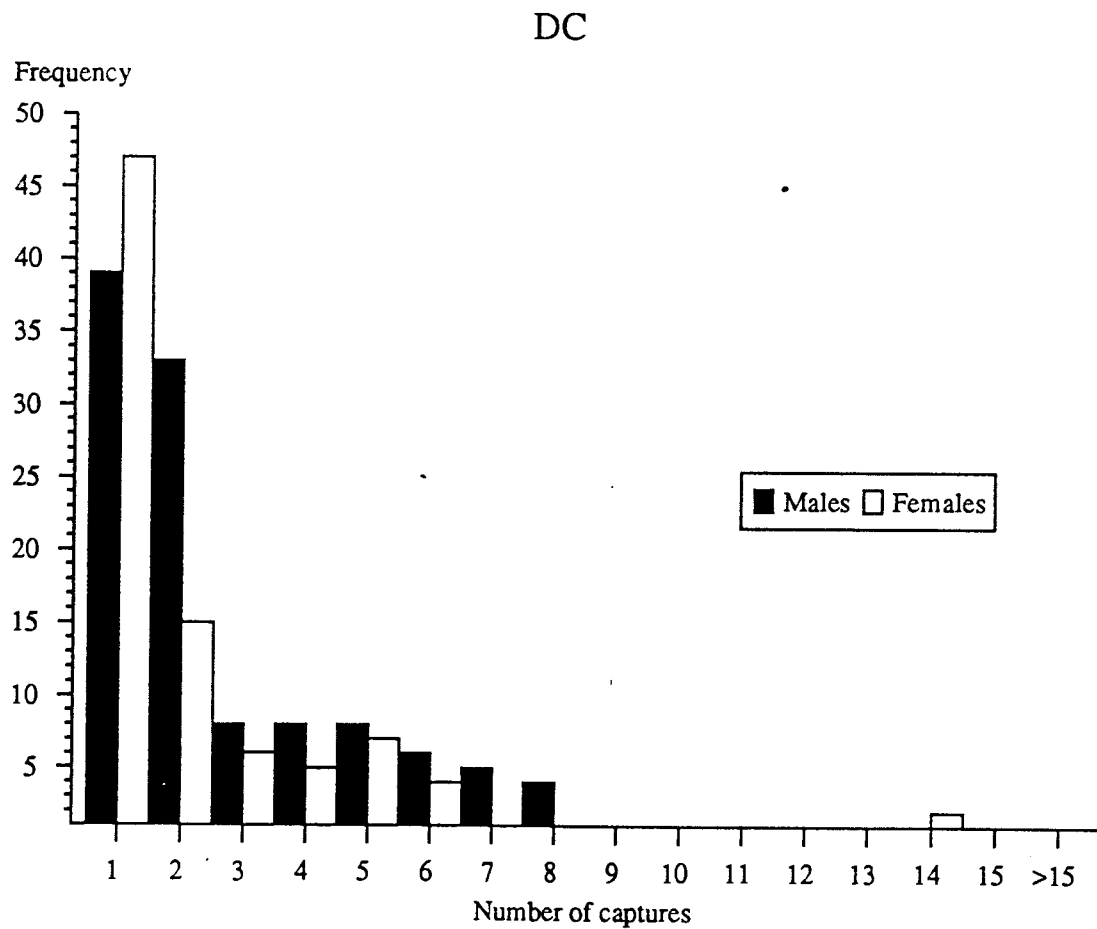
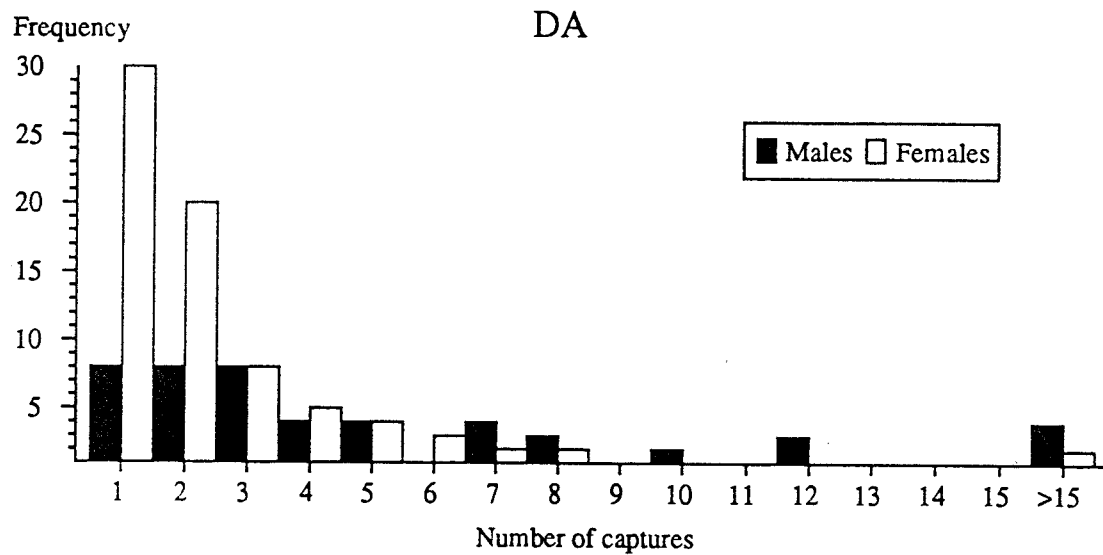


Fig. 3.4 Movements of a male (DA38) and a female (DA16) at DA from 1982 to 1986.

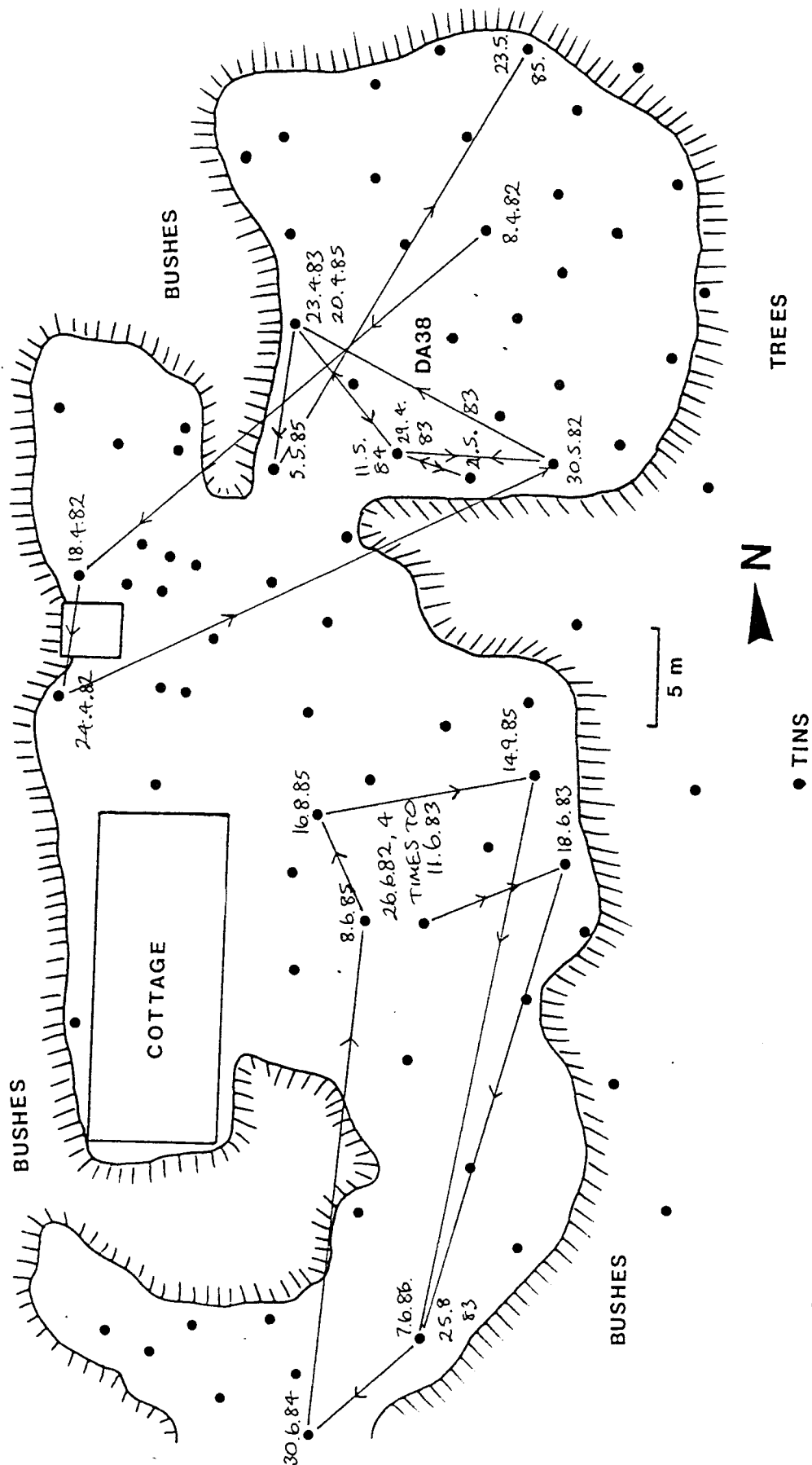


Fig 3.5 Frequency distribution of distance moved between successive captures for males and females at DA.

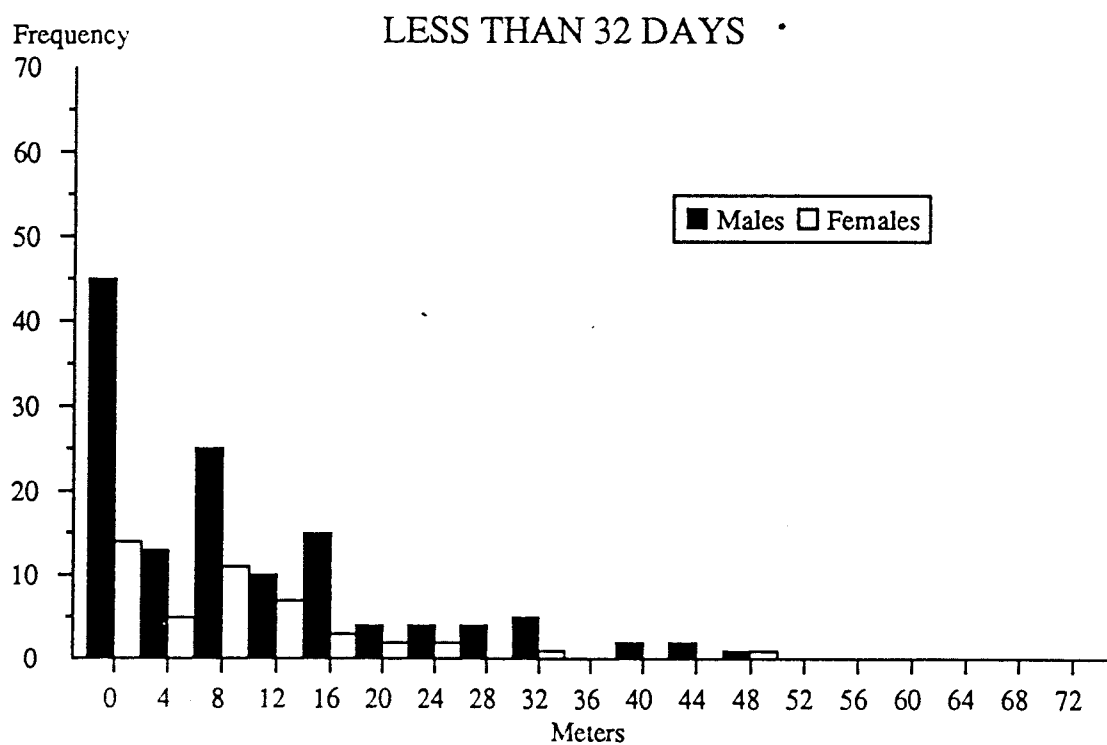
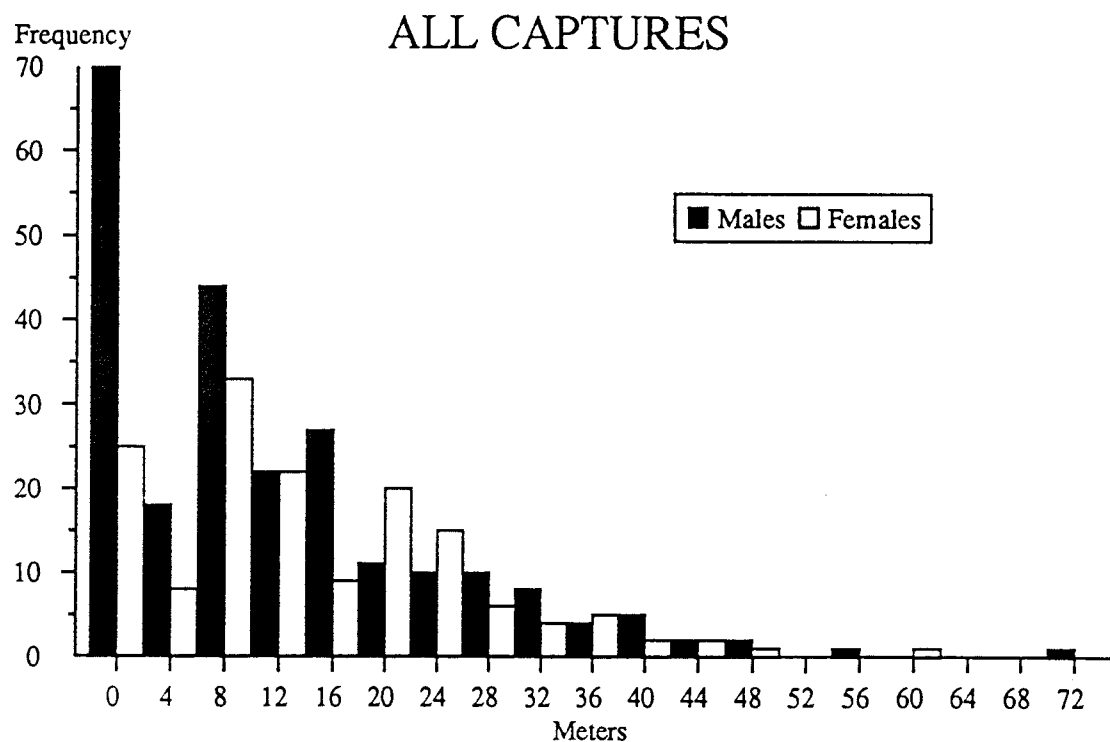


Fig. 3.6 Frequency distribution of rate of movement for males and females at DA.

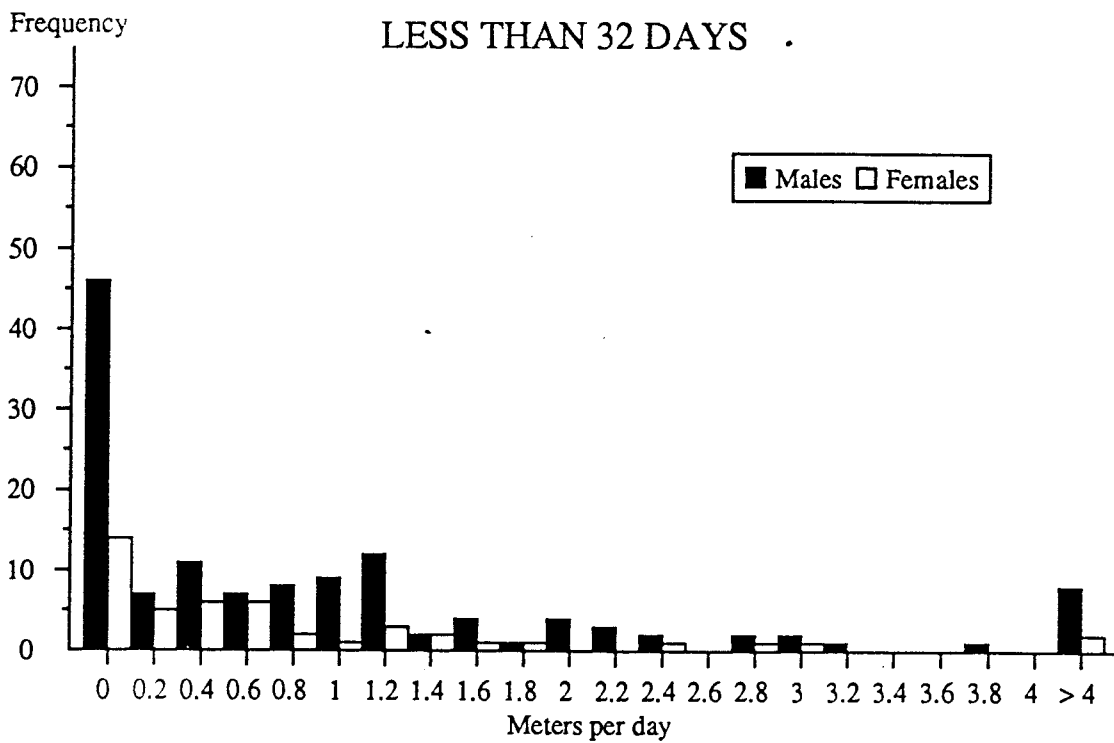
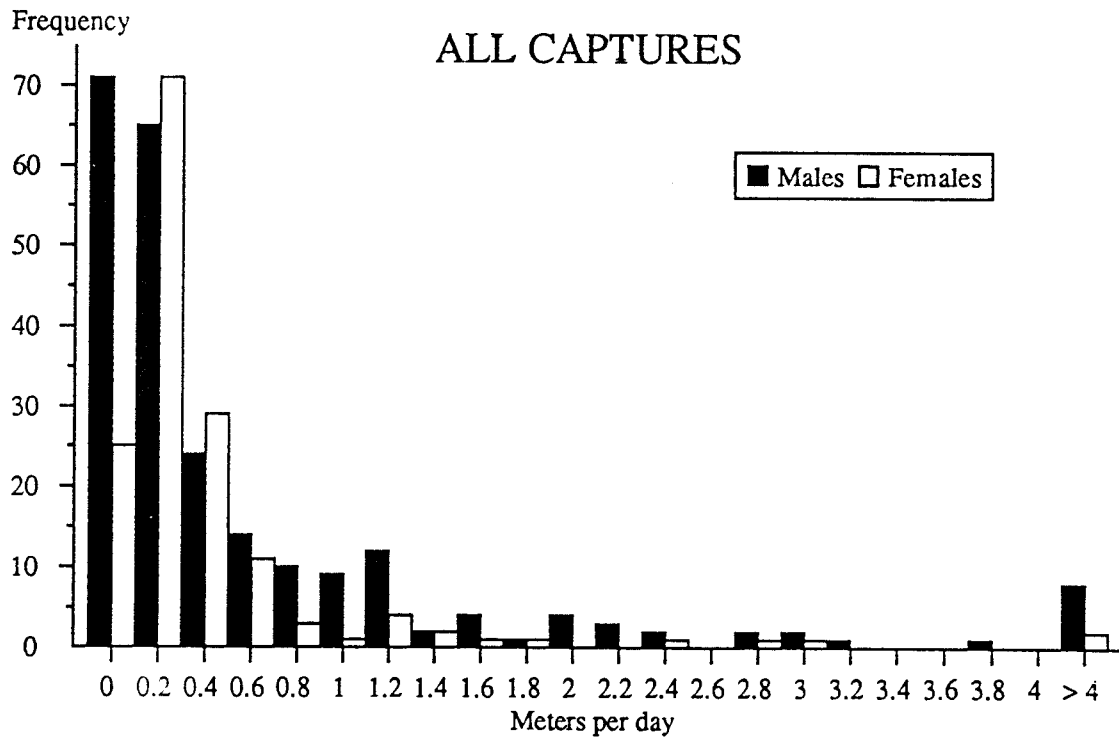


Fig. 3.7 Frequency distributions of the numbers caught per visit at DA and DC, all years.

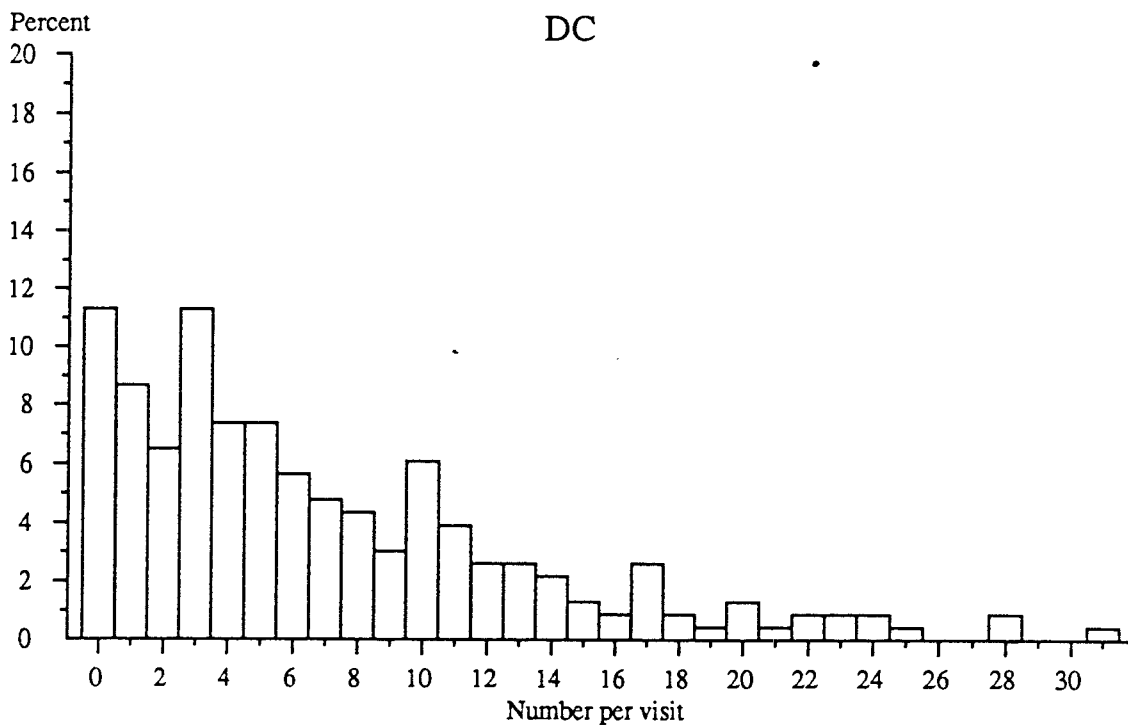
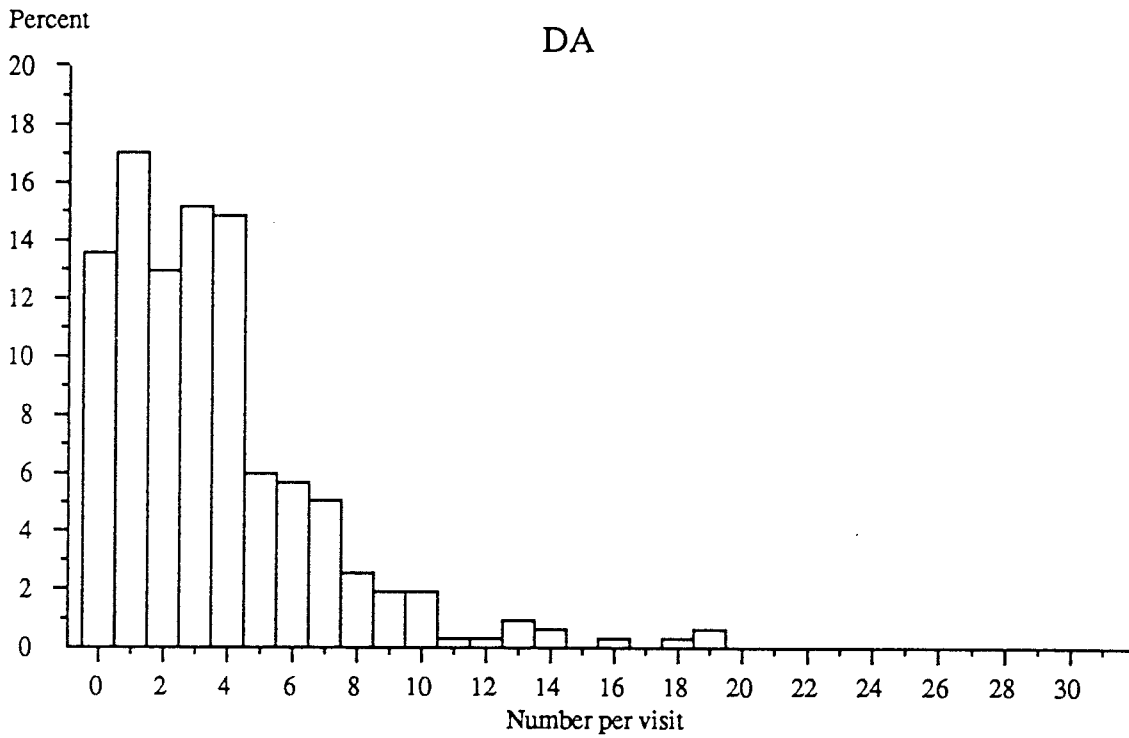


Table 3.1 Numbers of slow-worms found at DA by month and year.

		YEAR								
	VISITS	81	82	83	84	85	86	87	88	TOTAL
=====										
FEB	1	0	1	0	0	0	0	0	0	1
MAR	15	0	3	3	1	3	1	0	0	11
APR	44	0	65	30	15	16	14	7	3	150
MAY	65	0	39	77	46	50	41	14	1	268
JUN	53	18	31	52	22	51	76	13	2	265
JUL	46	16	16	16	8	27	18	24	0	155
AUG	50	9	25	13	22	59	24	6	2	160
SEP	36	7	8	13	16	42	15	9	7	117
OCT	22	0	10	1	12	24	7	7	0	61
NOV	1	0	0	0	1	0	0	0	0	1
TOT	333	50	197	205	142	272	226	82	15	1189
NO/ VISIT		5.0	3.0	3.5	2.3	4.6	4.8	3.3	3.0	3.57



Table 3.2 Numbers of other species of reptile found at DA,  
by month, 1981-1988.

Lv = Lacerta vivipara, Vb = Vipera berus, Nn = Natrix  
natrix, La = Lacerta agilis, Ca = Coronella austriaca.

	SPECIES									
	Lv		Vb		Nn		La		Ca	
	NO/		NO/		NO/		NO/		NO/	
	N	VISIT	N	VISIT	N	VISIT	N	VISIT	N	VISIT
=====										
FEB	1	1.00	0	0.0	0	0.0	0	0.0	0	0.0
MAR	9	0.60	2	0.13	0	0.0	0	0.0	0	0.0
APR	46	1.05	5	0.11	0	0.0	3	0.07	0	0.0
MAY	38	0.59	25	0.39	2	0.03	11	0.17	0	0.0
JUN	36	0.71	48	0.94	19	0.37	3	0.07	4	0.08
JUL	16	0.38	89	2.12	17	0.40	0	0.0	2	0.05
AUG	38	0.81	56	1.19	20	0.43	0	0.0	2	0.04
SEP	35	1.06	8	0.24	3	0.09	0	0.0	0	0.0
OCT	14	0.67	2	0.10	4	0.19	0	0.0	0	0.0
NOV	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
ALL	243	0.73	229	0.69	65	0.20	17	0.05	8	0.02

Table 3.3 Numbers of slow-worms found at DC by month and year.

	YEAR								
	82	83	84	85	86	87	88	TOTAL VISITS	
=====									
FEB	0	0	0	0	0	0	0	0	0
MAR	0	2	0	8	0	0	0	10	8
APR	0	47	17	17	9	3	4	97	26
MAY	54	138	69	189	134	32	2	618	57
JUN	57	67	46	170	92	33	3	468	50
JUL	24	32	23	58	64	19	0	220	41
AUG	30	14	40	57	13	4	0	158	40
SEP	26	22	29	60	22	7	8	174	30
OCT	8	1	19	37	3	5	0	73	19
NOV	0	0	0	0	0	0	0	0	1
ALL	199	323	245	596	337	103	17	1820	272
NO/ VISIT	5.9	6.2	4.8	8.8	8.0	5.4	2.8	6.7	

Table 3.4 Numbers of other species of reptile found at DC,  
by month, 1982-1988.

	SPECIES							
	Lv		Vb		Nn		Ca	
	NO/		NO/		NO/		NO/	
	N VISIT		N VISIT		N VISIT		N VISIT	
=====								
FEB	0	0.0	0	0.0	0	0.0	0	0.0
MAR	0	0.0	2	0.25	0	0.0	0	0.0
APR	8	0.31	12	0.11	0	0.0	0	0.0
MAY	12	0.21	21	0.38	5	0.09	8	0.14
JUN	7	0.14	36	0.72	3	0.06	7	0.14
JUL	2	0.05	24	0.59	1	0.02	2	0.05
AUG	8	0.20	27	0.67	2	0.05	0	0.0
SEP	5	0.17	8	0.27	1	0.03	0	0.0
OCT	0	0.0	0	0.0	0	0.0	1	0.05
NOV	0	0.0	0	0.0	0	0.0	0	0.0
ALL	42	0.15	130	0.46	12	0.04	18	0.06

Table 3.5 Numbers of slow-worms found at secondary sites by month.

	SITE						
	DB	DE	SB	GA	HA	OTHER	TOTAL
=====							
MAR	0	3	0	0	3	8	
APR	3	17	18	0	2	33	73
MAY	15	12	9	18	2	153	209
JUN	15	3	2	46	3	207	276
JUL	2	0	16	7	0	89	114
AUG	18	0	9	0	1	84	112
SEP	3	3	2	0	1	56	65
OCT	0	0	3	0	0	51	54
NOV	0	0	0	0	0	1	1

Table 3.6 Frequencies of capture by year of representative animals from DA and DC.

		YEAR								
NO	SEX	81	82	83	84	85	86	87	88	CAPTURES
=====										
DA2	F	1	2	1	3	4	2	3		16
DA7	M	1	4	4	5	7	8			29
DA19	M	2	11	8	3	4	5	1		34
DA22	F	1		2		3				6
DA46	F		3	3	5	8				19
DA98	F			1				1		2
DA103	F			1			1			2
DA111	M			1	1					2
DA141	M					1	1			2
DC18	F		1	2	3	5	6	2		19
DC31	M		1							1
DC36	F		1			2	2			5
DC47	M		2			2				4
DC67	F		1							1
DC112	M			3	1	2	1	1		8
DC128	F			1		3		1	1	6
DC132	M			3	1	4	6			14
DC133	F			2	2	7	3			14
DC135	F			1						1
DC157	M			1	1	1				3
DC231	SA				1	1				2
DC293	M					5	1			6

Table 3.7 Comparison between the two sites for distance moved and rate of movement, by Kruskal-Wallis tests.

L.QUART and U.QUART are lower and upper quartiles.

DISTANCE MOVED, ALL RECORDS

=====

SITE	SEX	N	MEAN	MEDIAN	L.QUART	U.QUART	H	p
DA	M	235	10.42	6.45	0.0	15.74		
DC	M	114	23.11	14.9	4.8	23.2	18.28	<0.0001
DA	F	153	12.85	9.25	4.60	19.85		
DC	F	132	18.35	6.95	2.0	21.0	1.162	>0.25

DISTANCE MOVED, RECORDS LESS THAN 32 DAYS APART

=====

SITE	SEX	N	MEAN	MEDIAN	L.QUART	U.QUART	H	p
DA	M	130	8.67	4.81				
DC	M	56	19.14	8.5	0.0	23.5	3.93	<0.05
DA	F	46	7.52	5.36				
DC	F	71	12.58	4.7	0.0	14.0	0.002	>0.95

RATE OF MOVEMENT, ALL RECORDS

=====

SITE	SEX	N	MEAN	MEDIAN	L.QUART	U.QUART	H	p
DA	M	235	0.645	0.136	0.0	0.707		
DC	M	114	0.970	0.259	0.033	1.000	5.68	<0.02
DA	F	153	0.432	0.113	0.044	0.302		
DC	F	132	0.824	0.168	0.019	0.569	2.52	>0.1

RATE OF MOVEMENT, RECORDS LESS THAN 32 DAYS APART

=====

SITE	SEX	N	MEAN	MEDIAN	L.QUART	U.QUART	H	p
DA	M	130	1.059	0.434	0.0	1.106		
DC	M	56	1.648	0.724	0.0	2.332	1.92	>0.1
DA	F	46	1.084	0.334	0.0	1.070		
DC	F	71	1.334	0.357	0.0	1.250	0.04	>0.8

Table 3.8 Areas and ranges of movement at DA for adults found at least 5 times under at least 5 different tins.

CAPS is the number of captures used to calculate the area, TINS is the number of different tins.

NO	SEX	SVL	TIME		CAPS	TINS	AREA (m²)	RANGE (m)
			(YEARS)					
=====								
DA2	F	170	6		15	9	177.9	25.0
DA7	M	145	5		27	9	207.4	22.2
DA10	M	151	4		10	8	156.7	47.8
DA16	F	170	4		10	7	292.9	32.8
DA19	M	178	5		32	13	485.6	43.6
DA20	M	176	1		16	7	207.6	27.2
DA32	F	166	6		13	19	306.3	29.2
DA35	M	164	4		22	11	401.5	48.2
DA38	M	154	3		12	10	358.2	41.0
DA42	F	159	4		8	8	261.6	37.2
DA45	M	153	4		8	5	200.1	37.0
DA46	F	173	3		18	6	214.0	21.4
DA49	M	169	4		14	9	333.2	45.1
DA58	M	119	2		12	10	241.5	28.0
DA78	M	140	2		7	5	78.6	13.8
DA80	M	144	2		7	5	88.4	26.4
DA81	F	160	2		6	5	97.5	25.4
DA84	M	173	2		9	7	137.2	34.6
DA91	M	168	4		11	10	798.0	47.2
DA92	F	152	3		7	5	48.4	19.8
DA96	F	138	4		5	5	58.7	26.1
DA108	F	157	3		5	5	131.2	32.3
DA114	M	147	3		8	5	114.5	22.2
DA115	F	132	2		6	6	77.5	14.5
DA125	F	151	3		7	5	88.7	21.8
DA152	F	127	2		7	5	296.2	34.7

Table 3.9 Ranges of movement at DC for adults found at least 5 times under at least 5 different tins.

The averages for the two main sites are given below.

Abbreviations are as Table 3.8.

NO	SEX	SVL	TIME		CAPS	TINS	RANGE (m)
			(YEARS)				
=====							
DC18	F	139	4		19	9	30.6
DC35	M	138	4		6	6	80.6
DC66	M	141	1		8	7	34.5
DC88	M	145	3		8	6	78.1
DC98	F	150	4		15	9	24.4
DC112	M	156	4		8	8	48.6
DC132	M	159	3		14	11	60.6
DC133	F	126	3		14	12	38.6
DC174	M	151	3		5	5	32.8
DC179	M	152	1		6	5	32.8
DC209	M	131	1		7	5	115.2
DC213	M	161	2		8	8	88.2
DC214	F	165	1		6	5	105.1
DC233	F	174	2		8	7	10.3
DC242	F	128	1		5	5	27.8
DC243	F	189	1		5	5	51.7
DC254	F	138	1		6	6	12.0
DC278	F	139	1		12	7	23.0
DC293	M	185	1		6	5	50.6

SITE	SEX	N	MEAN		MEAN	
			AREA	SD	RANGE	SD
=====						
DA	M	14	272.0	194.56	34.6	11.31
DA	F	12	170.9	99.59	26.7	6.76
DC	M	10	-	-	61.4	28.68
DC	F	9	-	-	35.9	28.86



## CHAPTER 4. REPRODUCTION

### 4.1 INTRODUCTION

Reptiles show a very wide variety of adaptations in their modes of reproduction. A distinction is made among these modes between oviparous and viviparous species. The former lay shelled eggs containing an embryo that has undergone little or no development and the latter retain the embryos in the mother until development is complete. Older concepts, such as ovo-viviparity, describing species that retain the eggs until the embryos are partially developed, are no longer used (Shine 1985).

All of the Crocodilia and Chelonia are oviparous. In the Squamata viviparity has evolved independently in both lizards and snakes a number of times. A few species have developed a placenta (Yaron 1985), and in others there is egg guarding and perhaps some care of the young after birth or hatching. Several species of anguid have developed egg guarding, including at least five species of Ophisaurus (Shine 1988). The slow-worm is a viviparous species, but there is no development of a placenta or post-natal care of the young (Yaron 1985). A general review of many aspects of reptilian reproductive biology is provided by Fitch (1970).

Shine (1985) has thoroughly reviewed all of the arguments for and against the various explanations for the evolution of viviparity in the Reptilia. He concluded that, in most cases, a species that had evolved viviparity was found in cooler climates than its nearest relatives. The slow-worm evolved from the genus Ophisaurus (Meszoely 1970), which in Europe is oviparous and not found further north than the Istrian peninsula, Yugoslavia (Obst 1981).

There are plenty of general statements on the basic parameters of the reproduction of slow-worms, such as number and size of young, time of birth and so on, but original data are few. Some notes and shorter papers give

a few more details as follows; date of birth (end of August to early October (Rollinat 1934)), number in litter (frequently given as seven to ten, with a maximum of 26 (Holder and Bellairs 1963)), size and weight of the young (65 to 90 mm TotL (quoted by many authors from Smith (1964)) and 0.4 to 0.6 g (Simms 1970)). Mating is stated to be in April or May, but has rarely been observed (Smith 1964).

This was the situation until the work of Patterson (1983), who was the first to study some of these parameters in any detail. He collected females from the Isle of Portland, Dorset (35 km west of the present study sites) in 1977 and 1979, counted oviducal eggs, and measured the energy and ash content of the eggs and the carcasses of the females. He found that less than half of the females in both years contained eggs. The proportion of smaller females (less than 150 mm SVL) that were reproductive in 1977 was much lower than in 1979. The proportion of larger reproductive females in each of the years was consistent with each female reproducing only in alternate years. In both years there was a significant positive correlation between female SVL and litter size, but more young per female unit length were found in 1979. The bodies of non-pregnant females had a higher energy content than those of pregnant ones of the same year. Clutches from 1979 had a higher energy content than those of 1977.

Patterson (1983) explained these results as follows. Biennial reproduction in reptiles was already known, mainly in viviparous species from cool temperate climates. Since slow-worms are born late in the season, there is little opportunity for building up fat reserves for reproduction in the following year, so these reserves must be built up in non-reproductive years. The difference between the years (1979 had more and larger eggs than 1977) was due to the exceptionally long, hot and dry

summer of 1976. The main food of the slow-worm, slugs and worms, would have been difficult to find, so fat reserves for reproduction in 1977 would have been poor. There were almost no smaller reproductive females in 1977, suggesting that there is a minimum threshold of fat reserves required for reproduction, that in lean years is only reached by larger females.

These data of Patterson (1983) provide some interesting pointers for further work. In the present study it was impossible to measure the energy content of eggs or females, but, because individuals could be identified, it was possible to determine if females did indeed reproduce in alternate years, as Patterson (1983) inferred from a chi-square test. It was also possible to compare years and sites, and to describe the relationships between size of female and the number, length and weight of the young.

## 4.2 ANALYSIS OF DATA

### 4.2.1 Introduction

The basic methods for the collection of reproductive data have been described in section 2.5. Females were kept in captivity until the birth of the young. The young were measured and weighed within 24 hours of birth. At all times in the following sections, a distinction is made between viable young (in the sense of Dunham et al. 1988) and those considered not viable. The latter included all young with obvious and significant deformities (whether alive or not), young born dead and unfertilised eggs. It is always indicated when only viable young were included in the following analyses. Where appropriate, monthly weather data were used in these analyses to discern the factors influencing time of mating and time of birth. The available data are described in more detail in the relevant section.

#### 4.2.2 Date of mating

With the paucity of data from directly observed matings, it was necessary to use less direct methods to estimate the date of mating. These were: (i) the dates of capture of pregnant females early in the season, i.e., before 30th June; they were plump in a way that suggested pregnancy rather than just being well fed; (ii) presence of motile sperm in the cloaca of a female, which indicated recent mating; (iii) presence of motile sperm in the cloaca of a male and (iv) the presence of "mating scars" on a female's neck. The presence of mating scars was taken to mean that mating had occurred recently and so was recorded as such. These data should be treated with a little caution. The finding of a pregnant female is only an indication of the fact of mating, not how long ago it occurred. The finding of a male with sperm in the cloaca is not an indication that it had mated recently, only that this was a possibility.

The median dates of categories (i) to (iv) above were compared between the years 1982 to 1986 using the median test (Siegel 1956) and to seasonal temperatures by correlation analysis. The median rather than the mean was used because the data were non-normal, is biased and is based on more than one method of collection. The seasons were defined as follows: winter was December to February, spring was March to May, summer was June to August and autumn was September to November. The average daily maximum temperatures for two sites, Winfrith and Swanage, were calculated for each season and year from the monthly data in the Meteorological Office publication "Monthly Weather Report".

#### 4.2.3 Date of birth

Section 2.5 indicated the conditions under which females were kept until the birth of the young. The date

was taken as that of the appearance of the first young if the birth of the whole litter lasted for more than a day. The dates were compared between years and to seasonal temperatures as outlined above. Average dates of birth, rather than medians, were used because the data were collected in one way and without apparent bias.

A natural progression from the date of mating (i.e., the date of "incidents") and date of birth is to subtract the first from the second to get a measure of the gestation period. As has been indicated, the estimate of the date of mating is a combination of factors and potentially biased, so such a subtraction would not be valid. These data can only give the most general indication of the true gestation period, and certainly should not be labelled as such.

#### 4.2.4 Frequency of reproduction

Patterson's (1983) suggestion that females only reproduce in alternate years was tested by following individuals by their photographs over as many years as possible. It was indicated in Chapter 3 that it was common for animals not to be found for a year or more. Thus it was impossible to ensure that any particular female was found in every year, or even at the right time of year, to be able confidently to determine pregnancy or its absence. Females classified as pregnant in May or June were of course kept in captivity until birth. No female found before May was found to be pregnant. By June it was normally possible to classify an animal by the plumpness characteristic of pregnant females, or lack of it.

These data can also be used to determine the smallest size at reproduction, both by following individuals as they grew to maturity and by analysis of the sizes of reproductive and non-reproductive animals in a given year.

#### 4.2.5 Size of litters

Descriptions of the numbers of young in litters include all young, viable or not. In analyses of litter sizes between sites and years only viable young are included.

#### 4.2.6 Size and weight of young at birth

These data were used to compare the sizes and weights of the young between sites and years. Only young with reliable measurements for all three of the following: SVL, TL (and therefore TotL) and weight were used in these analyses.

It was impossible to sex the young at birth.

#### 4.2.7 The possible effects of tail loss by the mother on litter size and size of young

It has been shown in some lizard species that females with autotomised tails have fewer and/or smaller young (or lay fewer and/or smaller eggs) than females with complete tails (Vitt and Cooper 1986; Dial and Fitzpatrick 1981). Whether or not this was true for the slow-worm was tested by one-way non-parametric anovas (Kruskal-Wallis tests), initially on the SVL of the females to see if allowance had to be made for the size of female. Kruskal-Wallis tests were then used to test for the possible effects of tail loss on the number of viable young, the litter averages of SVL, ToTL and weight, and the total weight of the litter. The two main sites were tested separately.

#### 4.2.8 Size of litters related to size of female

The measurement of the female used here was that taken immediately after birth, not that on first capture. SVLs of females taken during pregnancy are liable to error because of the distended abdomen. It was easier to take SVL measurements post-partum than during pregnancy. The

former were easier to take, and therefore probably more accurate.

In analyses of the relationships between linear dimensions of animals, it is usual to use a power equation of the form:

$$y = a \cdot x^b.$$

or:  $\log(y) = b \cdot \log(x) + \log(a).$

This type of equation is considered to be biologically the most "real", since they describe the allometric, or relative changes in size relationships between two variables (Peters 1983). Power least-squares regressions were calculated for the relationships of the sizes of female and number of young. They were also both used in the relationships discussed below in Sections 4.2.8 and 4.2.9. Only viable young are included in all these analyses.

Regression equations are the starting point for an analysis of population and density, since they allow predictions of the total numbers of young born to all females in a year at a given site (Chapter 5).

#### 4.2.9 Size and weight of young related to size of female

The averages of SVL, TotL and weight of the young within a litter were calculated for all litters that had at least three viable young. The weights of foetal membranes and umbilical cords were not included.

Calculating regressions of female size on the average of the measurement ensures that each litter has equal weight. One large litter can strongly bias a least squares regression equation. Power regression equations were used.

#### 4.2.10 Total weight of litter related to size of female

The total weight of the litter was only calculated for those where all the young were viable. This means that there are fewer litters for use in these regressions. The

calculated relationship gives an indication (not an estimate) of the reproductive effort put into a litter of viable young by a given sized female. The concept of reproductive effort is complex and should not be defined too simply.

Calculation of the relationships outlined in sections 4.2.8 and 4.2.9 is useful for a number of reasons. Comparisons can be made between sites and years. Any differences found can be related to seasonal, habitat and population factors to see which may influence, say, the number or size of young the most. The number of young born in a year at a particular site can be estimated as a starting point for the analysis of the population. These data will also tell whether the slow-worm is *r* or *K* selected or somewhere in between. Comparisons can be made with other reptile species, particularly those from cool temperate climates.

#### 4.2.11 Incidence of dead and deformed young

Dead and deformed have occasionally been reported before, but there has been no analysis of their incidence. All deaths and deformities were classified into one of the following categories: (1) Infertile eggs, recorded either at birth or from dissection of a female that died in captivity; (2) Partially or fully developed embryos with obvious and presumably lethal deformities; (3) Partially or fully developed, but dead, embryos with no obvious deformities; (4) Young born alive, but with obvious and presumably lethal deformities; (5) Young born alive, but with only minor and possibly non-lethal deformities, where the animal lived at least until release.

Deformities of types (2) and (4) were usually severe kinking of the spine, an incompletely closed umbilical opening or deformities to the head. Type (5) was most often a slight kink to the tail. These animals were often not able to move as well as normal ones, so their survival



once released may be questionable due to an increased likelihood of predation. No young with even the most minor post-natal deformities was found in the field. Albino young have been reported, but none were noted here. Dead near-term embryos frequently looked pale, suggesting that the pigment does not fully develop until late in gestation.

G tests were used to compare the incidence of deaths and deformities between sites and years.

For some of the young in categories 3, 4 and 5 it was possible to take measurements of the SVL. This was done only if the animal was not so deformed as to make the measurement less reliable than that of a viable young. Comparisons were made between the SVL of viable and dead and deformed young using one-way anovas.

#### 4.3 RESULTS

##### 4.3.1 Date of mating

Mating was only observed once during the study. This was at DC on 11th June 1983 at 1520 hrs, at an air temperature of 17.6 C. The SVL of the male was 171 mm, and that of the female 168 mm. On two further occasions pairs were observed in "courtship", with the male gripping the females head and neck prior to (and during) mating. The first pair, from Steep Holm, had been placed in the same carrying bag and were found in the evening of 4th June 1983. The other pair were found under a tin at DC on 19th May 1985 at 1530 hrs.

Fig. 4.1 shows all "incidents" as defined in section 4.2.3 recorded before June 30th, and Table 4.1 gives the median dates. Field work did not start until July in 1981.

There are clear differences between years. In 1985 the incidents were recorded early. 1986 was a late year, but the variance of the dates was high in all years. In the median test, counts are made of the numbers of incidents either side of the common median. G tests were performed

on the frequencies for each year except 1987, where the sample size was too small, and on the whole sample. For the whole sample,  $G = 11.687$  ( $p < 0.01$ , 4 d.f.), indicating that there was significant heterogeneity between years. Only 1986 was different from the common median ( $G = 5.884$ ,  $p < 0.025$ ; other years  $p$  all  $> 0.10$ ). Neither of the two main sites were different from the common median ( $G$  for DA = 0.143, and for DC = 0.291,  $p$  of both  $> 0.50$ ) or from each other ( $G = 0.096$ ,  $p > 0.90$ ).

The median dates for each year were correlated with the average daily maximum temperatures of the four seasons prior to and including the spring of the year. The temperature of the spring was significantly correlated with median date ( $r = 0.867$ ,  $p = 0.025$ , 6 d.f.). The other three seasons did not correlate with median dates of incidents ( $p$  of all  $> 0.4$ ). Warm springs are correlated with early observations of "incidents", but mild winters are not.

#### 4.3.2 Date of birth

Fig. 4.2 shows dates of birth for all sites for the years 1981 to 1987. There was no overall difference between the two main sites (Wilcoxon test,  $Z = 1.671$ ,  $p > 0.05$ ), but there were differences between the years (Kruskall-Wallis test,  $H = 68.6$ ,  $p < 0.001$ ). Again, 1986 was a very late year.

The date of birth did not correlate significantly with any seasonal temperature.

#### 4.3.3 Frequency of reproduction

Table 4.2 shows the incidence of reproduction of all females caught in more than one year at DA and DC. The table indicates if the female was considered too small for reproduction (i.e., had a SVL of less than 130 mm) and if the animal was not found at the correct time of year for

assessing reproductive state. The number of females found in more than four years was small. Despite this, all but two of the females can be seen to show a *possible* year-on, year-off breeding pattern. The alternate pattern can be seen clearly in several individuals, such as DA2, DA16 and DC4. It can be concluded that female slow-worms usually, but not exclusively, breed in alternate years.

#### 4.3.4 Size of litters

Figs. 4.3 and 4.4 show the frequencies of litter sizes (both total litter size and numbers of viable young only) for the two main sites for all years and all sites for two years, 1985 and 1986. Table 4.3 shows the totals of all and viable young and the average of viable young. There were a number of differences between years and sites. At DA, there were differences between the years as shown by the stars in Table 4.3 (Kruskal-Wallis test,  $H = 15.458$ ,  $p < 0.02$ ). At DC, there was no difference between the years, partly because there were small sample sizes for 1983, 1986 and 1987. It was possible to compare 1982, 1984 and 1985 between the sites, using Kruskal-Wallis tests. There was no difference in any of these three years (1982,  $H = 1.866$ ; 1984,  $H = 1.137$ ; 1985,  $H = 0.947$ ,  $p$  for all  $> 0.15$ ). There was no overall difference between DA and DC ( $H = 1.399$ ,  $p > 0.2$ ). The large litters of 17 and over at DC have not altered the overall picture. All the above analyses were conducted on the numbers of viable young only.

#### 4.3.5 Size and weight of young at birth

The basic data are shown in Tables 4.4, 4.5 and 4.6. The data were normal and so were analysed by one-way anova. It was also possible to make comparisons between the two main sites and samples from Steep Holm (GA), the results of which are shown in Table 4.7.

Multiple range tests (shown by stars in Tables 4.4, 4.5 and 4.6) show that there are similarities between the three measures (SVL, ToTL and weight) when compared within sites and between years. There are fewer differences between years when ToTL is compared to SVL, probably because the added component of the tail in the ToTL increases its variance.

When the years are compared, 1982 stands out as lower than most other years for all three measures. There were significant differences with other years except those with small sample sizes (1986 and 1987 at DC for SVL for instance). The only exception to this was 1987 at DA for weight. Although there are statistical differences between the years for all measures, no year stands out as does 1982. There are also clear differences between the two years for which samples were available from GA for all measures, with young being smaller in 1984.

#### 4.3.6 The possible effects of tail loss by the mother on litter size and size of young

There was no significant difference in the Kruskal-Wallis one-way anovas used to compare any juvenile parameter between females with complete or incomplete tails at either of the main sites.

At DA the statistics were; SVL of the mother,  $H = 2.672$ ,  $p > 0.1$ , 67 d.f.; number of viable young,  $H = 0.733$ ,  $p > 0.35$ , 46 d.f.; SVL of young,  $H = 0.482$ ,  $p > 0.40$ , 48 d.f.; ToTL of young  $H = 0.023$ ,  $p > 0.85$ , 48 d.f.; average weight of young in a litter,  $H = 0.112$ ,  $p > 0.7$ , 45 d.f.; total weight of the litter,  $H = 1.520$ ,  $p > 0.2$ , 40 d.f.

At DC the statistics were; SVL of the mother,  $H = 0.002$ ,  $p > 0.9$ , 35 d.f.; number of viable young,  $H = 0.031$ ,  $p > 0.85$ , 28 d.f.; SVL of young,  $H = 1.441$ ,  $p > 0.20$ , 28 d.f.; ToTL of young  $H = 1.097$ ,  $p > 0.25$ , 28 d.f.; average weight of young in a litter,  $H = 2.725$ ,  $p > 0.1$ , 28 d.f.; total

weight of the litter,  $H = 0.475$ ,  $p > 0.4$ , 28 d.f. There is thus no observable effect of the loss of the tail on any reproductive parameter measured here.

#### 4.3.7 Size of litters related to size of female

Power regression equations were calculated for the relationship of the number of viable young in a litter against female SVL for all years for DA and 1982, 1984 and 1985 at DC. Litters with no viable young were not included. At DA there was no significant regression coefficient for any year. This reflects the small sample sizes and the low numbers of large females at the site. When all years except 1986 are combined, the regression coefficient is significant ( $t = 3.925$ ,  $p < 0.0005$ , 46 d.f.). At DC, there were significant regression coefficients for 1982 and 1984. The relationship when all years except 1986 were combined was also highly significant ( $t = 5.006$ ,  $p < 0.0001$ , 28 d.f.). There was no significant difference in regression coefficients between the sites when all years except 1986 are combined.

The relationship of female SVL on number of viable young was compared between sites within years using analysis of covariance (ancova). There was no difference in any year, so the data from the two sites were combined. It was then possible to compare years using the data from all sites. There was no difference of any year from another, except for 1986, which was different from all other years.

Fig. 4.5 shows the relation of female SVL to viable litter size for DA and DC, and Table 4.8 gives the basic data of the regression equations of female SVL and the size, weight and number of young and the results of the  $t$  tests for differences between the sites.

#### 4.3.8 Size and weight of young related to size of female

Power regression equations were calculated for the two main sites on the averages for each litter of SVL, ToTL and individual weight against the SVL of the female. Table 4.8 shows that the regression coefficients of the power or log/log relationship of the female SVL to the litter averages of SVL, ToTL and weight were not significant at DA and DC. The relation is shown in Figs. 4.6, 4.7 and 4.8 for both sites.

There was also no difference in the relationship of female SVL to the juvenile parameter when the data from the two sites were combined within each year. This was as true for 1986 as for all other years.

These data indicate that larger females do not produce longer or heavier young.

#### 4.3.9 Total weight of litter related to size of female

The basic power regression equations are given in Table 4.8 and Fig. 4.9. The pattern of regression equations was similar to that for the number of viable young. It was possible to combine the data from both major sites within each year, where 1986 again showed a significant difference with other years. There was no significant difference in the regression coefficients between the sites ( $t = 0.848$ ,  $p > 0.4$ , 65 d.f.) when all years except 1986 were combined.

#### 4.3.10 Incidence of dead and deformed young

Table 4.9 shows the basic data on the numbers of dead and deformed young by category, and the percentages of young and litters affected. The definitions of the five categories were given in section 4.2.11. Category 3, dead at birth, but with no obvious deformities, was by far the most common in all years.

The oddest deformity noted was a case of siamese twins born to a small female from DA in 1987. The young were connected by an umbilicus. One was dead with a very severely twisted body. The other was small and just alive at birth. In another case, the young was born without a tail, i.e., with the cloaca terminal. These three did not survive. Of the 78 litters affected, 33 (42%) had only one or two young affected, but were of expected size for the SVL of the female. These litters accounted for 38 (16%) of affected young. A further 24 litters (31%), again of normal size, had all but one or two of the young affected. These litters accounted for 151 (63%) of affected young. Thus nearly three-quarters of the affected litters were affected either strongly or very little. Of the remaining litters, 13 (17% of affected litters, 19 (8%) of affected young) were of only one or two young in the first place; all had one or both affected. The last eight litters (10% of litters, 30 (13%) young) had roughly half of the young affected.

There was a significant difference in the incidence of dead and deformed young at the two main sites. At DA, 128 of 476 (27%) were affected, but at DC only 48 of 298 (16%) ( $G = 13.081$ ,  $p < 0.001$ , 1 d.f.). There were also highly significant heterogeneity between years at both sites. At DA,  $G$  was 64.079,  $p < 0.001$ , 4 d.f.; at DC,  $G$  was 42.109,  $p < 0.001$ , 2 d.f. Years with fewer than 5 affected young were not included. At both sites 1982, 1984 and 1985 had approximately the expected number of affected young, as did 1987 at DA. At DA in 1983 there were significantly more affected young than expected ( $G = 11.711$ ,  $p < 0.001$ , 1 d.f.), but the worst year was undoubtedly 1986, both sites having far more affected young than expected (at DA, 44 of 77,  $G = 33.166$ ,  $p < 0.001$ , 1 d.f.; at DC, 21 of 31,  $G = 30.165$ ,  $p < 0.001$ , 1 d.f.).

The average SVL of measurable affected young at DA was 43.2 mm, at DC 43.7 mm and for all other sites combined

43.8 mm. There was no difference between the sites ( $F = 0.291$ ,  $p > 0.7$ , 107,2 d.f.). These averages were significantly lower than those for viable young at all sites (DA;  $F = 35.308$ ,  $p < 0.001$ , 401,1 d.f.: DC;  $F = 4.686$ ,  $p < 0.05$ , 254,1 d.f.: Other sites;  $F = 9.486$ ,  $p < 0.005$ , 168,1 d.f.).

#### 4.4 DISCUSSION

##### 4.4.1 Comparison with older work on the slow-worm

Many of the reproductive parameters of the slow-worm are much as indicated by the older literature outlined in section 4.1, but there is considerable variation, mainly between years that has only been discussed by Patterson (1983). There are some discrepancies. Mating has frequently been stated to occur in April, but this is much earlier than most of the observed "incidents"; they tended not to occur until May or June. In 1986 the date of birth (as with many other parameters) was very different from average; females were still pregnant in late October, the normal time for entering hibernation, despite being kept in captivity at higher temperatures than those found in the field. This may be the explanation for the pregnant female found dead in February by Knight (1949). The ToTL at birth is here shown to be longer than the so often quoted 65 to 90 mm; indeed this is a considerable underestimate, since the average SVL is 45 mm, which, with a similar TL, gives an average ToTL of 90 mm and a maximum of over 100 mm.

##### 4.4.2 Possible effects of the loss of the tail

Section 4.3.6 showed that there were no data to indicate any difference in the number or size of young between females with complete tails and those with incomplete ones. Arnold (1988) has discussed the ecological factors surrounding autotomy, including the



known effects of tail loss on reproductive success. For example, Dial and Fitzpatrick (1981) have shown that females of the gekko Coleonyx brevis with autotomised tails produced fewer and smaller eggs. The fat stored in the tail was important in the production of yolk. In temperate lizards, such as Lacerta vivipara, these fat stores have also been shown to be important during hibernation (Avery 1970; Bauwens 1981). It is notable that regeneration in this and all other lacertid species is rapid and eventually complete (Arnold 1984), indicating that the tail is sufficiently important as a fat store, along with other possible uses such as in locomotion, for the animal to invest the energy for regrowth. Regeneration in the slow-worm on the other hand is very slow and always incomplete (Bryant and Bellairs 1967). Arnold (1988) noted that slow tail regeneration is associated with elongate, limbless species that burrow, or live cryptically close to the earth-vegetation interface or under objects. The slow-worm fits that description very well. The tail of the slow-worm is relatively long in comparison to the SVL, and it is possible for an individual to autotomise its tail two or more times (pers. obs.), although the length lost at an autotomy event is very variable and unpredictable. Of the very wide variety of possible uses of a lizard's tail, the one that seems to apply most strongly to the slow-worm is autotomy. There are no obvious uses in locomotion, as a weapon or any other use discussed by Arnold (1988), except possibly as a fat store for hibernation. Species with full regeneration always have uses other than autotomy for their tails. There is no point in a species regenerating its tail to enable further autotomy since the vertebral column of the regenerate is composed of a simple cartilaginous rod and therefore completely lacks intravertebral autotomy planes (Bellairs and Bryant 1985). This argument appears to make sense of the long but non-regenerating tail of the slow-worm.

#### 4.4.3 The slow-worm and viviparity

The most recent and thorough review of viviparity, its incidence and evolution, is due to Shine (1985). This author reviewed all of the earlier ideas in detail. All known cases of viviparity among reptiles were reviewed and analysed to see which life-history traits best correlated with the condition. All of the ideas concerning the selective forces which may give rise to viviparity have been based on "cost-benefit" type arguments; i.e., there is a cost associated with viviparity (the female may be more sluggish and therefore vulnerable to predators, for instance) so benefits in terms of increased survival of the young must be identified. A number of the early ideas, such as that which claimed that viviparity can be associated with large female size (the female, while gravid, is better able to defend herself against predators) or with venomousness (same reason) are hardly applicable to the slow-worm. Other ideas were concerned with the vulnerability of eggs to attack by predators or disease, or the ability of the female to ensure a more equable environment for the embryos by thermoregulating. This latter argument applies mainly to those species that live in higher latitudes and altitudes.

Shine (1985) found 95 known independent origins of viviparity among the squamate reptiles from many different families and genera. Viviparity has evolved relatively more times in the Anguidae than in most other squamate families. Of the 60 origins where there were sufficient data, 53 were associated with the viviparous species being found in cooler climates than their nearest oviparous relatives. The remainder were associated with damper soils and more fossorial habits. Shine predicted that viviparous species would be more diurnal and heliothermic than their oviparous close relatives, citing Anguis and Coronella as examples. Unfortunately, the original publications that Shine relied on for this prediction were based on casual

observations, not experimental data, so there is little basis in these species to arrive at any conclusions about the prediction. Three reasons were given by Shine (1985) for greater heliothermy in viviparous species: (i) heliothermy favours the evolution of viviparity; (ii) heliothermy evolved as an adaptation to viviparity; (iii) heliothermy is an adaptation to cooler climates by viviparous members of the taxa. Shine concluded; "Although the hypothesis that viviparity evolves in cold areas is supported, the exact nature of the selective force remains unclear" (Shine, 1985, p 677).

Viviparity, and half-way stages such as egg retention for part of the gestation period, have clearly evolved many times in reptiles, and can be seen as a successful reproductive strategy for a wide variety of taxa. The slow-worm has a very wide distribution for a temperate reptile. It is likely that viviparity has played a part in the spread of the species into (for a reptile) normally hostile environments. If Patterson (1983) and Bull and Shine (1979) are correct, the "price" payed by the slow-worm for viviparity is a reduced rate of reproduction in females, at least in certain parts of its range. The question of whether viviparity was a preadaptation, or evolved as a necessity after the slow-worm moved to climates that were marginal for survival, is unanswered and probably unanswerable.

#### 4.4.4 Size of female and size of young

It is clear from Figs. 4.5 to 4.9 and Table 4.9 that larger females do not give birth to larger young, but to more young. The best correlation was between SVL of the female and the total weight of the litter.

It has been shown that the size of the young at birth is larger than that given in the popular literature. Andrews (1982), in a review of reptilian growth, showed that there is a strong ( $r > 0.9$ ) correlation between the

average SVL of adults and the SVL of hatchlings for a very wide range of squamate species. This author produced a power equation for predicting SVL at birth from average female SVL. At DA the average SVL of reproductive females was 158.8 mm, at DC it was 164.3 mm. From these figures, the predicted SVLs are 49.3 and 50.6 mm respectively. i.e., about 5 mm longer than found. This could possibly be because the slow-worm is an elongate, limbless species. It may be that the slow-worm is too long for the size of young it produces, rather than the juveniles being too small. If the data were available, it could be interesting to produce a similar equation for the weight or volume of the female against the weight or volume of the young.

Andrews (1982) also calculated a power regression equation of average SVL on SVL at maturity from the same range of species for both sexes. The average SVL of males at DA was 153.8 mm, at DC it was 153.6 mm. From Andrew's predictive equations, the calculated SVL at maturity would be 122.2 and 122.1 mm respectively. For females, using the above figures, the SVL at maturity was 131.6 and 136.1 mm at DA and DC. Although data are few, these estimates correspond to observations made in this study. It was noticed that males with an SVL of about 125 mm had lost the subadult pattern and colour and were similar in all respects except size to obviously adult animals. The smallest females known to be pregnant had SVLs in the range 132 to 140 mm. However, they were only found in certain years, such as 1986. In other years, the smallest pregnant females had SVLs of 150 mm or more.

#### 4.4.5 Incidence of dead and deformed young

There have been very few data given on the incidence of deaths and deformities among hatchlings or neonates in reptiles. Dunham *et al* (1988) have remarked on the lack of field data on the proportion of fertile embryos to total

embryos, even in turtles, the most thoroughly studied group in this regard.

At first sight, figures of 58% of litters and 25% of total young being affected may seem high, but there are few data for comparison. Goddard (1981), in his study of Coronella austriaca, found 7 of 14 litters and 19 of 58 young (33%) affected in similar ways to the slow-worms in this study.

Goddard's (1981) female smooth snakes were kept in captivity from the time when they were first noticed as pregnant to the birth of the young. The question that arises is; what affects, if any, did the conditions under which the animals have on the developing embryos? There is no direct answer to this question, since there are no data from non-captive females for comparison. There is a little indirect evidence. The female slow-worms were kept under slightly more equable conditions than those that pertained in the field. If the captive conditions adversely affected the development of the embryos, then it might be expected that the proportion of affected young would be similar between years and between sites. The data available indicate that there were considerable differences between sites and years.

The causes of the apparently large numbers of dead and deformed young are unknown. It may be significant that 1983, with its hot, dry summer and 1986, which was very cool and wet, both showed increases in the frequencies of affected young. In other years there were no affected young at all (1981), or, in most of the litters, there were just one or two affected young. In the case of one female, there was the possibility that too many young was the problem. The female had an SVL of 163 mm, very close to the average size, but gave birth to 14 full term, dead young. All the young were of a normal length, but were very light in weight, averaging 0.27 g, or a little over half the average for all litters. A female of that size

would be expected to have 7 or 8 in a litter. It may be inferred that a female of that SVL is too small to provide sufficient yolk for so many embryos to survive.

#### 4.4.6 The work of Patterson (1983)

The present study has shown that, by following individuals over several seasons, reproduction in females is normally biennial. This confirms Patterson's (1983) argument from a chi-squared analysis of the number of females in a collection that were reproducing in one year. It is not possible to confirm or otherwise Patterson's other arguments on "good" and "bad" years, since either there were few differences between years or samples were too small. There were no obvious effects of the hot, dry summer of 1983 on clutch sizes or the size of young in 1984 as Patterson's argument would predict. On the other hand, 1986 was notable for the very small clutch sizes, very late births and very high incidence of dead young and eggs. That summer was particularly cool and wet, so here may be the other side of the Patterson argument, since 1985 was also cool. Two consecutive cool summers may have led to poor reproductive success. Low air temperatures and reduced sunshine hours may have meant reduced opportunities for finding food and reduced efficiency of digestion, leading to low fat reserves and therefore small clutch sizes in 1986. It may be possible to produce experimental evidence for or against this argument if sufficient animals were to be available.

The slow-worm lives in climates that are much cooler as well as warmer than that of southern England, but there are no data on reproduction from (say) the Iberian Peninsula and the Peloponese peninsula on the one hand, or central Scandinavia on the other. If female slow-worms reproduce biennially in England, is this reduced to triennially in Finland and increased to annually in Greece or Spain? It would be very interesting to have such data

for comparison, since there is some evidence that there is geographic variation in at least one temperate reptile. Vipera aspis females reproduce annually, biennially or triennially according to the climate; the most frequent reproduction is in the warmest climate (Saint Girons 1957). The northern limits of the distribution of the slow-worm may be determined by this reduced rate of reproduction. If cool climates reduce the rate of reproduction, the climate in certain areas may be so cool that the females have too little time to build up fat reserves during fallow season(s), so that reproduction is too infrequent to counter mortality rates and sustain the population.

In all known cases of reduced rate of reproduction, it is only the females that are affected (Bull and Shine 1979). This is true in the only other Anguid that is known to reproduce biennially. The species is Barisia (= Mesaspidis) monticola, a viviparous tropical montane species with a very long gestation period (Vial and Stewart 1985). In the slow-worm there is no evidence that males are only fertile biennially. If the sex ratio is 1:1, as it may be in the slow-worm, there may be greater competition between males for females. What form this competition may take is unknown; no agonistic behaviour was observed in this study. Older males are sometimes stated to have scars from fighting for females (Smith 1964), but this is an assumption, not direct observation. It is also possible to explain such scars as the results of unsuccessful attempts at predation by birds.

The data presented here may be used to discuss a few other aspects of the reproductive biology of the slow-worm. The age at first reproduction is very variable. Available data agree with Patterson (1983) that in some years females of 140 mm SVL and less may breed, in others they will not. In the present study only four females of less than 140 mm SVL were known to have bred, 3 in 1986

and 1 and 1987. In most years, the smallest known reproductive females were 145 to 155 mm SVL, at a probable age of 4 years. This probably represents the more typical size for first reproduction.

Another possibility that can be considered is of estimating the total production of young at a site for each year, and over the lifetime of a female. Such an estimate would involve many assumptions and would have to take into account wide variations from year to year. These inaccuracies may make the estimate so vague as to be useless.



Fig 4.1 Finds of pregnant females (vertical lines), observed matings (arrows) and presence or absence of sperm in the cloaca. Lower case letters = sperm absent, upper case = sperm present.

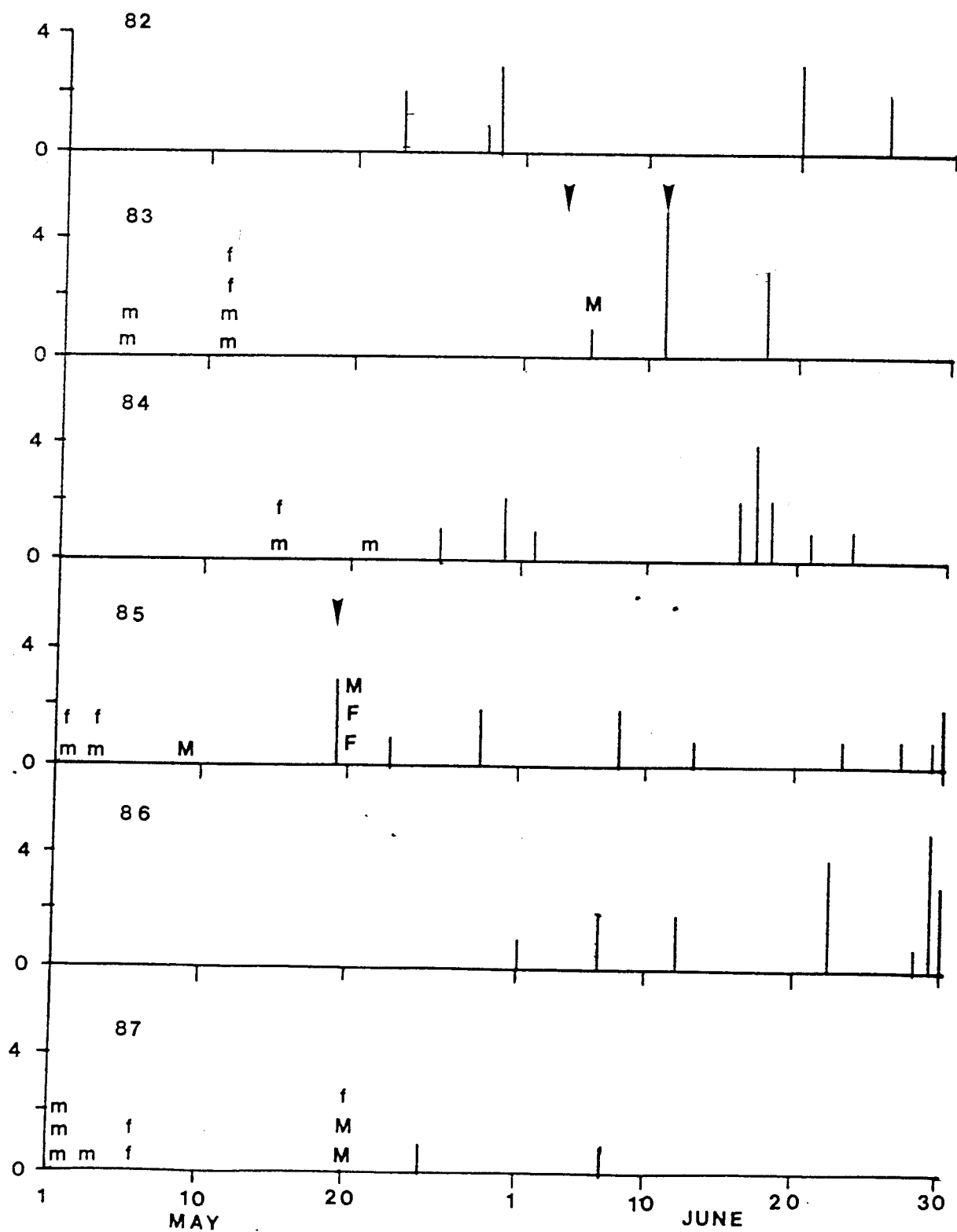




Fig. 4.2 Dates of birth, all sites, 1981-87.

Solid bars = DA; open bars = DC; hatched bars = other sites.

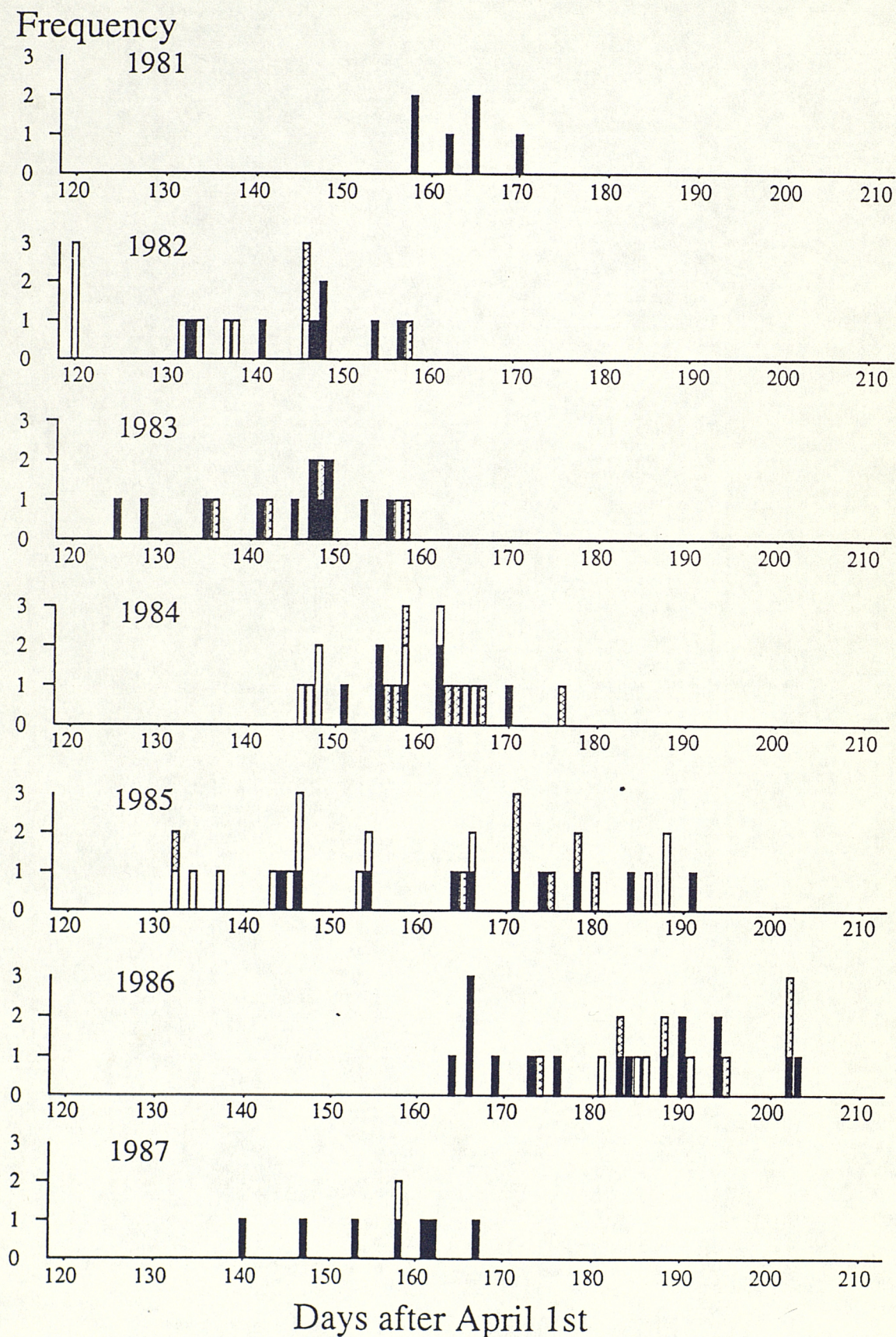




Fig 4.3 Frequency distributions of litter sizes, 1985 and 1986, all sites

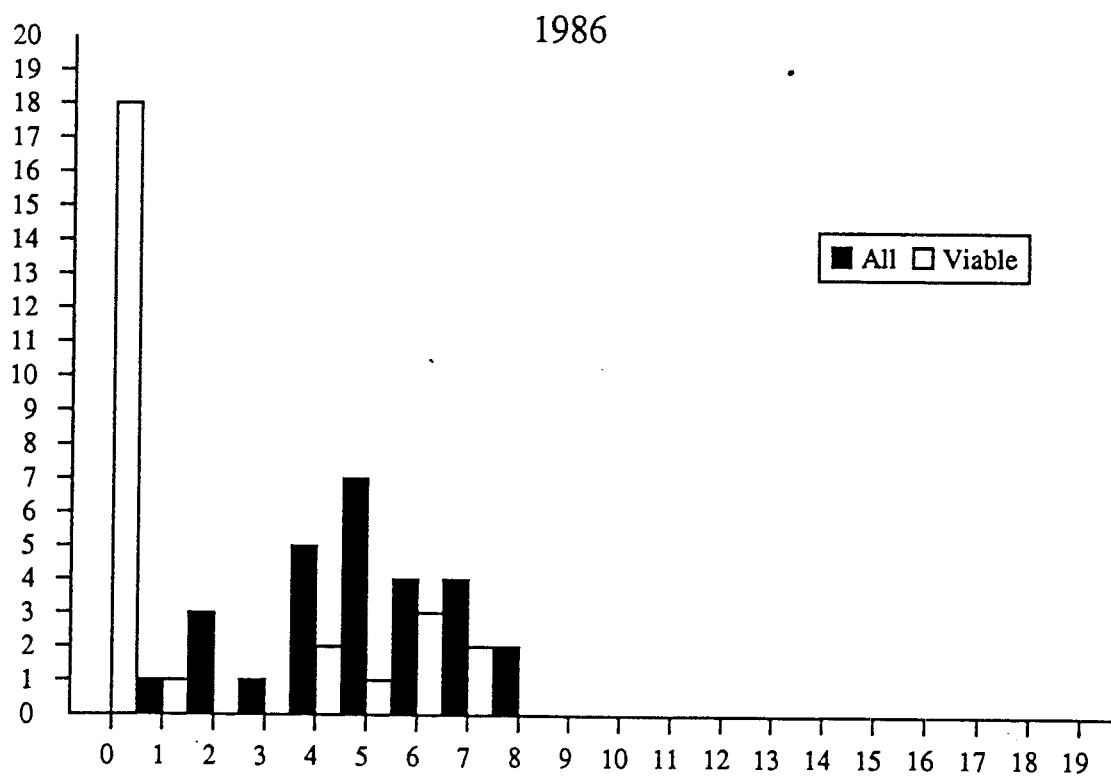
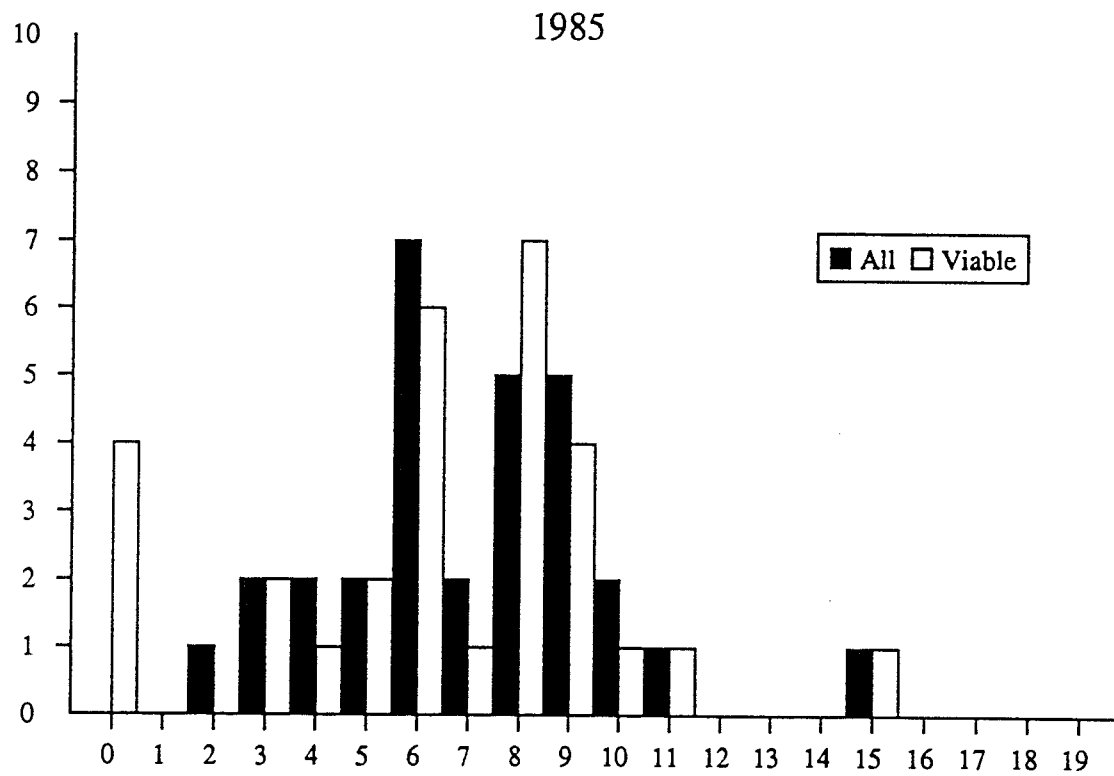


Fig 4.4 Frequency distributions of litter sizes of all and viable young at DA and DC, all years.

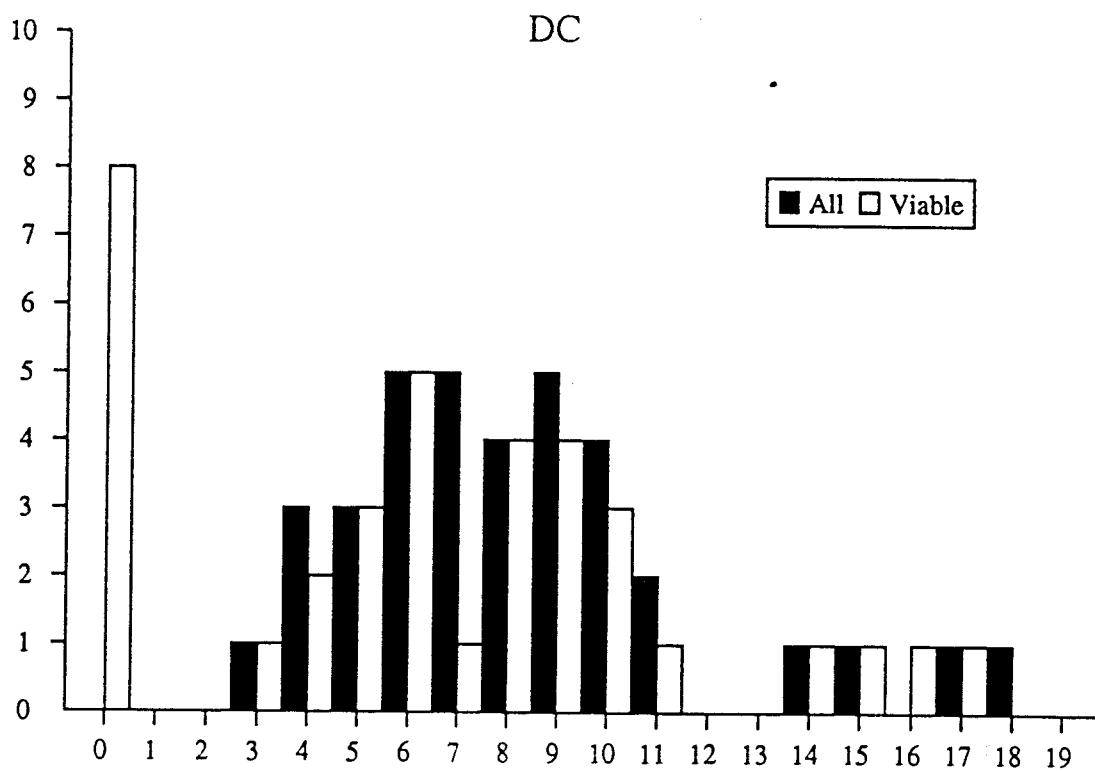
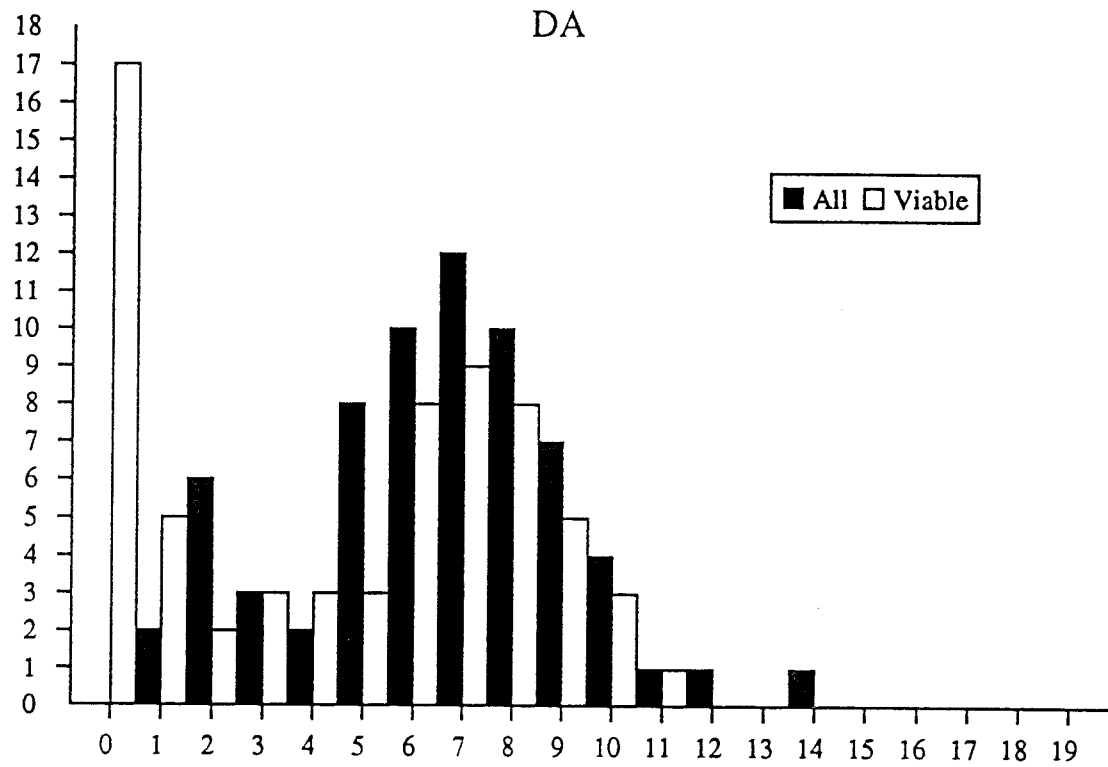


Fig 4.5 Relationship of female SVL to the number of viable young in the litter at DA and DC.

Data for 1986 is not included

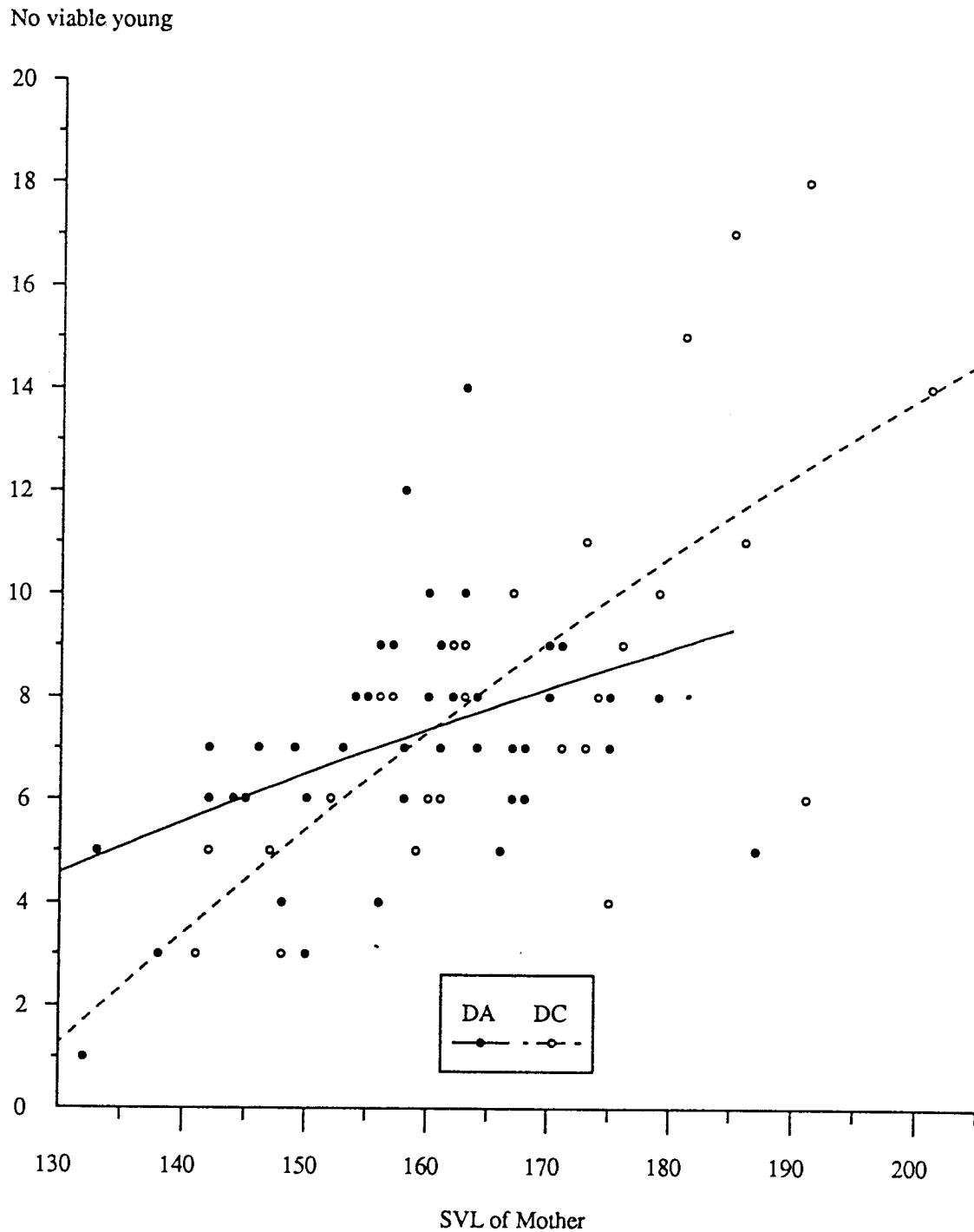


Fig. 4.6 Relationship between female SVL and average SVL of the litter at DA and DC.

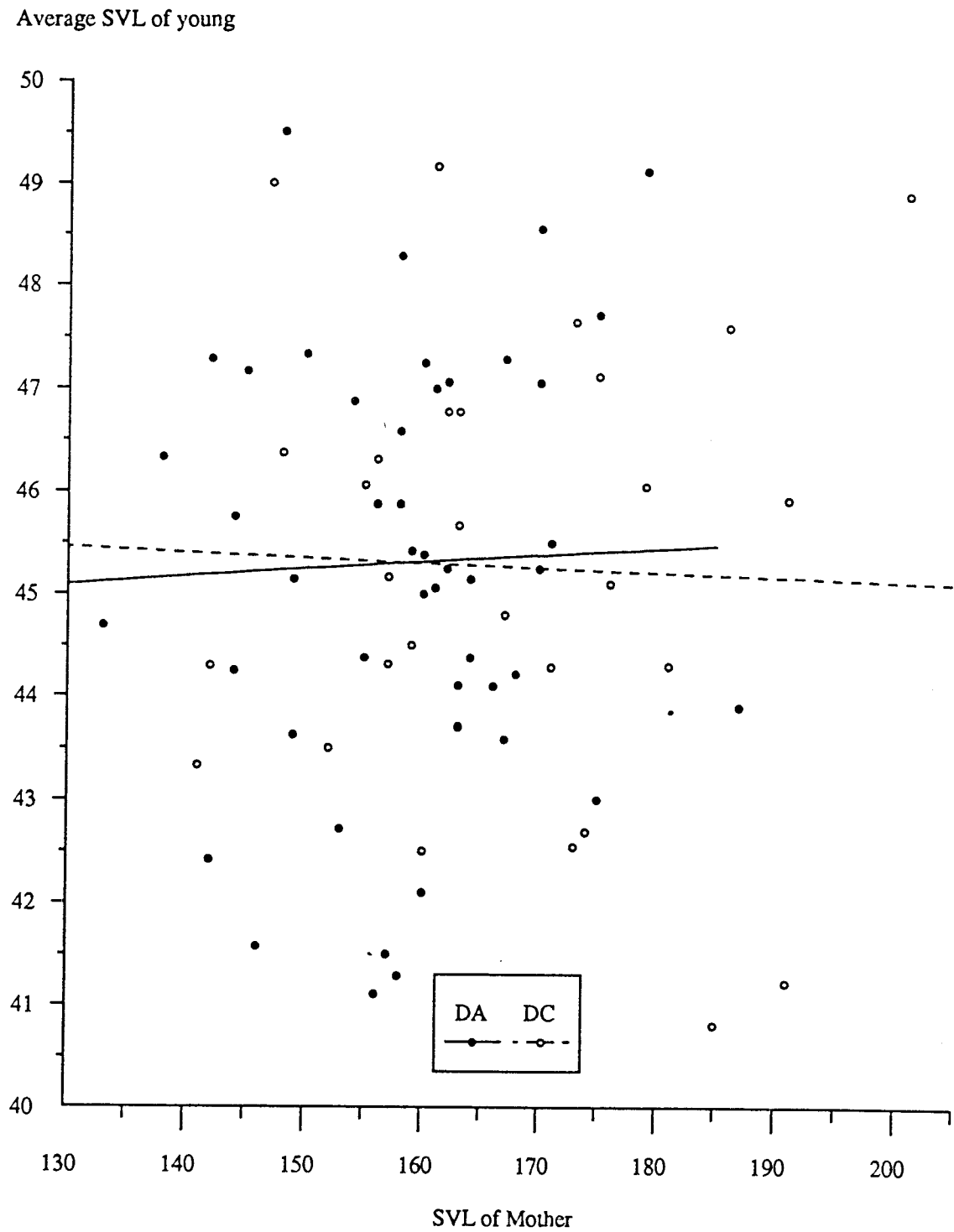


Fig 4.7 Relationship of female SVL to average ToTL of the litter at DA and DC.

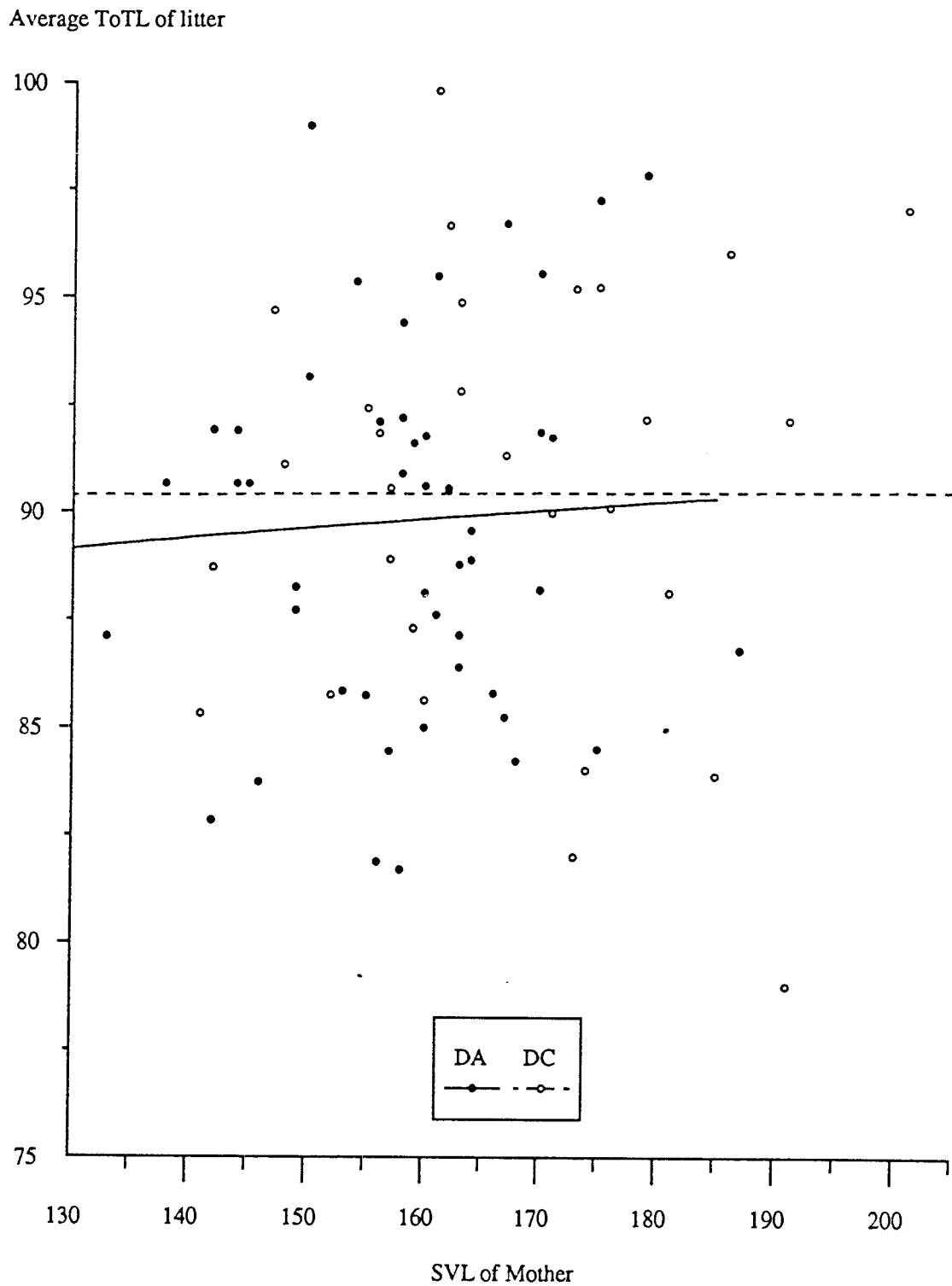


Fig. 4.8 Relationship of female SVL to average weight of young in the litter at DA and DC.

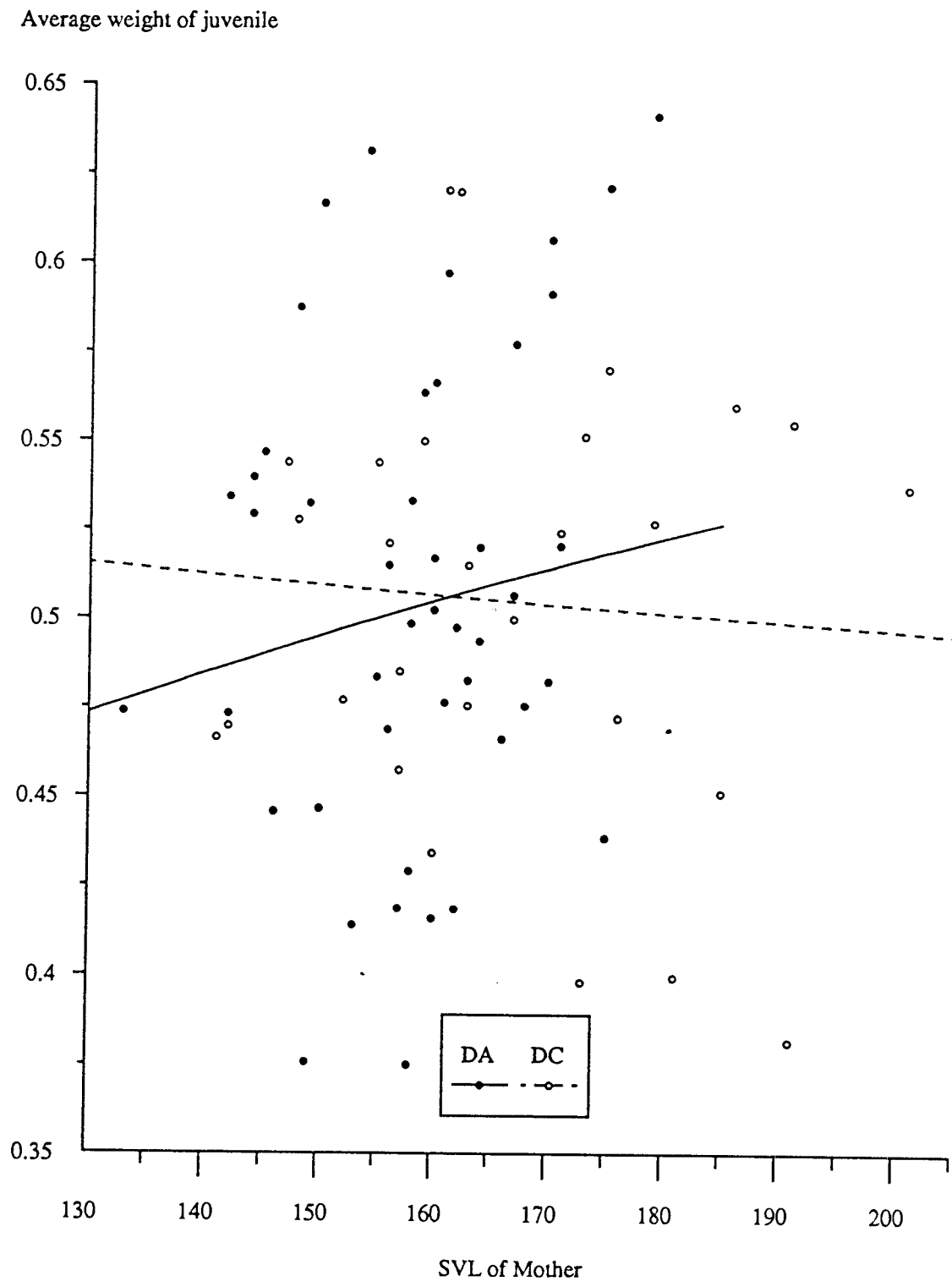




Fig 4.9 Relationship of female SVL to the total weight of the litter at DA and DC.

Data for 1986 is not included.

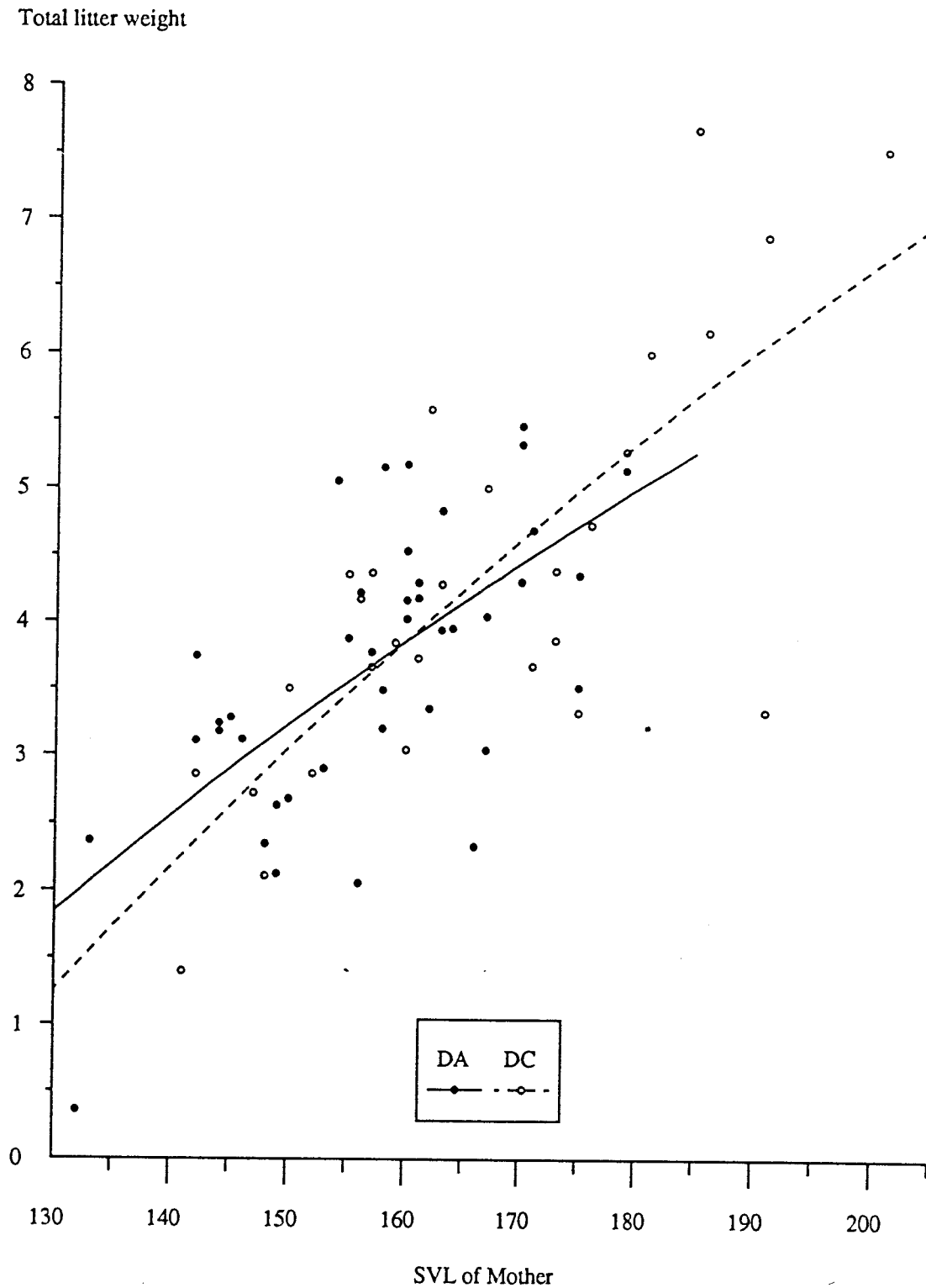


Table 4.1 Median dates of "incidents", and average date, median date and variance of dates of birth, by year.

"INCIDENTS"			DATE OF BIRTH			
		MEDIAN	AVERAGE		MEDIAN	
YEAR	NO.	DAY	NO.	DAY	VARIANCE	DAY
=====						
1981			6	11 SEP	21.6	12 SEP
1982	11	30 MAY	15	23 AUG	72.5	24 AUG
1983	12	11 JUN	17	24 AUG	90.7	26 AUG
1984	14	17 JUN	22	7 SEP	61.6	6 SEP
1985	18	29 MAY	30	10 SEP	339.7	13 SEP
1986	18	25 JUN	26	2 OCT	148.0	4 OCT
1987	4	22 MAY	8	4 SEP	81.1	6 SEP
1988			2			31 SEP
ALL	77	12 JUN	120	9 SEP	335.7	6 SEP

Table 4.2. Indication of pregnancy or otherwise of all females found in more than one year at DA and DC.

! = known to be pregnant; ? = not found in that year, or found at the wrong time of year; X = found between June and August and shown not to be pregnant; < = too small to be pregnant, i.e., less than 130 mm SVL.

NUMBER	81	82	83	84	85	86	87	88
=====								
DA 2	!	?	!	X	!	X	X	?
4	!	X						
14	X	?	!					
16	X	!	X	!	X	!	?	?
22	X	?	!	?	!			
24	X	!						
27	!	X						
28	X	!						
32	?	X	?	!	X	!	?	!
42		<	!	!	X	?		
46		X	X	!	X			
54		!	?					
68		X	!					
72		X	!	X				
76		X	!					
90			X	?	!	?	!	
92			<	!	?	!		
94			!	?	!	X		
96			<	?	!	X	!	
99			<	<	X	!		
101			!	?	!			
102			!	X	!	X		
103			!	?	X	!		
108			!	?	X	!		
123				<	?	X	!	
125				!	X	X	?	
130				X	!			
161					X	!		

Table 4.2 (continued).

NUMBER	YEAR							
	81	82	83	84	85	86	87	88
=====								
DC 4		!	X	!	X			
18		<	<	X	?	?	X	
22		<	?	X	!			
36		<	?	?	!	X		
98		<	<	X	!	?		
125			<	?	!			
143			X	!	?			
151			!	?	!			
165			<	X	!	X		
224				X	!			
233				X	!	?		

Table 4.3. Numbers of litters, total young, viable young and averages for all years.

Stars on the same row link averages within sites that are not significantly different.

	YEAR								
	81	82	83	84	85	86	87	88	TOTAL
=====									
<u>DA</u>									
LITTERS	6	7	15	7	10	17	7	1	70
LITTERS WITH									
VIABLE YOUNG	6	6	12	7	8	8	6	1	54
TOTAL YOUNG	52	49	129	55	63	77	45	6	476
VIABLE YOUNG	52	35	84	47	56	27	37	5	343
VIABLE YOUNG/ LITTERS WITH VIABLE YOUNG	8.7	5.8	7.0	6.7	7.0	3.4	6.2	5.0	6.4
	*	*	*	*					
	*	*		*	*		*		
		*		*	*	*	*		
 <u>DC</u>									
LITTERS	0	5	2	9	13	6	1	0	36
LITTERS WITH									
VIABLE YOUNG		5	1	8	11	2	1		28
TOTAL YOUNG		62	15	79	108	31	3		298
VIABLE YOUNG		58	5	73	91	10	3		240
VIABLE YOUNG/ LITTERS WITH VIABLE YOUNG		11.6	5.0	9.1	8.3	5.0	3.0		8.6
		*	*	*	*	*	*		

Table 4.4. Snout-vent lengths of viable young for the two main sites and for Steep Holm, by year.

Stars in the same column join SVL values within a site that are not statistically significantly different.

SITE	YEAR	N	AVERAGE	STD	MINIMUM	MAXIMUM		
			SVL	DEVIATION				
=====								
DA	1981	52	45.4	2.44	42.0	53.0	*	*
	1982	35	42.0	2.18	35.0	46.0	*	
	1983	84	46.1	1.96	41.0	50.0	*	*
	1984	48	45.0	2.99	39.5	50.5	*	
	1985	56	45.5	1.79	41.0	49.0	*	*
	1986	30	46.5	2.20	43.5	50.5		*
	1987	36	46.7	2.00	43.0	52.0		*
DC	1982	58	42.3	2.29	38.0	46.0	*	
	1983	5	49.0	1.37	47.5	50.0		*
	1984	67	46.6	1.96	41.5	50.5	*	*
	1985	92	45.6	1.76	42.0	50.5	*	
	1986	10	44.2	3.11	40.0	49.0	*	*
	1987	3	43.3	2.52	41.0	46.0	*	*
GA	1983	11	50.0	1.42	48.5	52.5	*	
	1984	31	46.4	1.68	43.0	49.0		*

Table 4.5. Total Lengths of viable young for the two main sites and for Steep Holm, by year.

Stars in the same column join ToTL values within a site that are not statistically significantly different.

SITE	YEAR	N	AVERAGE	STD	MINIMUM	MAXIMUM		
			TOTL	DEVIATION				
=====								
DA	1981	52	90.6	5.42	82.0	103.0	*	*
	1982	35	84.1	4.65	69.0	92.0	*	
	1983	84	92.0	4.67	83.5	103.5		*
	1984	48	88.8	6.12	79.0	101.5	*	
	1985	56	89.8	3.82	78.5	98.0	*	*
	1986	30	91.9	4.87	82.5	101.5	*	*
	1987	36	91.1	4.39	83.0	102.0	*	*
DC	1982	58	84.3	6.31	72.0	98.0	*	
	1983	5	94.7	2.39	92.0	98.0	*	*
	1984	67	93.6	4.05	82.0	101.5		*
	1985	92	91.3	4.15	83.0	105.0	*	*
	1986	10	89.2	6.19	79.0	99.0	*	*
	1987	3	85.3	4.16	82.0	90.0	*	*
GA	1983	11	101.5	3.18	97.0	106.5	*	
	1984	31	95.2	3.86	87.0	102.0		*

Table 4.6. Weights of viable young for the two main sites and for Steep Holm, by year.

Stars in the same column join SVL values within a site that are not statistically significantly different.

SITE	YEAR	N	AVERAGE	STD	MINIMUM	MAXIMUM			
			WEIGHT	DEVIATION					
=====									
DA	1981	52	0.53	0.080	0.41	0.69			*
	1982	35	0.44	0.061	0.30	0.54	*		
	1983	84	0.48	0.073	0.30	0.69		*	
	1984	48	0.51	0.079	0.33	0.67		*	*
	1985	56	0.53	0.058	0.36	0.62			*
	1986	30	0.53	0.059	0.36	0.67		*	*
	1987	36	0.49	0.074	0.30	0.68	*	*	*
DC	1982	58	0.44	0.062	0.29	0.54		*	
	1983	5	0.54	0.015	0.53	0.57			*
	1984	67	0.53	0.053	0.42	0.64			*
	1985	92	0.50	0.064	0.38	0.65			*
	1986	10	0.49	0.074	0.42	0.60		*	*
	1987	3	0.47	0.32	0.43	0.49		*	*
GA	1983	11	0.61	0.024	0.57	0.65		*	
	1984	31	0.60	0.054	0.51	0.72		*	



Table 4.7. Differences in viable new-born juvenile SVL, ToTL and weight between the two main sites and Steep Holm for each year.

Sample sizes of less than 10 are not included.

\* =  $p < 0.05$ , \*\* =  $p < 0.01$ , \*\*\* =  $p < 0.001$ , NS = not significant.

DIFFERENCES BETWEEN:										
DA AND DC				DA AND GA				DC AND GA		
YEAR	t	p	d.f.	t	p	d.f.	t	p	d.f.	
=====										
SVL	82	0.586	NS	91						
	83				6.336	***	93			
	84	3.398	***	113	2.261	*	77	0.575	NS	96
	85	0.400	NS	146						
	86	2.591	*	38						
ToTL	82	0.197	NS	91						
	83				6.569	***	93			
	84	5.006	***	113	5.196	***	77	1.911	NS	96
	85	2.140	*	146						
	86	1.419	NS	38						
WGHT	82	0.303	NS	91						
	83				5.863	***	93			
	84	1.180	NS	113	5.310	***	77	6.148	***	96
	85	2.613	**	146						
	86	1.438	NS	38						

Table 4.8. Power regression equation values and differences of the relationship of female SVL to number of viable young (NV), average SVL of young in a litter, average ToTL of young in litter, average weight (Wg) of young in litter and total litter weight (ToTWg), by site, all years combined.

\*\*\* =  $p < 0.0005$ , NS = not significant.

	SITE	d.f.	b	c	SE(b)	t(b)	p	r <sup>2</sup>
=====								
NV	DA	47	2.8020	-12.2781	0.7140	3.925	***	0.255
	DC	28	3.4710	-15.7099	0.6934	5.006	***	0.491
SVL	DA	49	0.0250	3.6855	0.1022	0.245	NS	0.001
	DC	29	-0.0221	3.9244	0.1026	0.215	NS	0.002
ToTL	DA	49	0.0373	4.3076	0.1056	0.353	NS	0.003
	DC	29	-0.0045	4.5264	0.1166	0.039	NS	0.000
Wg	DA	46	0.2559	-1.9947	0.3751	0.6823	NS	0.010
	DC	28	-0.1176	-0.0895	0.2610	0.4505	NS	0.008
ToTWg	DA	41	3.8434	-18.1999	0.7912	4.858	***	0.377
	DC	28	3.0319	-14.1003	0.5066	5.985	***	0.579

Differences between regression coefficients of DA and DC.

	d.f.	t	p
=====			
NV	71	0.6630	NS
SVL	74	0.3259	NS
ToTL	74	0.2695	NS
Wg	70	0.8051	NS
ToTWg	65	0.8477	NS

Table 4.9. Numbers of dead and deformed young by year, all sites combined.

For category definitions, see section 4.2.11.

There were no dead or deformed young in 1981.

CATEGORY	YEAR								%
	82	83	84	85	86	87	88	ALL	
=====									
1	0	11	5	2	13	0	0	31	12.9
2	3	0	4	5	10	1	0	23	9.6
3	20	43	15	18	60	6	2	164	68.3
4	3	0	0	0	2	1	1	7	2.9
5	2	1	7	2	2	0	1	15	6.3
		82	83	84	85	86	87	88	ALL
TOTAL									
AFFECTED		28	55	31	27	87	8	4	240
TOTAL									
LITTERS		15	21	23	30	29	8	2	134
TOTAL									
YOUNG		137	182	182	216	137	48	15	969
LITTERS									
AFFECTED		12	10	14	11	26	3	2	78
% LITTERS									
AFFECTED		80	48	61	37	90	37	100	58
%YOUNG									
AFFECTED		20	30	17	12	64	17	27	25
NUMBER									
AFFECTED									
/LITTER		1.9	2.6	1.35	0.9	3.0	1.0	2.0	1.8

Totals and percentages include data for 1981 (52 young in 6 litters from DA).

## CHAPTER 5. POPULATION ECOLOGY

### 5.1 INTRODUCTION

There have been considerable advances in the study of the population parameters of the reptiles of northern and central Europe in recent years. Many of these studies have been autecological in character, and often have a perception that such data are necessary for the effective conservation of the species in question. Examples are Spellerberg and Phelps (1977) on Coronella austriaca, Avery (1975), Heulin (1985) and Pilorge (1981, 1987) on Lacerta vivipara and Prestt (1971) on Vipera berus. Dunham et al. (1988) have given a very useful review of the methods of studying reptile populations, and has there is a thorough review of the data on populations until the mid 1970's by Turner (1977). Stumpel (1985) is the only worker to attempt any study of the slow-worm, but he was unable to obtain many data on population density or structure. As noted in Chapter 3, his data are unlikely to represent a true picture of the population he studied, since his samples were heavily biased towards females.

### 5.2 ANALYSIS

#### 5.2.1 Introduction

In the present study, the estimation of some parameters is much easier than others. Calculation of the sex ratio is a matter of counting the numbers of adults of both sexes known to be present at a given time. The problem here is allowing for individuals not found in the relevant time period. There is no way of estimating immigration or emigration from the available data, so it must be assumed that an individual was present in the population for the whole time between two captures. The same applies to the estimation of population density and structure. If an animal was not found after a given time,

it must be assumed to have left the population, say from predation.

The estimation of population structure is dependant on further assumptions. Chapter 6 indicates that growth rates are very variable, both for a given individual and between individuals and size classes. It is therefore not possible to determine age from size with any confidence. Analysis of population structure thus has to be based on size classes, which are to a certain extent arbitrarily defined, not on age classes. The size class of an animal not found in a given year must be determined from highly variable growth rate data. The situation is helped by the ability to follow individual adults and larger sub-adults by photography. It was not possible to do this for animals of less than 100 mm SVL, so alternative methods had to be used to estimate their numbers and density. There are several possible approaches. One is to argue that the number of captures in each size class is proportional to the absolute numbers in the population at the time in question. It is easy to see that this is not so from Chapter 3, where the changes in the proportions are very large, and change in unpredictable ways. It is quite possible that smaller animals differ in their reactions to the environment under the tins, or to a set of weather conditions, leading to differential rates of capture. A possible point of departure is that the number of young born in a year can be estimated within known confidence limits. For many females in a year the number of young born is known precisely, either from the litter measured and counted in captivity (Chapter 4), or from the animal found at the right time to be correctly classified as non-pregnant. The number of young born to females not found can be estimated from the equations of part 4.3.6, after deciding whether or not the female was present in the population and the probability of reproduction that year. It may then be possible to relate the number of young born

in a year to the number of captures of juveniles caught the following spring. The unknown is the rate of predation. Whether this can be extended for the years following the first year after birth is unfortunately very questionable, since many more unknown factors come into play, such as different survival rates of older over younger juveniles and unknown differences in behaviour.

A life table is the aim of this analysis. Such a table is dependent on a number of assumptions, and would be a table of size classes rather than ages. This is because of very variable growth rates, long periods between recaptures, the lack of a suitable method of identifying juveniles and last (but not least) the relatively long potential life span of the slow-worm. This is quite a lot longer than the length of this study, since adults found at the start of the study were known to be still alive in 1987. The study itself is a little longer than is usual for such work.

#### 5.2.2 Estimation of the total numbers of young born

The number of young born to females of known size was given in Chapter 4. The next step was to estimate the numbers born to females in the population that were not caught in a particular year. The presence or otherwise of each identified female was determined from recapture data. If an animal was found in, say, 1985, it was assumed to be present for all previous years. If 1985 was the last year in which the animal was found, it was assumed to have left the population and was not counted in any estimates for the years following. Chapter 4 has also shown that females generally are pregnant in alternate years. Those females which were not found in a given year had their reproductive status for that year determined by their previous and later reproductive history and the pattern of being pregnant in alternating years. Although the alternating pattern was found not to be a fixed rule, it

was assumed to be so for this analysis. The SVL of each female in the population was estimated from the growth rates in Chapter 6, taking 1st September as the date for the number of days of growth. The number of young born to these females was then estimated from the regressions of female SVL and number of viable young given in Chapter 4. This figure was then rounded up or down to the nearest integer. These regression assumed that the year in question was "average", i.e., not like 1986 with the low numbers of viable young born. Very few females of less than 140 mm SVL were found to be pregnant in any year except 1986. If the growth estimate predicted an SVL of less than this, it was taken to be too small to be reproductive. Excluding these animals did not alter the estimate to any degree, since they were few in number and tended to have small litters.

#### 5.2.3 The sex ratio

The total numbers of individuals the sexes were taken for the two main sites. These data were compared by a two-way table for comparing the sites and G tests for comparing the numbers of the sexes within a site on the assumption of a 1:1 sex ratio.

#### 5.2.4 Size classes

Histograms of the SVLs of sub-adults and first-year juveniles were generated and the distributions compared by Kruskal-Wallis tests, which were carried out on the raw data rather than size classes. The size classes of adults were formed by taking the SVL of each individual on its first capture. These distributions were then compared between sexes and sites by Kruskal-Wallis tests.

#### 5.2.5 Density estimates

The area of DA suitable for the placing out of tins was 0.1 ha. At DC a similar area was assumed (Chapter 2) but this estimate may not reflect the area from the slow-worm's point of view because of the nature of the terrain. The simplest estimate of density was taken as the number of adults alive in 1982.

### 5.3 RESULTS

#### 5.3.1 Total numbers of young born

The totals of the numbers of viable young in each year at the two sites was given in Table 4.3. The numbers of young born to females known to be alive and thought to be reproductive in each year are given in Table 5.1. It can be seen that fewer females were not found in a given year at DA than at DC. There were two years at DC when very few pregnant females were found at all.

From the growth rate estimates in the next chapter, and the regressions of female SVL against the size of the litter, it can be estimated that an average female at DA could produce 33 young in a lifetime. The first reproduction at an SVL of 145 mm would give a litter of four, the second (two years later), at an SVL of 169 a litter of eight, the third at an SVL of 180 mm a litter of ten. The final litter, at an SVL of 185 would have 11 in it. The two regressions have large variances and this estimate will have wide confidence limits. At DC some females were larger than at DA, although the growth rates were similar. The larger numbers of juveniles captured may be because of better survival at DC, allowing a further litter of 12 to be born.

#### 5.3.2 The sex ratio

At DA there were a total of 50 males and 82 females individually identified. A further 28 sub-adults of more



than 100 mm SVL were captured. These were not assigned to a sex since they were not caught at a large enough size to determine it with certainty. There were 160 photographed animals at the site. A G test showed that the numbers of males and females was significantly different ( $G = 7.835$ ,  $p < 0.01$ , 1 d.f.).

If only those animals known to be alive and adult at the beginning of 1982 are considered, the difference remains, since there were 39 males and 53 females, but the difference was not significant ( $G = 2.139$ ,  $p > 0.1$ , 1 d.f.).

At DC the bias was in the opposite direction. There were 115 photographed males, 89 females and 58 sub-adults that were not known to have progressed to adulthood. These frequencies were not quite significantly different ( $G = 3.323$   $p > 0.05$ , 1 d.f.). There were 77 males and 59 females known to be alive in 1982. This difference was not significant ( $G = 2.389$ ,  $p > 0.1$ , 1 d.f.).

The difference in sex ratio between the sites was highly significant when all animals were considered (2 x 2 contingency table,  $G = 11.051$ ,  $p = 0.001$ , 1 d.f.). When those animals known to be alive and adult in 1982 were considered, the difference was less significant ( $G = 4.458$ ,  $p < 0.05$ ).

### 5.3.3 Size classes

Fig. 5.1 shows the distribution of SVLs for sub-adults and first-year juveniles for the two sites. The frequencies are shown as percentages because the data are numbers of captures, not numbers of individuals. There is no difference in this distribution between the sites ( $H = 1.049$ ,  $p > 0.3$ , 1464 d.f.).

Fig. 5.2 shows the distribution of SVLs of adults at the two sites. The SVLs are of each individual at the time of its first capture. The average SVL of males at DA was

151.7 mm (standard deviation = 12.90, n = 42) and of females 153.5 mm (s.d. = 12.14 mm, n = 69). At DC, as might be expected from the histogram (Fig. 5.2), the averages were slightly greater; that of males was 156.3 (s.d. = 19.71, n = 103), while for females it was 157.5 (s.d. = 17.97, n = 76). Although there were some very large animals at DC, there was no difference in the SVLs of males ( $H = 0.562$   $p > 0.4$ ) or females ( $H = 1.221$ ,  $p > 0.25$ ) between the sites. There were also no differences when the sexes were compared within a site (DA,  $H = 0.556$ ,  $p > 0.4$ ; DC,  $H = 0.441$ ,  $p > 0.5$ ). The small numbers of very large animals at DC did not change the overall picture.

#### 5.3.4 Density estimates

Section 5.3. showed that there were 92 adults at DA and 136 at DC alive in 1982. If the area of both sites was 0.1 ha, the densities were 920 and 1360 adults/ha respectively. It was not possible to estimate the numbers of sub-adults and juveniles, but it is worth noting that the numbers caught per visit were higher at DC than at DA.

#### 5.4 DISCUSSION

There have been no previous reports of the size class distribution of slow-worms. Stumpel (1985) gave some data on weight classes, but there are problems with this approach, such as autotomised animals, which can bias the samples if included, or seriously reduce sample sizes if they are not. There were no differences between sexes or sites and the pattern in Fig. 5.2 is typical for many other species. It is obviously not possible to differentiate age classes from size class data as Pilorge (1987) was able to do for the common lizard.

There are no clear reasons why the sex ratios should be different between the sites. In some reptiles there is

temperature dependent sex determination, where the temperature experienced by the developing embryo effects its sex at hatching. This phenomenon is widespread in crocodilians and chelonians, but has not been found in a lizard with sex chromosomes (such as the slow-worm), nor in a viviparous species (Bull 1980). Viviparous reptiles are unlikely to be species with temperature dependent sex determination since the female can control the temperature of development to a certain extent. There may be sampling bias, but the ratios at the two sites were in opposite directions, so it is difficult to see from where the bias may have come. Pilorge (1987) showed that the sex ratio in the common lizard could fluctuate markedly, but was generally near 1:1. Prestt's (1971) populations of adders had a ratio of almost exactly 1:1.

The average sizes of the sexes in Stumpel's sample were, in females at least, similar to those reported here. His sample of males was small in numbers and SVL at 142.7 mm, but the average SVL for females was 156.4 mm.

The density estimates are comparable to those of Pilorge (1987) for the common lizard, of the order of several hundred per hectare, and much greater than those for the smooth snake given by Goddard (1981). Stumpel (1985) had too few recaptures for estimates of population size or density.

Fig. 5.1 Distribution of SVLs of non-adults at DA and DC.

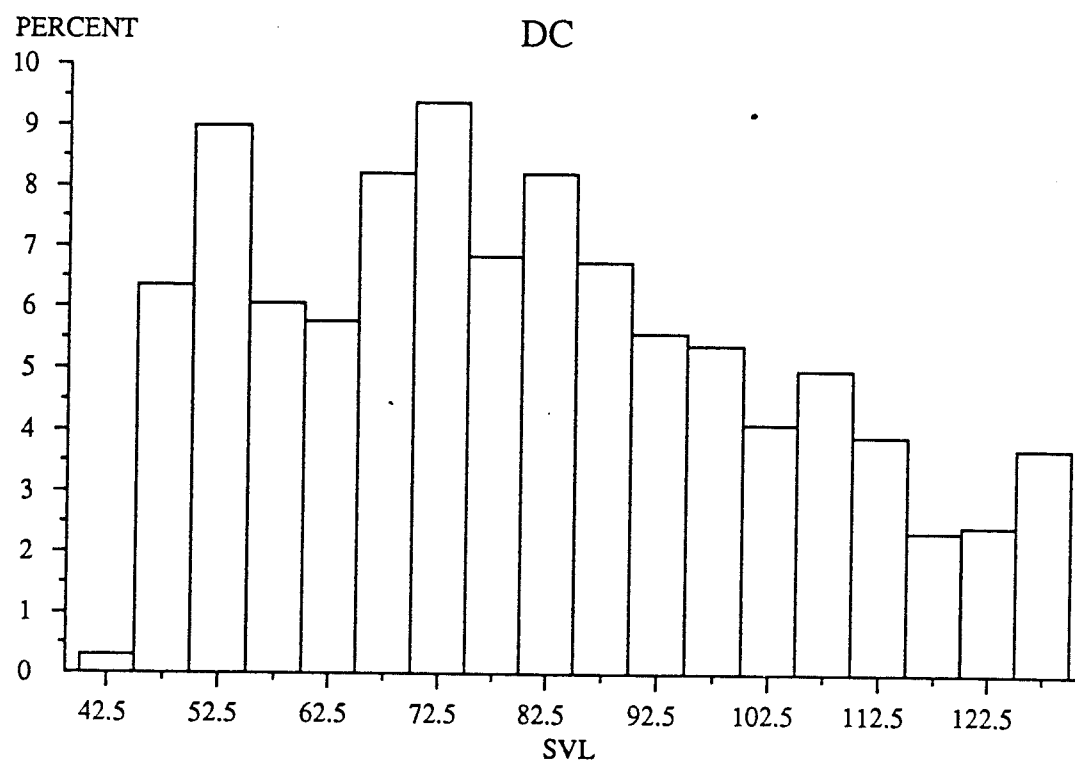
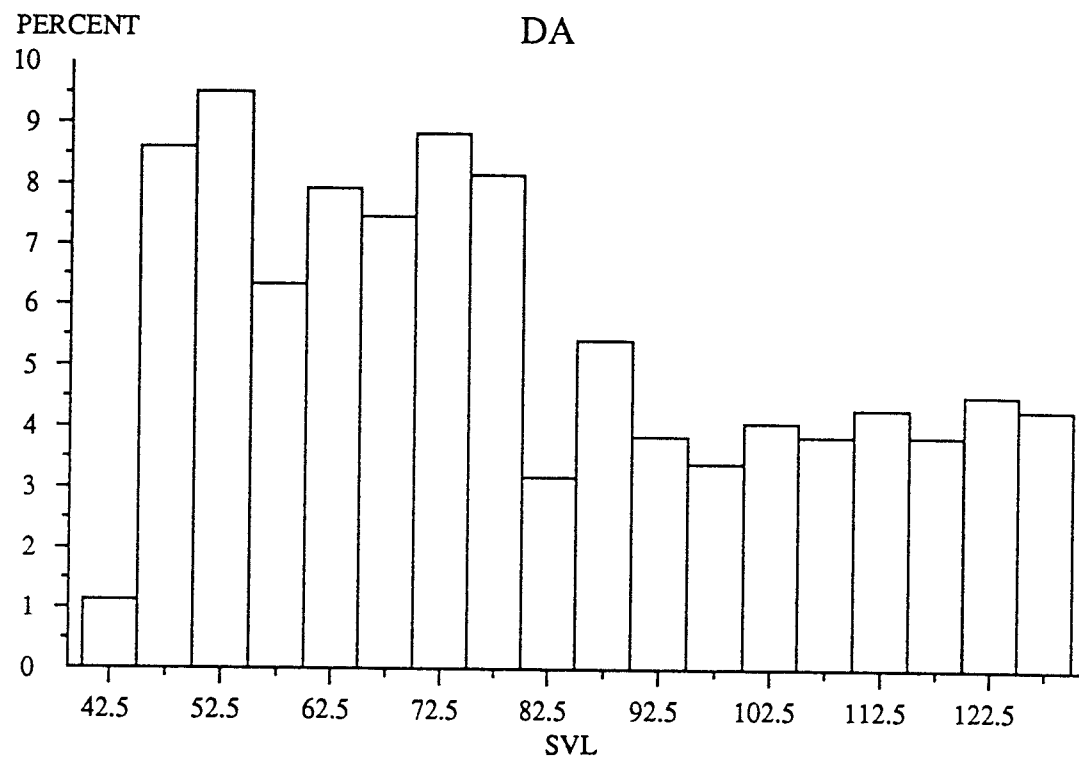


Fig. 5.2 Distribution of size classes of adults at DA and DC.

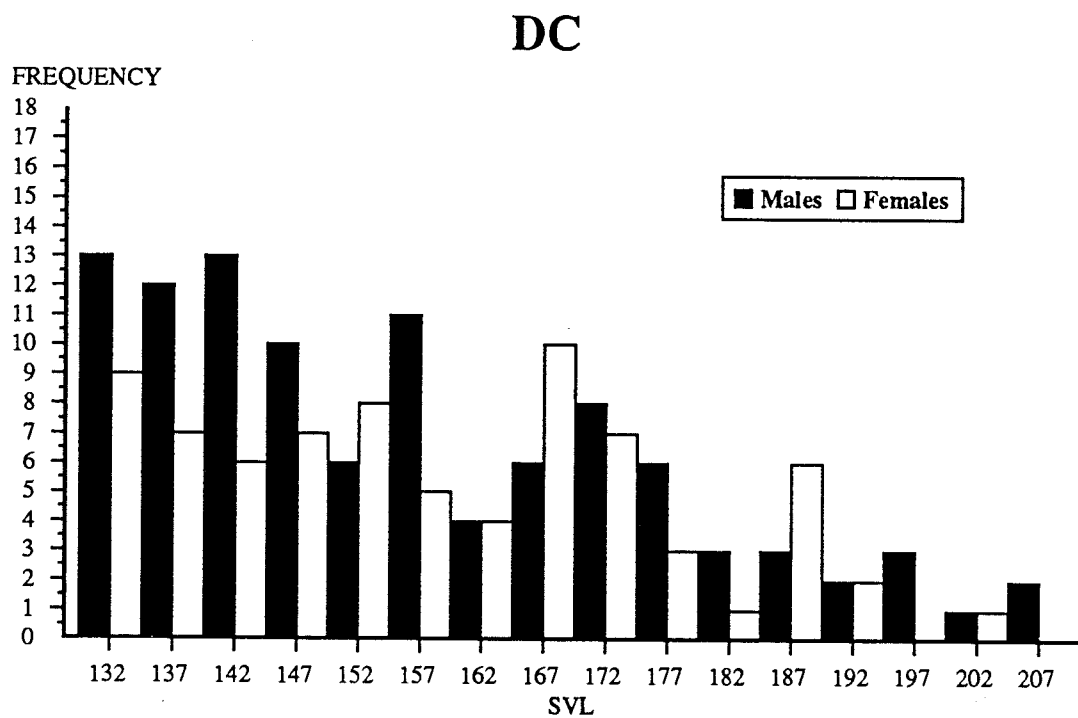
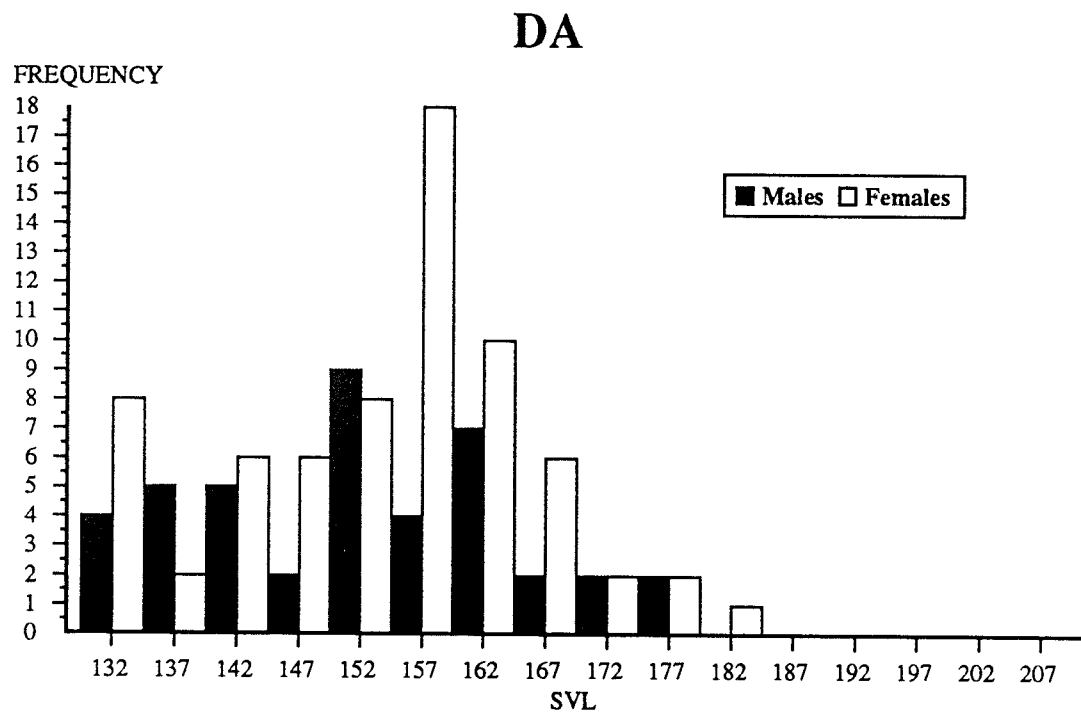


Table 5.1 Estimated total numbers of young born in each year at the two main sites.

	YEAR	VIABLE YOUNG	EXTRA FEMALES	EXTRA YOUNG	TOTAL YOUNG
=====					
DA	1981	52	9	59	111
	1982	35	5	32	67
	1983	84	2	14	98
	1984	47	4	28	75
	1985	56	2	12	68
	1986	27	1	9	36
DC	1982	58	12	82	140
	1983	5	7	52	57
	1984	73	8	53	126
	1985	91	2	11	102
	1986	10	0	0	10

## CHAPTER 6 GROWTH

### 6.1 INTRODUCTION

The study of reptilian growth, defined as the change in a linear dimension or mass with time, has progressed greatly in recent years. A number of models have been used on a very wide variety of species (Andrews 1982), all of which necessarily have made assumptions about the growth of the species. It is now known that reptiles do not continue to grow throughout life, as was previously thought, but reach a maximum size asymptotically. This asymptote can vary markedly between the individuals and populations of a species. Thus, growth does not proceed at a near constant rate, but varies with size. Growth rates can vary markedly due to both extrinsic factors (season, food supply, climate) and intrinsic (size, sex, individual variation); this is as true of tropical as of temperate species (Andrews 1982). This author identifies three important stages in the postnatal growth of a reptile; birth or hatching, sexual maturity and maximum length. Embryonic growth rates have been little studied.

There has been very little published on the growth of slow-worms. Smith (1964) gives some ranges of total lengths for various age groups, but these are of little use since he did not give SVLs, and there was no indication of how the figures were calculated. Stumpel (1983) gave almost no data for growth in his mark-recapture study of the slow-worm in the Netherlands because of inaccuracy in the measurements of SVLs.

### 6.2 METHODS AND ANALYSIS

#### 6.2.1 Possible growth models

This study, as has previously been pointed out, was often hampered by a low numbers of recaptures and long and irregular intervals of captures of known individuals, and

the inability to identify juveniles and smaller subadults. This made it desirable to keep the analyses as simple as possible, hopefully at the not making too many simplifying assumptions.

Although there are a number of possible approaches to the study of growth, the most practical from the point of view of a long-term mark-recapture study is to assume a functional relation of size (viewed as a linear dimension such as SVL) with time (Andrews 1982). If this assumption is valid, then the model most widely used to describe and analyse growth rates is the Bertalanffy, which is a negative linear function of growth rate with time:

$$GR = b \cdot SVL + c;$$

where GR is growth rate in mm/day, b and c are the regression coefficient and constant calculated from the set of mm/day data. In its integrated form it is a decaying exponential which reaches an asymptote. The integrated form can be used to estimate the new SVL after growth in a given time and is normally stated as;

$$SVL_t = A(1 - k \cdot e^{-bt});$$

where  $SVL_t$  is the new SVL after the time period t (in days), A is the asymptotic length ( $= -c/b$ , i.e., the regression constant divided by the coefficient, and is thus the value of the SVL where growth equals 0 from the linear equation), e is the base of natural logarithms and k is the proportion of growth remaining, i.e.,  $(1 - SVL_t/A)$ ,  $SVL_0$  being the initial SVL.

The Bertalanffy has been found to be most appropriate for longer lived species and both linear and exponential forms of the model are relatively easy to manipulate. Another commonly used model, the logistic, assumes that the maximum growth rate occurs at the mid-point of minimum



and maximum sizes, and has been found to be useful in short-lived, fast growing species such as the small iguanid Sceloporus merriami (Andrews 1982; Dunham 1978).

In the present study, the Bertalanffy model was used in the analysis of the growth of individually identified, i.e., adult and larger subadult slow-worms.

#### 6.2.2 First year and older juveniles

The Bertalanffy model could, however, not be used for the analysis of growth from birth to one year of age, since individuals could not be identified. Over a short time period (i.e., relative to the life-span of the species) it is reasonable to use a simple linear regression of SVL on day of year, and indeed this method has been used in cases where there was a clear relation between size time of year (Shine 1978). In a linear regression of length on date, for instance, the regression coefficient is the estimate of the growth rate, normally expressed as mm/day.

The initial classification of first-year juveniles in the field was found on later analysis to be not as clear cut as hoped (Chapter 3), since first-year juveniles and older animals did not always form two clear groups. Fig 6.1 illustrates this by showing SVL by date for all non-adults at DA in a single year. Records classified as first-year juveniles are bounded. Similar decisions had to be made at both sites and in nearly all years. Four types of regression were used, linear, reciprocal, exponential and logarithmic to see which gave the best least-squares fit, i.e., that which gave the largest  $r$ . Sufficient data were available for 1982-86 at DA and 1983-86 at DC to make comparisons between sites and years.

Fig. 6.1 also shows that juveniles older than a year could not be split into clear size/age groups. To have done so would have meant making assumptions on large numbers of individual field records with no way of testing

those assumptions. This unfortunately meant that their growth rates could not be analysed in the same way as the first year animals. However there were records of larger subadults, and some of smaller, that allowed the gap to be partially filled.

Neonate juveniles were found in the autumn of most years. Regressing SVL on day could also be used to see if there was significant growth from birth to the first hibernation. Caution must be exercised because of great variation in birth dates and the possibility of size-related mortality. On the other hand, it was possible to compare the average size of the young at birth (Chapter 4) with the predicted size (from the regression equations of SVL on date) on emergence from hibernation the following spring.

#### 6.2.3 Sub-adults and adults

Adults and sub-adults of more than 100 mm SVL (as well as some smaller) were photographed and could be identified on recapture (Chapter 2). On recapture the number of days between successive captures was calculated, using 1st April as a base and discounting winter if relevant. The growth rate was taken as the change in SVL divided by the number of days between successive captures. This rate, as mm/day, was then related by least-squares regression to the initial SVL, and to the mean SVL of the initial capture and recapture.

There was some inaccuracy in the measuring of SVL, even with practice, so that growth between two captures a few days apart could easily be overshadowed by errors in the measurement of the SVL. Therefore, growth rates calculated from captures less than seven days apart were not used in the initial analysis. The growth rate calculated from one capture and recapture thus became one point in the regression of SVL on growth rate. It was found that this did not remove large sources of variation

in the regression estimates. Regression equations of mm/day on SVL were then calculated using the data for captures which were successively not less than 14, 19, 24, 29, 39, 49, 74, 99, 149 and 199 days apart. The equation with the highest  $r$ , of the 11 calculated was taken to be that which best described the relationship. This process was repeated for males, females and subadults, using initial and mean SVL estimates, at each of the two main sites. The time spent in captivity by pregnant females was not counted in the calculation of their growth rates. Males, females and subadults were analysed separately, but it was not possible to separate the years, as sample sizes were too small.

#### 6.2.4 Maximum size of adults

There have been many statements in the popular literature on the maximum size of slow-worms and the relative sizes of the sexes. These sizes almost always ignore SVL and are given as total lengths. Females are usually stated to grow larger than males, although the opposite is sometimes said to be true (Dely 1981; Smith 1964; Street 1979).

The maximum size is defined by Andrews (1982) as "the largest individual in the study population". This assumes that a researcher finds that particular animal; it is also unusual to define a parameter of a population on the basis of a single animal. There is no readily accepted method of characterising the largest size to which an average individual in a population may attain should it survive to the normal maximum age. In this study a number of different ways were used to estimate the largest size to which an individual might grow; some may be a little artificial, but all but one use more than a single animal. In all cases the two main sites and males and females were treated separately, and it was also possible to use the relatively small amount of data from Steep Holm for

comparative purposes. Although it may be possible to place confidence limits on some of these estimates, it is only intended that these estimates be used as a rough guide to the possible differences between sexes and sites, not for statistical comparisons.

The various estimates of maximum size are defined as follows:

- (i) The largest recorded individual,
- (ii) The third largest recorded individual,
- (iii) The average SVL of the 5 largest animals,
- (iv) The average SVL of the 10 largest animals,
- (v) The upper quartile of the largest 20% of individuals,
- (vi) The average SVL of the largest 10% of individuals,
- (vii) The estimate from the equations of growth rate against SVL of the asymptotic length, using the equation with the highest  $r$ , in each case.

It was possible to make estimates of all but the last for Steep Holm.

### 6.3 RESULTS

#### 6.3.1 Growth from birth to the first hibernation

Fig 6.1 shows all captures from birth to the first hibernation for all 1984 at both sites. The other years were similar: there was no clear growth and the data were too few for comparing years or sites. Although it is not possible to conclude that there is no growth from birth to the first hibernation from these data, for the reasons outlined above, neither is it possible to decide that there is growth.

#### 6.3.2 Growth in the first full season

Table 6.1 shows the coefficients of determination for all years at the two main sites for four regression

models; linear, exponential, reciprocal and power. The  $r$ , values are similar for all years and sites, suggesting that no model describes the data very much better than any other. The  $r$ , values for the linear equation are greatest in four of the nine year/site combinations, while reciprocal has the greatest in three and power in two. Further analysis was done on the linear equations.

Figs. 6.2 and 6.3 show the regression lines for DA and DC for 1982-86 (DA) and 1983-86 (DC) respectively. There are too many data points to show them all; both figures show the data for a single year to illustrate the typical spread of data. The coefficients and constants of the regression lines are given in Table 6.2, along with the comparisons between years and sites. There are no significant differences in the regression coefficients (i.e., growth rate) between any two years at DA. At DC 1983 is significantly different from all other years, but there are no other differences. Comparing sites within years, only 1983 showed a significant difference between DA and DC, although 1985 was nearly so at the 0.05 level. In most years, therefore, there is an estimated growth rate of 0.12 to 0.13 mm a day. It is not possible to tell from these data that the rate changes over the first year of life of an animal. If there is a change in rate it is probably small and could probably be detected only by experiment under controlled conditions.

Table 6.2 also shows the constants for the regression equations. These are the estimates of the SVL at day 0, i.e., 1st April. Again 1983 is noteworthy, because of the low values at DA and DC. There was also a high value at DC in 1984. It is possible to compare these estimates with the known sizes of juveniles born in captivity the year before. These data are given in Table 4.4. There is a high correlation between the two ( $r = 0.941$ ,  $p < 0.0001$ , 8 d.f.). The estimates of SVL in spring are higher than the known sizes of neonates in all years at both sites. The

average estimated increase in SVL is 1.5 mm (range 0.7 - 2.5 mm). There is thus evidence of only a small amount of growth from birth to emergence from hibernation. Alternatively, if there had been higher rate of growth, then there would have had to have been a compensating selective mortality of larger juveniles. If there had been growth at a similar to that of the following season, i.e., 0.12 mm/day, the neonates would have grown by approximately 7 mm SVL by the end of October and so would have been 4.5 to 6 mm longer than estimated from the regression equations of growth for the following year.

### 6.3.3 Growth of sub-adults and adults

The initial task of the analysis was to determine which of the two SVL figures (initial or the mean of the initial and second) gave the highest  $r$ , values for the linear regression equations of SVL on growth rate. It was found that the highest  $r$ , values for these equations were obtained by using the SVL on initial capture for all sex/size groups, and sites. The initial SVL was used in all further analysis. The growth rate of sub-adults is shown for the two main sites in Fig. 6.5. The regression lines represent the equations with the highest  $r$ , i.e., after all SVLs taken more than 149 days apart were excluded. Table 6.3 gives the basic data on these equations. There is no significant difference between these equations ( $t = 0.55$ ,  $p > 0.3$ , 51 d.f.). These equations indicate that a sub-adult of an SVL of 100 mm would have an instantaneous growth rate of 0.097 mm/day at DA and 0.116 mm/day at DC. The growth over a season (taken as 200 days, from the beginning of April to the third week in October), calculated from the integrated Bertalanffy equation, would be 17.6 mm at DA and 20.8 mm at DC.

If these equations represent the real growth rates of the animals, then the rate estimated from them for the largest sub-adult of 130 mm should be the same as that for

the smallest adults. At DA the growth rate for a 130 mm sub-adult was calculated as 0.066 mm/day and at DC as 0.082 mm/day.

Growth rates for males and females were estimated in the same way as for sub-adults. Figs. 6.6 and 6.7 show the basic data points and three regression lines for growth rates calculated from SVLs taken not less than 6 and 29 days apart and that for the number of days producing the equation with the highest  $r$ , for males and females at DA and DC. These data are also shown in Table 6.3.

These equations suggest that a male of an SVL of 130 mm at DA would have a growth rate of 0.069 mm/day, and a female one of 0.060 mm/day. A male of 130 mm SVL at DC would have a growth rate of 0.085 mm/day and a female 0.088 mm/day, all of which data are consistent with the values calculated from the equivalent equations for sub-adults.

An average sized male of 160 mm SVL at DA would have an estimated growth rate of 0.0351 mm/day and a female one of 0.0356 mm/day. A male of 160 mm SVL at DC would have an estimated growth rate of 0.0463 mm/day and a female one of 0.0357 mm/day.

The equations for the growth of first-year juveniles indicate that at the end of the first full season, assuming that it was 200 days long, an average animal would have an SVL of 75 mm. If the integrated growth equations are used thereafter, at DA a sub-adult would have an SVL of 96 mm at two years, 115 at three and 130 at four. At DC these estimates would be 75 mm at one year, 100 mm at two, 121 at three and 137 at four.

#### 6.3.4 Maximum size of adults

Table 6.4 shows the estimates for maximum size for males and females at the three sites. All measurements are given as SVLs. There is considerable consistency among and between categories despite the widely differing ways by

which they were calculated. Males are larger than females in all but three estimates over all sites; of those, two of the differences are less than 5 mm. The differences within estimates between the sexes is consistently larger at DC than at DA. Males at DC are larger than those at DA in all seven estimates. Females at DC are larger than those at DA by six estimates. This is fairly consistent with the growth rates calculated from the Bertalanffy equations in the previous section, where those at for males DC were higher than those at DA. The estimates of growth rates for females were similar between sites. At DA the asymptote estimates agree within 3 mm with the largest animal found for both sexes, but at DC the asymptotes considerably underestimate the largest animals.

The situation in the Steep Holm samples is less clear. Males are larger than females in three of the five estimates where calculation was possible, as well as in an average of the estimates, but females are larger in the other two, in one case by a considerable amount. This reflects the relatively small number of visits made to the island, leading to relatively few captures of adults. The large difference in estimate (iv) (average SVL of the largest 10 animals) is due to the finding of a number of females in range 190 to 210 mm SVL. The male sample is biased by the capture of a few very large animals (the largest, at 250 mm SVL, is the longest animal recorded in Britain whose SVL has been noted) while the rest were of more modest sizes.

#### 6.4 DISCUSSION

In the introduction it was noted that the analysis of growth rates in the slow-worm had to be simple because of the low rates of recaptures of known individuals. The results given here are reasonably consistent with those that may be expected. In most longer-lived reptiles juveniles grow faster than sub-adults, which in turn grow



faster than adults (Andrews 1982). The present data are consistent with this, although there are notable differences between sites. The growth rates at of first-year juveniles was similar between the two main sites, biut subadults and males at DA grew more slowly than at DA.

There are, of course, gaps in these data. Sample sizes were too small to separate individual years except for first-year juveniles, and the data for sub-adults were marred by the paucity of records of animals of less than 100 mm SVL. The slow-worm is a relatively slow growing species, which means that there has to be a fairly long time between captures to ensure that errors in the measurement of the SVL are masked as much as possible by true growth. The effect can be seen in Table 6.3, where the sample sizes used to calculate the regressions tend to be small. Even so,  $r$  values are still low in several cases.

The model chosen to describe the data is very important for the success of the analysis. The Bertalanffy model has been used in many studies and was felt to be the most appropriate for the present data. The data set was too small to fit to a number of possible models to see which, if any, fitted the data best. This has been done for the American alligator, Alligator mississippiensis by Jacobsen and Kushlan (1989), using six types of growth function. They concluded that an exponential, non asymptotic growth curve fitted their data best. It is worth noting that, while the maximum sizes for males and females predicted from the Bertalanffy equations at DA agree with the largest animals found, at DC they underestimated them considerably.

It is clear that a great deal more data are required on the growth rates of the slow-worm for more precise models to be fitted.

Fig 6.1 Records of all animals of less than 130 mm SVL at DA and DC in 1984

Records between the two lines were considered as first-year juveniles. Records above line A are sub-adults, those below line B are neonates.

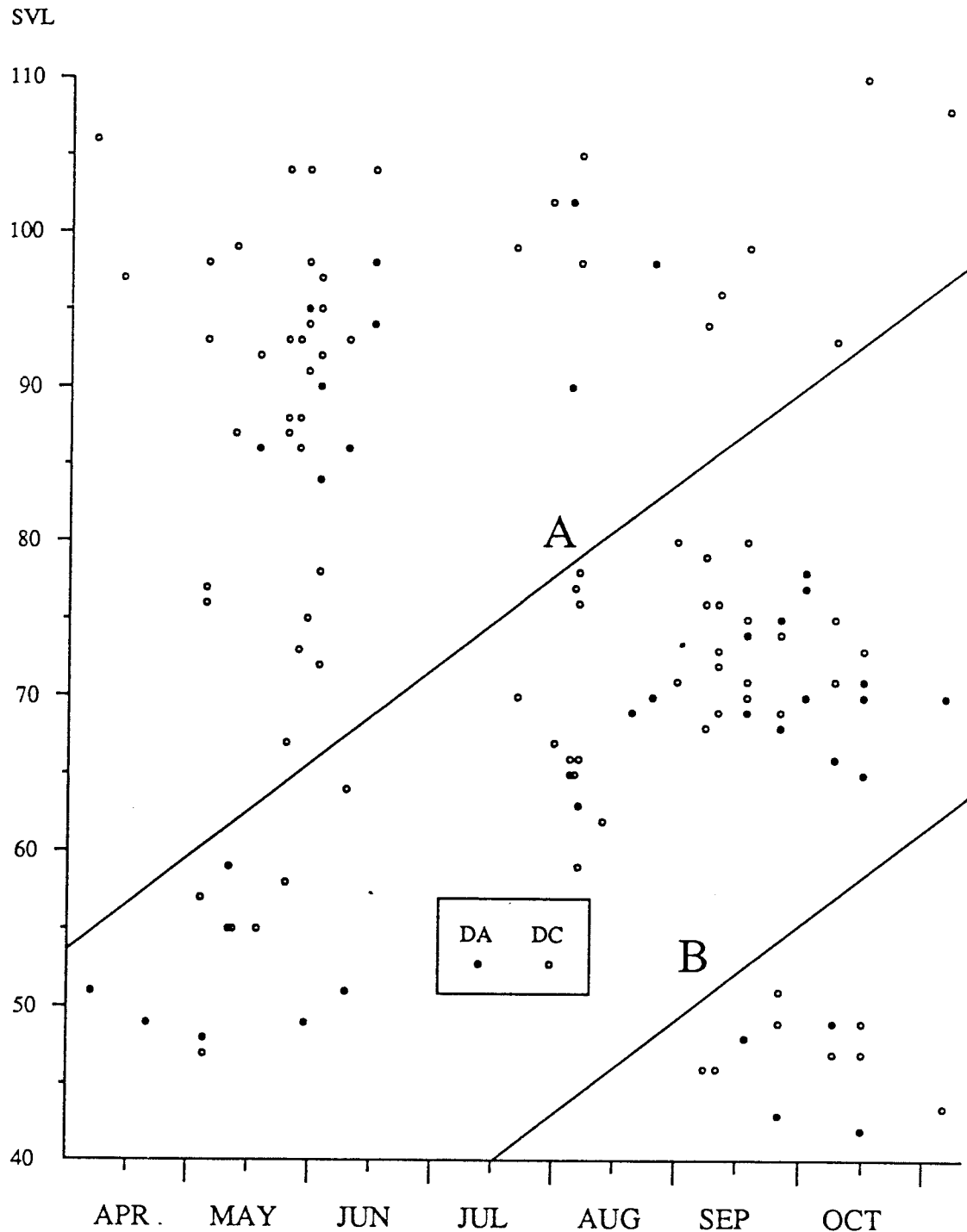


Fig 6.2 Linear regression lines of SVL on date for first-year juveniles at DA 1982-1986  
The points for 1984 are shown for illustration.

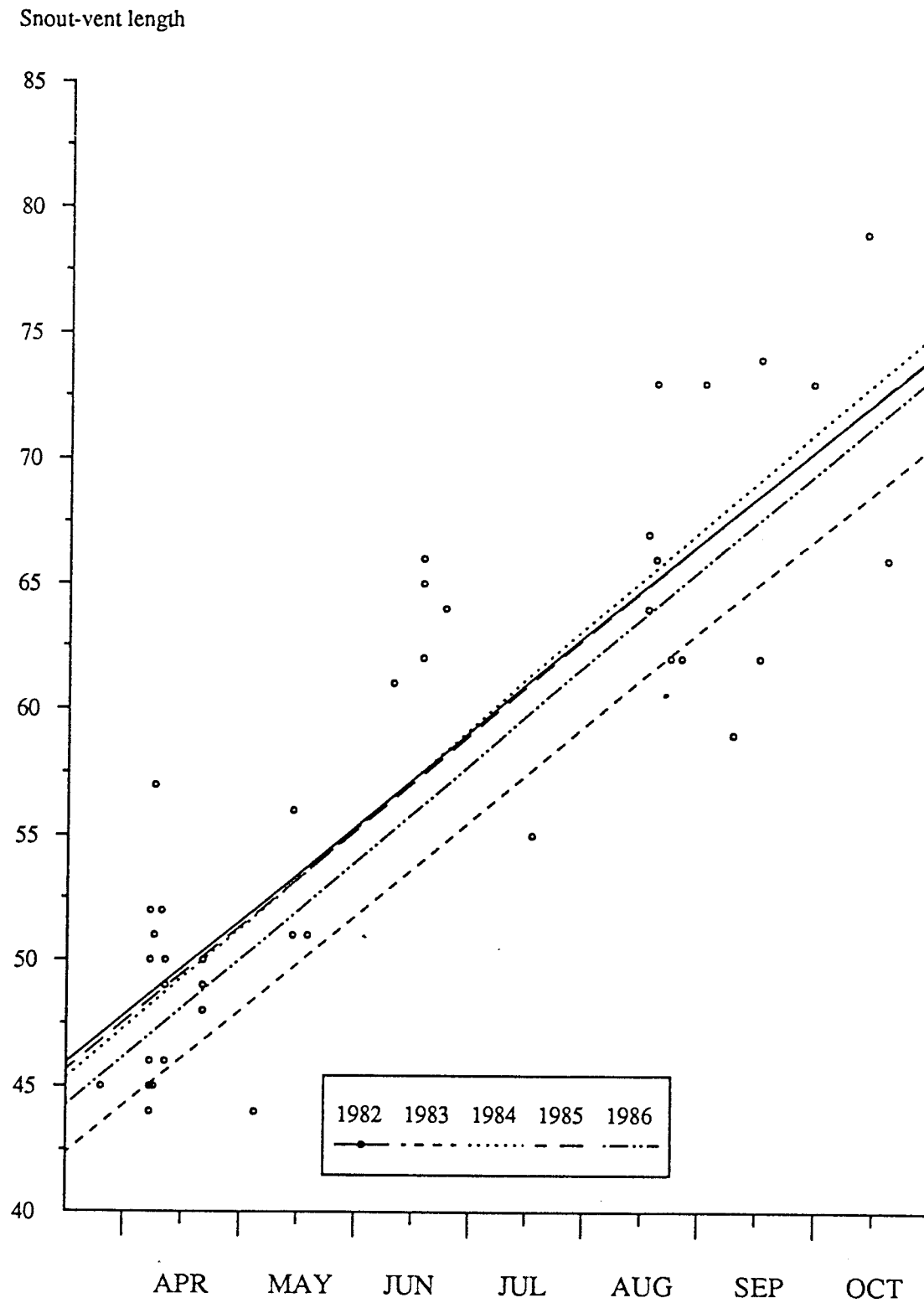


Fig. 6.3 Linear regression lines of date on SVL for first-year juveniles at DC, 1983-1986.

The points for 1984 are shown for illustration

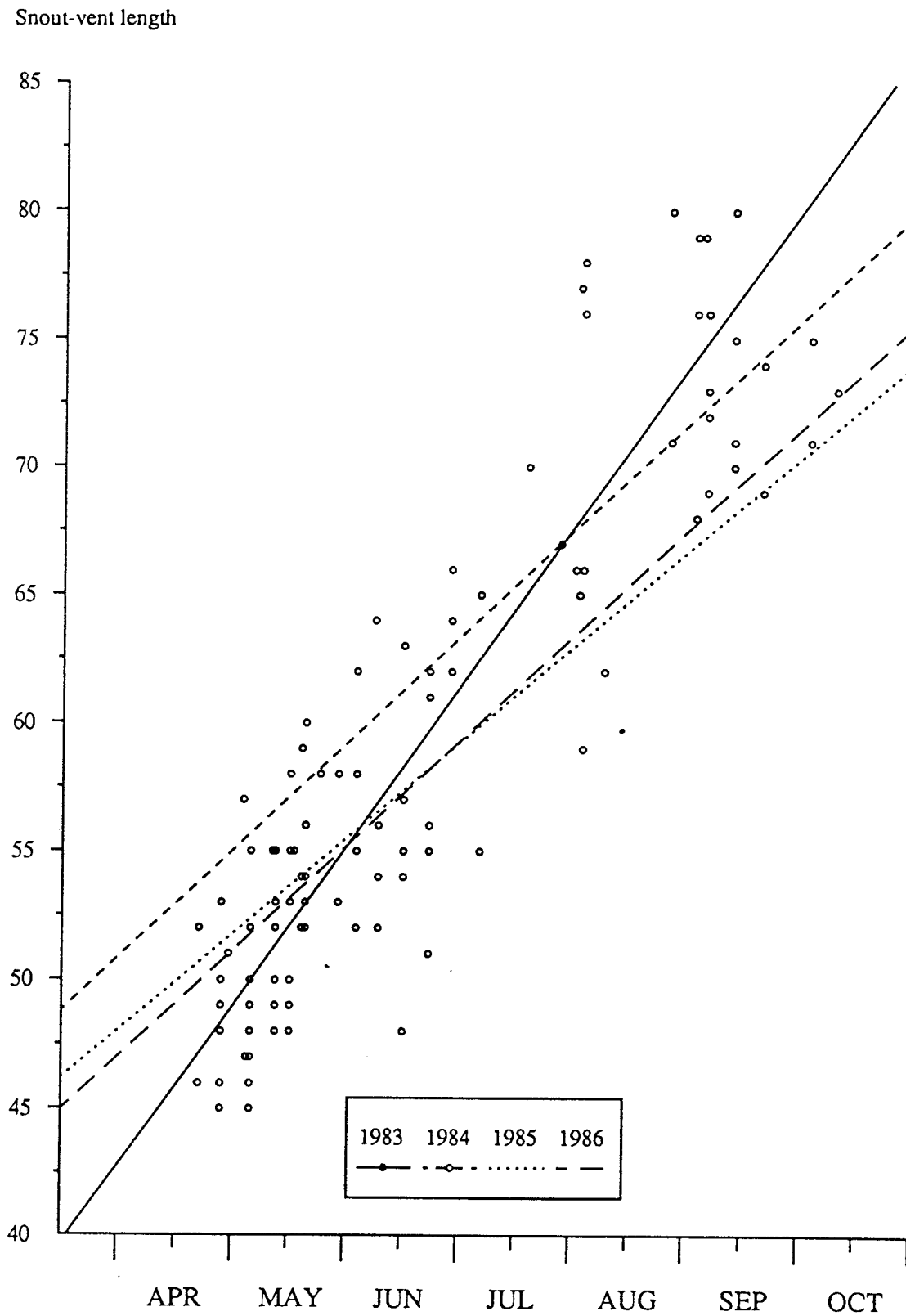


Fig. 6.4 Relationship between growth rate and SVL for sub-adults at DA and DC.

Table 6.3 gives the data for the regression lines.

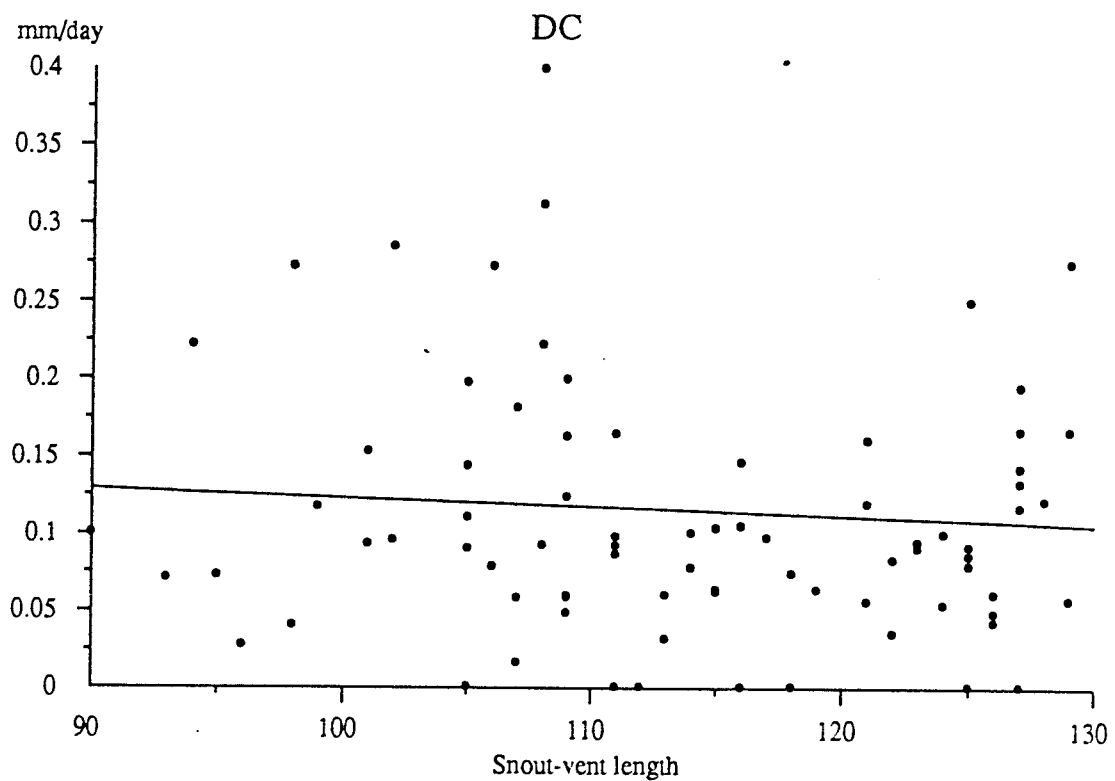
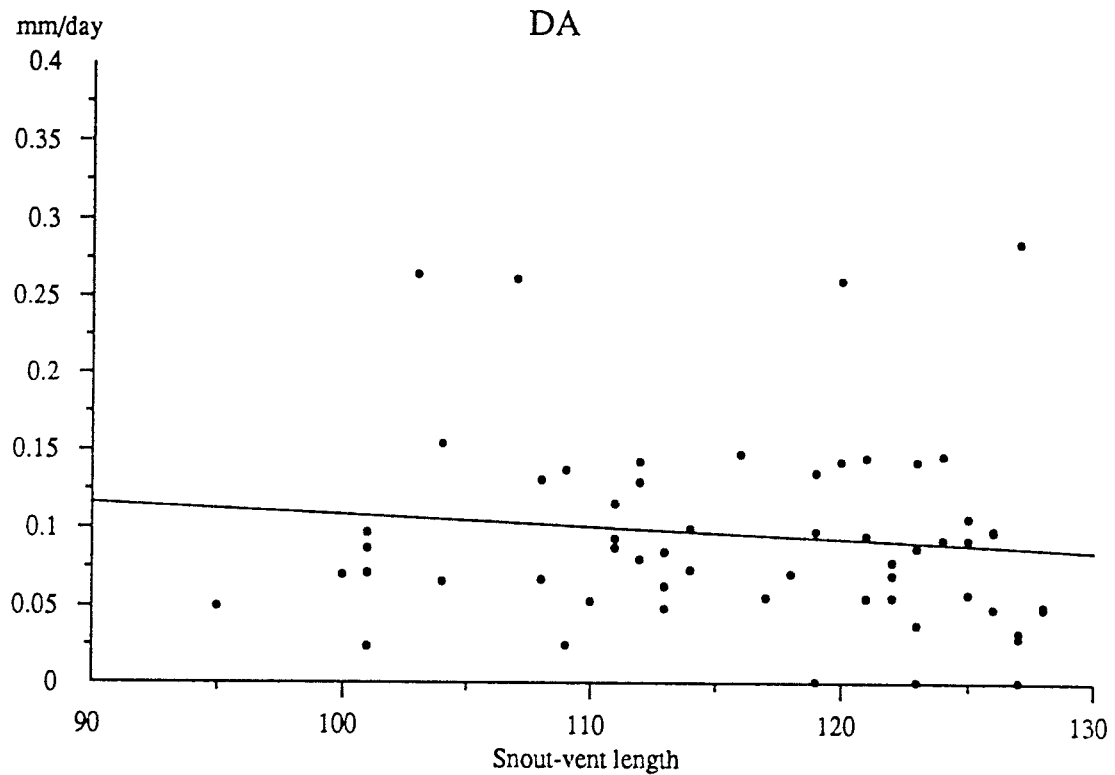


Fig. 6.5 Relationship between SVL and growth rate for males and females at DA.

Table 6.3 gives the data for the regression lines.

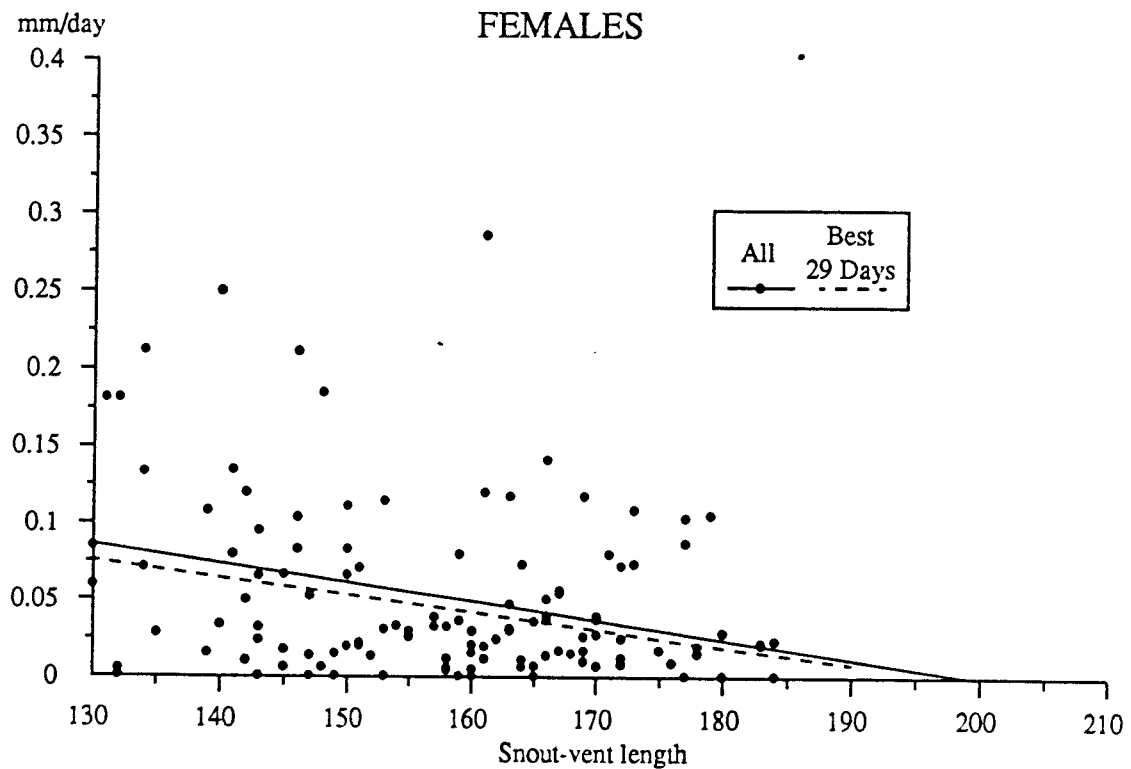
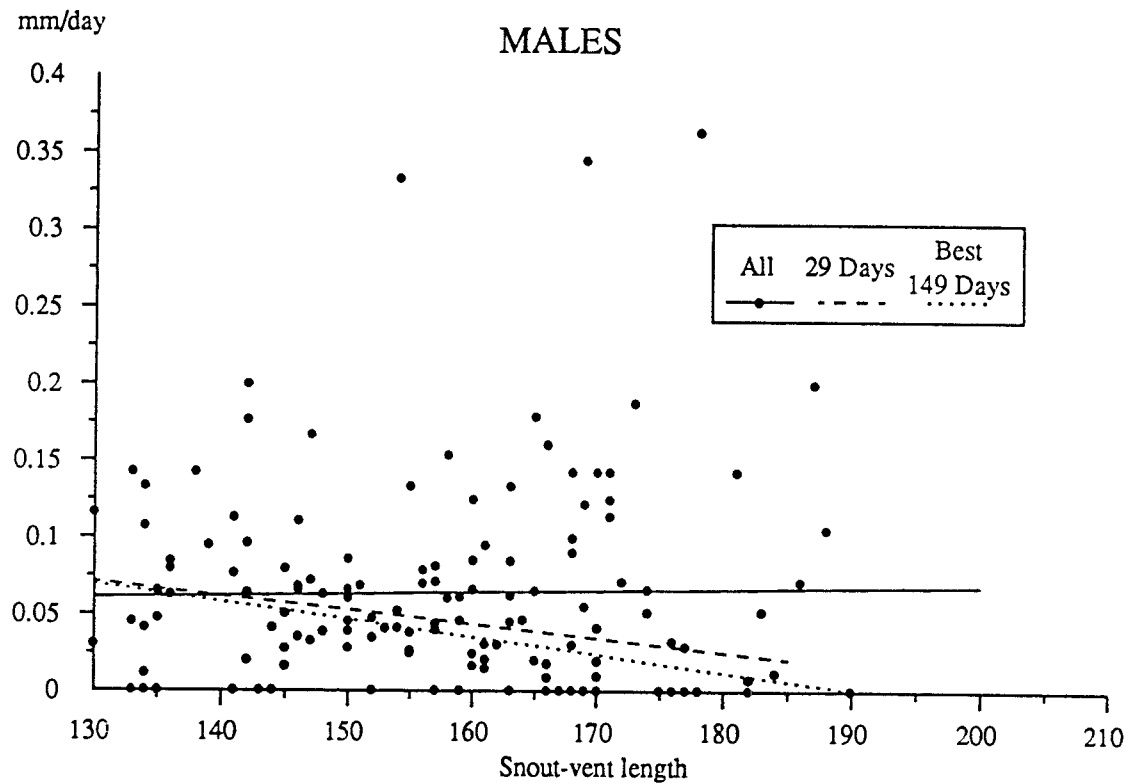


Fig. 6.6 Relationship between growth rate and SVL for males and females at DC.

Table 6.3 gives the data for the regression lines.

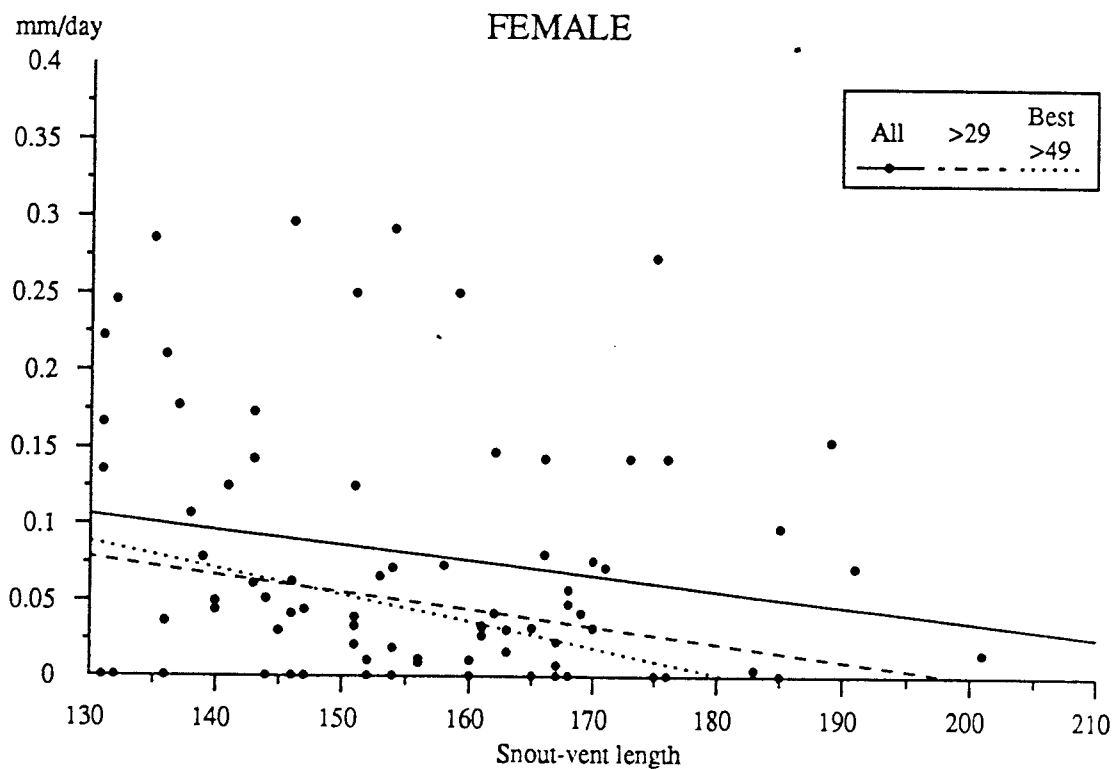
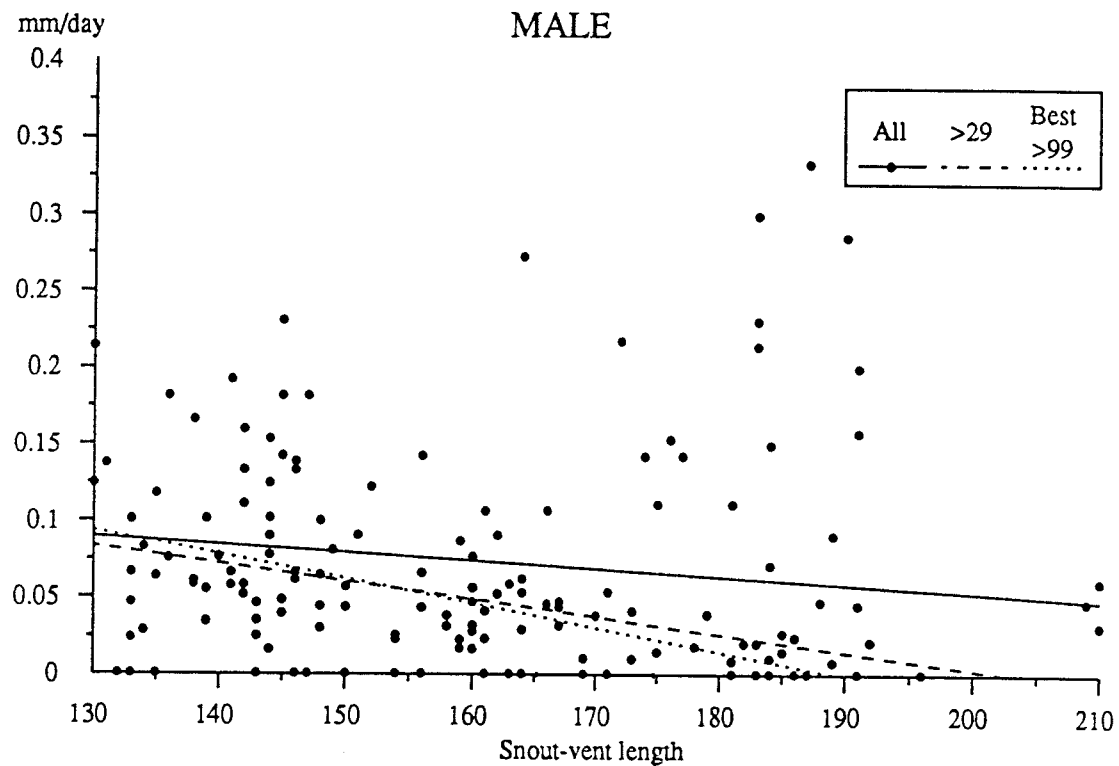


Table 6.1. Coefficient of determination ( $r^2$ ) values for four regression models of the relation between the SVL of first-year juveniles and date, by year and site.

The highest values are underlined.

	LINEAR	EXPONENTIAL	RECIPROCAL	POWER
<u>DA</u>				
1982	<u>0.762</u>	0.761	0.749	0.761
1983	<u>0.735</u>	0.707	0.676	0.707
1984	0.784	0.794	<u>0.796</u>	0.794
1985	0.702	0.729	<u>0.747</u>	0.728
1986	0.702	0.707	0.702	<u>0.707</u>
<u>DC</u>				
1983	<u>0.648</u>	0.632	0.611	0.632
1984	0.607	0.633	<u>0.648</u>	0.634
1985	0.675	0.682	0.681	<u>0.683</u>
1986	<u>0.723</u>	0.697	0.666	0.698

Table 6.2. Statistics of the linear regression equations of SVL of first-year juveniles on day of year, by year and site.

	N	b	c	SE (b)	t (b)
<u>DA</u>					
1982	42	0.12151	47.807	0.010727	11.328
1983	15	0.12170	44.225	0.020254	6.008
1984	24	0.12800	47.305	0.014326	8.935
1985	46	0.12290	47.559	0.012075	10.178
1986	52	0.12424	46.232	0.011444	10.856
<u>DC</u>					
1983	84	0.20034	42.705	0.016293	12.296
1984	37	0.13369	50.861	0.018183	7.353
1985	110	0.11993	48.031	0.008016	14.962
1986	105	0.14241	46.341	0.008694	16.379



Table 6.3 Regression statistics of growth rates for sub-adults, males and females at DA and DC.

The days column refers to the minimum number of days between successive captures that was found to produce the highest  $r^2$ .

SITE	DAYS	N	b	c	SE(b)	$r^2$
=====						

SUB-ADULTS

DA	149	23	-0.001032	0.20061	0.0006274	0.109
DC	149	30	-0.001123	0.22816	0.0005555	0.124

MALES

DA	149	33	-0.001147	0.21861	0.0002221	0.455
DC	99	48	-0.001291	0.25287	0.0001654	0.565

FEMALES

DA	29	98	-0.001125	0.22165	0.0003277	0.108
DC	99	39	-0.001741	0.31428	0.0005016	0.241

Table 6.4 Estimates of the maximum size of males and females at DA, DC and Steep Holm (GA).  
 For details of the seven methods, see section 6.2.4.  
 Differences in brackets indicate females larger than males.

SITE	METHOD	MALES	FEMALES	DIFFERENCE
=====				
DA	i	190	188	2
	ii	183	182	1
	iii	184.0	183.2	0.8
	iv	180.0	180.5	(0.5)
	v	183.0	180.5	2.5
	vi	184.0	181.4	2.6
	vii	190.3	185.4	4.9
	Average	184.9	183.0	1.9
DC	i	216	202	14
	ii	203	201	2
	iii	203.8	193.8	10.0
	iv	199.1	189.5	9.6
	v	195.0	191.0	4.0
	vi	198.5	190.3	8.2
	vii	195.8	180.5	15.3
	average	201.6	192.6	9.0
GA	i	250	219	31
	ii	201	204	(3)
	iii	213.8	209.0	4.8
	iv	192.0	202.5	(10.5)
	v	-	215.0	-
	vi	237.5	212.7	24.8
	average	218.9	210.4	8.5

## CHAPTER 7. TEMPERATURE RELATIONS

### 7.1 INTRODUCTION

Reptiles are ectotherms, that is they obtain the great majority of their body heat from the environment, rather than from internal physiological processes. It is now accepted that, far from being "cold-blooded", i.e., passive and un-sophisticated in their adaptations to the thermal environment, reptiles have evolved a great variety of strategies that try and overcome constraints of physiology and climate (Huey 1982). Early studies on reptilian thermal relations tended to concentrate on a fairly small number of North American species, (many of them in the genus Sceloporus), but in the last fifteen years or so, species from other geographical areas and with very different life-histories have become the focus of attention. Avery (1982) and Huey (1982) provide fairly recent reviews of this work and the concepts that underlie it. Seigel et al. (1987) give a more recent review of the work on snakes.

Thermal relations has been a major area of reptilian biology that has suffered from a confusing excess of terminology. The terms used here, with their definitions in brackets, are those of Pough and Gans (1982), unless stated otherwise. The extremely important concept of thermoregulation is there defined as the maintenance of body temperatures within a specified and usually narrow range when ambient temperatures extend above or below that range. Huey (1982) refined this definition to specifically include the idea that thermoregulation is dynamic, i.e., it is an active, homeostatic process. Not all species thermoregulate, however. Those that do not are called thermoconformers, to indicate that their body temperatures are usually extremely close to ambient, and that they make no attempt to actively regulate them (Hertz 1981). Such species, perhaps not surprisingly, are almost all found in

tropical climates. The distinction between thermo-regulators and thermoconformers is, however, not absolute since a species at a given time and under a given set of conditions can behave as though it were on the continuum between the two extreme types (Huey, 1982).

One concept that has been applied particularly to burrowing and secretive species is the "maximum tolerated temperature" (Elick et al. 1979). This is defined functionally rather than conceptually as the temperature at which the animal is forced to move from a retreat by the excessive temperature of the substrate. It is not immediately obvious how this differs from the accepted concept of the voluntary maximum temperature, but it is noted here because it has been applied to small North American snakes, such as Carphophis vermis, that show some similarities in size and behaviour to the slow-worm.

The physiological and behavioural adaptations of a number of British and European species have now been studied in a little detail, but from several viewpoints. Examples are Lacerta vivipara (Avery 1984), Natrix maura (Hailey and Davies 1987), several Vipera species (St. Girons 1978) and the geckoes Hemidactylus turcicus and Tarentola mauritanica (Martinez Rica 1974).

The slow-worm itself has not been studied in any detail, particularly in the field. In a laboratory thermal gradient Spellerberg (1976) found that the mean selected temperature (the arithmetical mean of body temperatures in a thermal gradient) of two animals was 23 °C (range 14 to 29). There was a bimodal selection of higher temperatures in the morning and evening. The critical minimum temperature (that which produces cold narcosis) was 4.0 °C, or 2.7 °C after acclimation. On the other hand, Kirk and Hogben (1946) estimated the lethal maximum temperature (that which leads to irreversible physiological damage and death) to be 37.5 °C over 24 hours. The slow-worm may

survive higher temperatures than this for short periods (see below, section 7.2.2).

Gregory (1980) measured the temperature of the substrate immediately adjacent to two juveniles and two adults in a laboratory substrate preference experiment. The average of 24 measurements of the juveniles was 24.7 °C (range 9 to 30), and that of 33 adult measurements was 24.2 °C (range 14 to 32). This author did not examine the relation between body and substrate temperatures.

The only reported cloacal temperature of the slow-worm measured in the field was 27.1 °C, from a male in the Valle de Tazzo, Italy (Bruno 1979).

The small amount of data summarized above suggests that the slow-worm has a low mean activity temperature (the arithmetic average of body temperatures within the normal activity range) and a low lethal maximum compared to many other species, but obviously data are very sparse, so that firm conclusions should not be drawn.

The thermal relations of the slow-worm are of interest for a number of reasons. It has adapted to the cool-temperate climates of northern Europe. Only Lacerta vivipara and Vipera berus are found at higher latitudes in the Old World. At the same time it is found in the relatively warm climates of some parts of the northern Mediterranean region. The little that is known of its behaviour suggests that it is different from many of the species studied so far, since it does not bask readily. Where the slow-worm is on the thermoregulator-thermoconformer continuum is a point of considerable interest in this cool-temperate species. Reptiles with the slow-worm's type of "life history strategy" have been studied least of all, so that any field data would be of considerable interest for comparative purposes.

## 7.2 METHODS AND ANALYSIS

### 7.2.1 Field measurements

The measurement of cloacal temperatures has already been described and discussed in some detail in Chapter 2.

There were a number of factors with available data that were potentially relevant to the study of the temperature relations of the slow-worm. They were analysed with respect to their relationship to field measured cloacal temperatures. These were: site, sex, SVL, date, time, air temperature, wind speed, cloud, the proportion of the tin in direct sun and whether or not the animal was under a part of the tin that was in direct sun. Sex (male or female, sub-adults were not measured; see Chapter 2), cloud (in octels), SVL and air temperature were defined and measured as described in Chapter 2. After some preliminary analysis, date was categorised to month, and time was categorised to hour (e.g. 0931 to 1030 BST equalled hour 10 and so on). The percentage of the tin in sun was divided into four categories; 0 to 20% equalled category 1, 30 to 50% equalled 2, 60 to 80% equalled 3 and 90 to 100% equalled 4. Wind speed was also divided into four categories; 0 equalled calm, 1 equalled light breeze, 2 equalled strong breeze and 3 equalled very strong wind. Whether or not the animal was under a part of the tin that was in direct sun was divided into three categories; 0 equalled not in sun, 0.5 equalled part of the body in sun and part out or not possible to tell, 1 equalled in sun.

There are many other factors that may be analysed in relation to cloacal temperatures. They may or may not have a considerable influence on a slow-worm's behaviour. There were considerable practical limitations in measuring these factors, which are discussed in later sections.

### 7.2.2 Measurement of the "maximum tolerated temperature"

The method used followed that of Elick et al. (1979). A pre-calibrated Yellow Springs Instrument Company type 511 thermistor probe was inserted 2 cm into the cloaca and secured by sticky tape. Temperatures were read to 0.1 °C on a YSI type 44 telethermometer. The animal was placed into an arena 50 cm square with a vermiculite substrate. A piece of thin metal sheet, 20 cm square, was placed over the animal, at the same time ensuring that there was free movement of the thermistor lead. The animal was allowed to settle for 30 minutes. All runs were started at cloacal temperatures that are well within the range of temperatures found in the field. The metal sheet was then heated from above by a 275 W infra-red lamp. The "maximum tolerated temperature" was taken as being the cloacal temperature at the time when the whole animal had emerged from under the metal. The initial cloacal temperature and the time taken to emerge were noted. Three animals, all male, were tested a total of fourteen times. Five of these tests were discarded for various reasons, such as loss of the probe from the cloaca. One test was abandoned when the cloacal temperature reached 41.2 °C. The righting response had been lost, indicating that this temperature is higher than the critical maximum. The animal recovered satisfactorily.

### 7.2.3 Analysis

Initial analysis concentrated on determining the normality or otherwise of the data. Normally distributed data were analysed by t tests and ANOVA. Data that departed significantly from normal were analysed by Mann-Whitney U and Kruskal-Wallis tests. Bartlett's test was used to test for equality of variances.

The difference between cloacal temperature and air temperature was subjected to the same tests. The

relationships of this difference to the factors outlined above could provide information that is as useful as the cloacal temperatures themselves, since they may show by how much the slow-worm can warm up under various conditions, and may give some indication whether or not slow-worms thermoregulate.

Cloacal temperatures and their differences from air temperatures were analysed for all factors by the appropriate tests as outlined above. The first factor considered was sex, with the intention that, if a significant difference were found, all the other factors should be analysed for the sexes separately. A second independent factor that was considered was date (i.e. month).

### 7.3 RESULTS

#### 7.3.1 Differences between the sexes

There was considerable variation within and between the sexes. Males had cloacal temperatures that ranged from 9.8 to 33.2 °C, females from 13.3 to 32.0 °C. The average for males was 24.2 °C, that for females 25.0 °C. The distribution of both sexes was non-normal, being skewed to the left (for males  $g = -0.6002$ ,  $t = 4.237$ ,  $p < 0.001$ ,  $n = 299$ ; for females  $g = -0.5127$ ,  $t = 2.737$ ,  $p < 0.01$ ,  $n = 171$ ). Fig. 7.1 shows a histogram of the distribution for both sexes. The distributions of the cloacal temperatures of the sexes were significantly different (Kruskal-Wallis test,  $H = 4.521$ ,  $p < 0.05$ ).

In males the differences between cloacal and air temperatures ranged from -3.2 to 19.0 °C, with an average of 8.9 °C. In females the range was -3.4 to 16.1 °C, with an average of 7.9 °C. The distribution of temperature differences was normal for both sexes, but the means were significantly different ( $t = 2.230$ ,  $p < 0.05$ . Bartlett's test = 1.0033,  $p > 0.25$ ). Fig. 7.2 shows histograms of the distributions of the differences for the sexes.



May and June were the only months with large enough sample sizes for analysis between the sexes. There were no differences between males and females in May for the distributions of cloacal temperatures or temperature differences (cloacal temperatures,  $H = 0.7084$ ,  $p > 0.3$ ; differences,  $H = 0.0004$ ,  $p > 0.9$ ). The distribution of cloacal temperatures was strongly negatively skewed ( $t = 3.016$ ,  $p < 0.01$ ). The mean ( $24.5^{\circ}\text{C}$ ), standard deviation (4.19) and median (25.2) of cloacal temperatures were all similar to the sample as a whole.

June cloacal temperatures and differences were normally distributed. There was no difference between males and females ( $t = 1.159$ ,  $p > 0.2$  for cloacal temperatures;  $t = 0.792$ ,  $p > 0.4$  for differences).

#### 7.3.2 Comparison of the two main sites

DA and DC were compared to see if separate analyses were necessary. There was no difference in cloacal temperatures in either sex ( $H = 2.262$ ,  $p > 0.1$  for males;  $H = 0.017$ ,  $p > 0.8$  for females). The same conclusions applied to temperature differences ( $t = 1.708$ ,  $p > 0.05$  for males;  $t = 0.313$ ,  $p > 0.75$  for females).

#### 7.3.3 Relationship between cloacal and air temperatures

It has been argued that the regression coefficient of air temperature on cloacal temperature may represent the "intensity" of thermoregulation (the "k" of Huey and Slatkin, 1976, where  $k = 1$  equals thermal passivity and  $k = 0$  equals perfect thermoregulation).

There were significant positive regressions of cloacal temperatures on air temperatures for both males and females. Cloacal temperatures measured when there was no sun, i.e., when octels equalled 8 and there were no opportunities for thermoregulation, were excluded. For males the equation was cloacal temperature =  $0.583 \times \text{AIR} +$

15.248, and for females it was cloacal temperature equals  $0.510 \cdot \text{AIR} + 16.623$ . The significance of both regression coefficients was high (for males  $t = 7.569$ ,  $p < 0.0001$ , 186 d.f.; for females  $t = 4.928$ ,  $p < 0.0001$ , 110 d.f.). There was no significant difference between the sexes ( $t = 0.556$ ,  $p > 0.25$ , 294 d.f.). There was a difference of less than 1 °C in the predicted values of cloacal temperature over the total range of observed air temperatures between the sexes. Fig. 7.3 shows this relationship for both sexes; the lines of equality of air and cloacal temperature are also indicated. There are very few cloacal temperatures lower than air in both sexes. Increases of cloacal over air temperatures are lower at higher air temperatures, which may give an indication of the voluntary maximum. Cloacal temperatures of over 30 °C can be attained at air temperatures of 15 °C in females and even lower in males.

#### 7.3.4 Relationship between SVL and temperatures

Product-moment correlation coefficients were calculated between SVL and cloacal temperatures and differences for the two sexes. There was no significant correlation of cloacal temperatures with SVL for either sex (for males  $r = -0.0249$ ,  $p > 0.6$ ; for females  $r = 0.1035$ ,  $p > 0.15$ ). The same was true for temperature differences (for males  $r = 0.0515$ ,  $p > 0.45$ ; for females  $r = -0.0028$ ,  $p > 0.95$ ). There was no indication that any size class of animal had cloacal temperatures different from any other, nor do these data indicate that the heating rates of larger animals are different from smaller ones. It is possible that measurements of sub-adults could have changed this picture, but the data are not available.

### 7.3.5 Variation of temperatures with month

Cloacal temperatures were measured in all months of the normal activity season. The animals found in the unusually mild November of 1984 were juveniles and therefore not measured. There are no measurements of males in October. The pattern of the numbers of animals measured in each month closely follows that of the total numbers of captures (Chapter 3).

Non-parametric Kruskal-Wallis tests were used to test for homogeneity or otherwise of cloacal temperatures between months, since there was significant non-normality of the distributions in several months. There was significant overall heterogeneity between months in both sexes (for males  $H = 17.205$ ,  $p < 0.01$ ; for females  $H = 28.476$ ,  $p < 0.0005$ ). Table 7.1 shows the median and interquartile cloacal temperatures for each month. There are no differences in cloacal temperatures between the sexes in any month. July showed the greatest difference; females had cloacal temperatures  $1.9^{\circ}\text{C}$  higher than males, but this was not quite significant at the 0.05 level. High temperatures ( $> 30^{\circ}\text{C}$ ) can be attained from April to August.

Table 7.1 also shows the means and standard deviations of temperature differences for each month. The pattern is slightly different since the highest increases over air temperatures tend to occur earlier in the season. Fig. 7.3 has shown that higher air temperatures are correlated with higher cloacal temperatures at lower air temperature values, since the voluntary maximum is soon reached and is a ceiling by definition. There is significant heterogeneity between months for males ( $F = 7.138$ ,  $p < 0.001$ ) and females ( $F = 3.048$ ,  $p < 0.01$ ; 1-way ANOVAS). Again there are no differences between the sexes for any month, but July is nearly significant at the 0.05 level.

#### 7.3.6 Variation of temperatures with hour

A similar analysis to that performed on months was carried out on hours. Table 7.2 shows the medians and interquartile ranges of cloacal temperatures, and the means and standard deviations of the temperature differences.

There are few differences between the hours for either males or females. High cloacal temperatures ( $> 29^{\circ}\text{C}$ ) were attained by both sexes for every hour, as were high increases over air temperature. The only differences between the sexes are hour 13 (= 12.31 to 13.30 BST) for cloacal temperatures (Kruskal-Wallis  $H = 5.349$ ,  $p < 0.05$ ) and hour 15 for differences ( $t = 2.882$ ,  $p < 0.01$ ).

#### 7.3.7 Variation of temperatures with cloud cover

There was significant heterogeneity between cloacal temperatures under different cloud cover levels (octels) for males ( $H = 41.582$ ,  $p < 0.0001$ ). The highest medians and maxima were found under the lightest cloud cover. Complete cloud cover produced the lowest median as well as the lowest recorded temperature ( $9.8^{\circ}\text{C}$ ). Females, on the other hand, showed homogeneity in cloacal temperatures ( $H = 5.676$ ,  $p > 0.6$ ). Total cloud cover tended to give the lowest temperatures, but the difference was smaller than in males and was not significantly different from other values.

The differences between cloacal and air temperatures showed a similar pattern in both sexes. There was significant heterogeneity in males ( $F = 3.816$ ,  $p < 0.001$ , 8,201 d.f.), but not in females ( $F = 0.835$ ,  $p > 0.5$ , 8,114 d.f.). Higher increases can be seen in the lower and middle categories of cloud cover. There is no significant difference between the sexes at any level of cloud cover. The basic data are shown in Table 7.3.

#### 7.3.8 Variation of temperatures with proportion of tin in sun

The four categories used here were derived from the original collection of the data as percentages. There was strong heterogeneity between these levels for both sexes for cloacal temperatures (for males  $H = 21.191$ ,  $p < 0.0001$ ; for females  $H = 15.613$ ,  $p < 0.002$ ). The lowest temperatures were found at the lowest factor level, i.e. the lowest proportion of the tin in direct sun. The highest temperatures, however, were not found in animals that were under tins that were nearly or wholly in sun. The cloacal temperatures attained in all three of the higher categories of proportion were similar in both sexes. There was no difference between the sexes at any level.

Temperature differences again showed a similar pattern. There was significant heterogeneity between levels and temperature differences in both sexes (for males  $F = 11.363$ ,  $p < 0.0001$ , 3,111 d.f.; for females  $F = 10.235$ ,  $p < 0.0001$ , 3,53 d.f.). The lowest levels showed the lowest increases. Spearman rank correlation coefficients of level on difference were highly significant for both sexes (for males  $r = 0.391$ ,  $p < 0.001$ ; for females  $r = 0.567$ ,  $p < 0.001$ ). The basic data are summarised in Table 7.4.

#### 7.3.9 Variation of temperatures with whether animal in sun or not

The three levels of this factor were significantly heterogeneous for both sexes for cloacal temperature (for males  $H = 21.510$ ,  $p < 0.00005$ ; for females  $H = 24.421$ ,  $p < 0.00001$ ). Whether or not the animal was under a sunny part of a tin had a considerable effect on cloacal temperatures. There was also a significant difference

between the sexes at level 1 (animal completely under a sunny part of tin;  $H = 7.751$ ,  $p < 0.01$ ).

Temperature differences show very much the same pattern. The variation is heterogeneous for both sexes (males  $F = 16.855$ ,  $p < 0.0001$ ; females  $F = 18.477$ ,  $p < 0.0001$ ) There is, however, no difference between the sexes at any level. The increases in cloacal temperature or temperature difference between two adjacent levels are the same at 2 to 3 °C. Care must be taken not to make too much of these results. Common sense should indicate that the proportion of the tin in sunshine and whether or not the animal was under a sunny part of tin are very highly correlated. It is rather difficult for an animal under a tin that is 90% in sunshine not to be under a sunny part of that tin. Conversely, it is rather difficult for an animal under a tin that is completely shaded to gain much benefit from the sun. A Spearman rank correlation analysis confirms this ( $r_s = 0.850$   $p < 0.0001$ ). Thus, a Figure to illustrate the variation of this factor is not given here.

#### 7.3.10 Variation of temperatures with level of wind strength

There were no differences between the sexes, or between any level of this factor, for either cloacal temperature or the difference between air and cloacal temperatures. Spearman Rank correlation analysis indicates that wind strength is not significantly correlated with any other factor, so there is no possibility of a spurious covariation as with the above factor.

#### 7.3.11 "Maximum tolerated temperature"

The results of the nine successful experiments on three male slow-worms are given in Table 7.5. All of the "maximum tolerated temperatures" shown were above the maximum field measured cloacal temperature (33.2 °C). Five

of the temperatures are in the range 35 to 36 °C and all but one (37.8 °C) are lower than the lethal maximum of 37.5 °C measured over 24 hours by Kirk and Hogben (1946).

#### 7.4. DISCUSSION

##### 7.4.1 Methods and results of the present study

In this study, as in many others, the data available for analysis are cloacal temperatures measured by a simple mercury thermometer at points in time. The ideal is to measure continuously over a period of time (preferably days), so that the animal's behaviour can be related to environmental and other factors such as nutritional state. This has been the rationale behind studies in laboratory temperature gradients; the environmental conditions are controllable and easily measurable, and it is easy to monitor the cloacal temperature and other behaviours of the subject. The aim is to reduce "noise" by controlling as many factors as possible. Field data are obviously preferable if they can be obtained, but, depending on the species studied, there are simplifications and compromises that have to be taken into account as well as problems in the interpretation of data and their relationship to the environmental factors.

In the present study, it was impossible to monitor the cloacal temperature in the field as has been done with a number of snake species. The slow-worm is just too small for the available transmitters. Single measurements of the cloacal temperature at the point of capture are therefore the only way to gain field data. To be of any use these data should be related to as many environmental and other factors as it may be possible or relevant to measure. Considerable care must be taken in interpreting these data in relation to the cloacal temperatures. A good example is relating the temperature under the tin to cloacal temperature. Temperatures can be taken at many points under a tin, but where is the most relevant place in

relation to the position of the slow-worm? The under surface temperature, or that on the surface of the substrate, or both? The answer may well depend on the behaviour of the slow-worm prior to being captured, but we cannot know what that behaviour was. Another problem is that of the actual measurement of these temperatures. Some initial work suggested that it was not possible to take any single temperature as the true one on the under surface of a tin. Conditions changed too rapidly (as cloud obscures and then reveals the sun on windy days for instance) for reliable measurement. The tins were very good conductors of heat, and indeed heated and cooled so rapidly that it became impossible to relate a measurement to the "true" value that pertained a minute or so before when the slow-worm was found. Turning over a tin also changed the environment underneath it.

Continuous measurement of the temperatures under a representative tin may have provided some reliable data that could have been related to cloacal temperatures. The problem here was security, since leaving the necessary equipment in the field for extended periods was not possible. There was also no guarantee that the environment under one tin was applicable to that under another.

With present methods, there is no way of knowing the influences on the behaviour of the slow-worms that immediately preceded the cloacal measurements taken at a point in time in the field. Care must thus be taken not to label any temperature, range of temperatures or a mean or median as "preferred" as this carries the unproven implication that the animal is exercising choice when in fact it is making none. "Voluntary" is perhaps permissible, since in this study the animals were under no restraint. Using the phrase "normal activity range" makes the so far unproven assumption that all the cloacal temperatures were taken from active slow-worms.



The use of the tins by slow-worms is relevant and interesting to the study of their relation to the abiotic environment. Because almost all of the captures in this study were made under tins, it is tempting, but unproven, to argue that the tins represent a resource to the slow-worms. There is no comparative evidence from slow-worms found in other situations that there is an advantage to be under a tin. If it could be shown, for instance, that slow-worms found under tins could maintain higher, or more constant, body temperatures, it could be argued that it is beneficial to a slow-worm to find a tin and use it.

On the other hand, field measured cloacal temperatures compare well with the few data already available. The averages and ranges given by Gregory (1980) and Spellerberg (1976) from temperature gradient data were very similar to those found in this study.

It is possible that, in the field, the slow-worm attains cloacal temperatures higher than that found in this study, but if the "maximum tolerated temperature" as given here represents the real behaviour of the animal, an animal with a cloacal temperature in the range 34 to 36 °C would be very close to seeking shelter from a potentially lethal situation. The "window of opportunity" for finding it would be small, since having reached a high body temperature it would tend to leave the area under the tin. Note the rapid reduction in the frequencies of finding animals with cloacal temperatures higher than 30 °C (Fig. 7.1).

#### 7.4.2 Comparison of data with other species

Reptiles that live in high latitudes have had to become adapted to climate and weather conditions that alter hourly, daily and seasonally. A variable environment will lead to variable body temperatures (Huey, 1982). This can be seen in the slow-worm in the figures given above. Other British species show similar patterns, although in

some the range of temperatures is smaller and higher temperatures are tolerated.

Damme et al. (1987) compared field measured temperatures to those in a temperature gradient for each month of the activity season in Lacerta vivipara. The former varied considerably over the season in a similar way to the slow-worm, but the latter varied little, and tended to be higher in all months, except for gravid females. Lacerta vivipara was thermally passive (i.e., it allowed its body temperature to rise as high as possible) in early spring, but actively thermoregulated in other months. The averages of field and laboratory cloacal temperatures was higher than in the slow-worm at 24.2 °C (males, field, March) to 34.0 °C (non-gravid females, laboratory, June). Most averages were over 30 °C. Lacerta vivipara has been found to have differences between populations in its selected (i.e., laboratory) temperatures (Damme et al., 1986). It is an active basker, so that its emergence in the morning (Avery and McCardle, 1973) and predatory efficiency (Avery et al., 1982) have been related to thermoregulatory behaviour.

The cloacal temperatures of European Vipera (such as V. berus), measured in a semi-natural out-door enclosure in central France, varied from 32.4 to 30.5 °C, depending on how recently a large prey item had been eaten (Saint Girons, 1978). Northern European species had similar temperatures to those from the south.

Of the British species studied to any extent, the smooth snake, Coronella austriaca most resembles the slow-worm. It is relatively reluctant to bask (Goddard, 1981), and has similar measured cloacal temperatures, both in the field and the laboratory. The average of 88 field temperatures in southern England was 25.8 °C, range 17.0 to 31.0. The daytime averages of two animals in the laboratory were 25.8 and 28.4 °C (Spellerberg and Phelps, 1975). Goddard (1981), in his study of the species in the

New Forest, showed that the mean field measured cloacal temperatures varied from 22.8 to 25.9 °C in males and 24.0 to 26.2 °C in females according to the time of day. Temperatures were lowest in the morning, rising to a fairly level plateau for the rest of the day. Temperatures were lower on overcast days. There were also seasonal differences, with March and April showing the lowest temperatures. Temperatures tended to remain fairly constant for the rest of the season. Females tended to have slightly higher cloacal temperatures to males. It is useful to compare these patterns to the relevant figures for the slow-worm, above.

Bont et al. (1986) force-fed smooth snakes with temperature sensitive transmitters and followed them in the field for several months. On cloudy days, body temperatures were very variable. On sunny days the body temperatures rose rapidly and remained at 29 to 33 °C until evening, even if substrate temperatures exceeded 40 °C. These authors concluded that the ingested transmitter did not affect the behaviour of the snakes.

Among the slow-worm's close taxonomic relatives, only a few species of the limbless Ophisaurus have been studied. The North American O. attenuatus, an inhabitant of open grassland in the Mid-West and with an SVL similar to a large slow-worm (200 mm), showed a high precision of cloacal temperatures in a temperature gradient. The range of averages for three animals was 31.0 to 32.8, with an overall range of 30.3 to 34.5 °C. Lower temperatures were to be expected in the field (Johnson and Voight, 1978). The European O. apodus had a lower average (27.7 °C, with a range from 24 to 35 °C) in a temperature gradient than in the field (Hailey, 1984). This species also had a lower standard metabolic rate than would be predicted for its large size whereas that of the slow-worm is similar to predicted values for its size (Hailey, 1984; Bennett and Dawson, 1976; Davies et al., 1981). The slow-worm also

shows the "metabolic shift" of a number of temperate reptiles, where the metabolic rate remains relatively high as body temperature reduces to about 10 °C (Davies et al., 1981). This is interpreted as an adaptation to activity at low temperatures, particularly those of a temperate spring, which allows the animal to remain active for longer periods.

Bury and Balgooyen (1976) measured the preferred temperature of Anniella pulchra (family Annielidae), a limbless relative of the Anguidae that lives in the coastal dunes of California. It is sometimes called the Californian slow-worm, and may prefer even lower body temperatures than the European species. The average cloacal temperature under moist conditions was 24.9 °C, and under drier conditions 23.6 °C. This species lives on sand dunes under overhanging vegetation, where the temperatures approximate to the preferred. Anniella rarely seems to bask.

There are indications that the family Anguidae as a whole tend to have low preferred temperatures, frequently coupled with low precision of thermoregulation (Avery, 1982). The present data on the slow-worm support this, even though one must be careful about claiming that the slow-worm thermoregulates. It can indeed be found under a wide variety of thermal conditions and body temperatures, but as mentioned above, variability of body temperatures is not the same as thermoregulation. Data to show that the species is "choosing" its body temperatures are lacking here because temperatures at a point in time were taken and there were no data on the behaviour before or after measurement.

Huey and Slatkin (1976) discussed the regression of air on body temperatures in their analysis of the costs and benefits of thermoregulation. This coefficient is the "intensity" of thermoregulation ( $k$ );  $k$  equals 1 means thermoconformity;  $k$  equals 0, perfect thermoregulation.

These authors produced a model of the costs and benefits which depended on the amount of energy gain associated with a particular thermoregulatory behaviour. They summarised a list of predictions based on the model which unfortunately cannot be tested on the slow-worm because of lack of data, or because they may not be applicable. Whether or not  $k$  really measures the intensity of thermoregulation has come into question. Hertz and Huey (1981) could not distinguish between two possible strategies in Anolis cybotes (Iguanidae) on Hispaniola. As altitude increased,  $k$  decreased, i.e., as the thermal environment became more variable at higher altitudes, the precision of thermoregulation increased. At low altitudes there was a shift in habitat use, but it was not possible to say whether this was due to a difference in thermoregulatory strategy or merely the fact that the lizards died out in a thermally extreme environment.

A similar argument applies to slow-worms, since it is not possible to say whether the animals are choosing, or seeking out the pieces of tin; or are merely easily found there, and are in fact randomly distributed in the habitat. It is therefore possible to argue that the slow-worms found under tins have cloacal temperatures higher than air temperatures because the tins warm up rapidly in sunshine, and animals under tins are those that are easiest to capture because they are easily discovered.

There is, however, no doubt that the slow-worm remains of interest as a species that has low body temperatures, even for an Anguid.

Fig. 7.1 Distribution of cloacal temperatures for males and females.

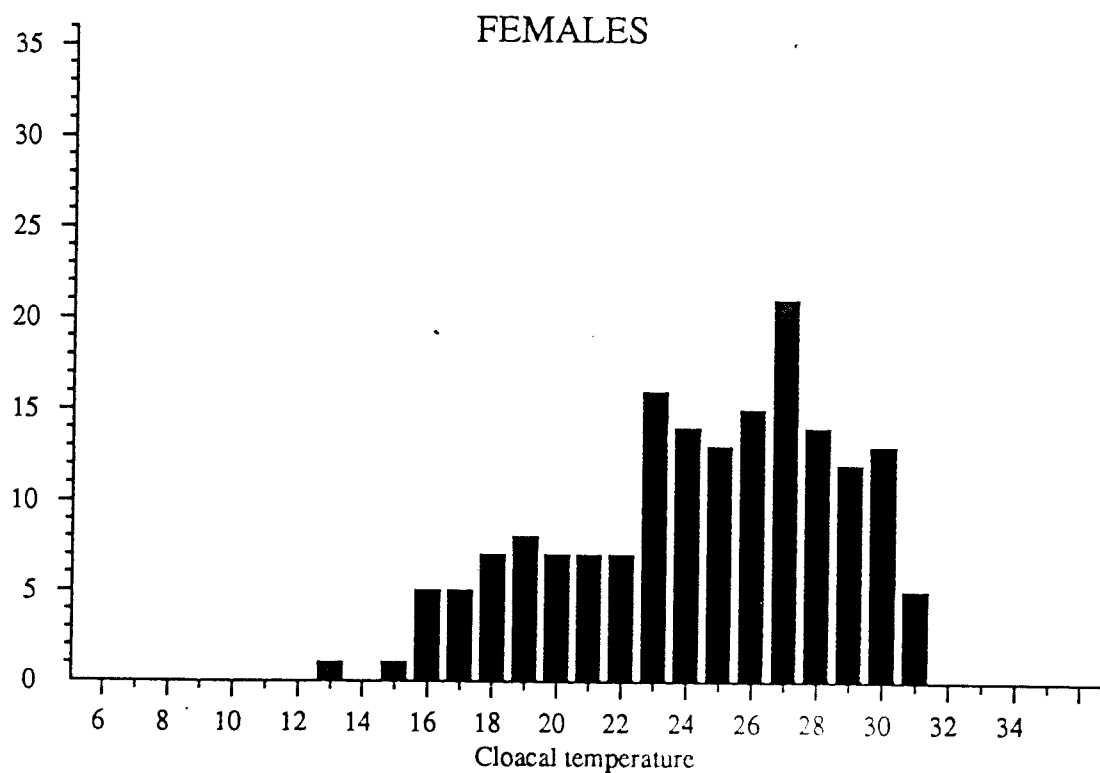
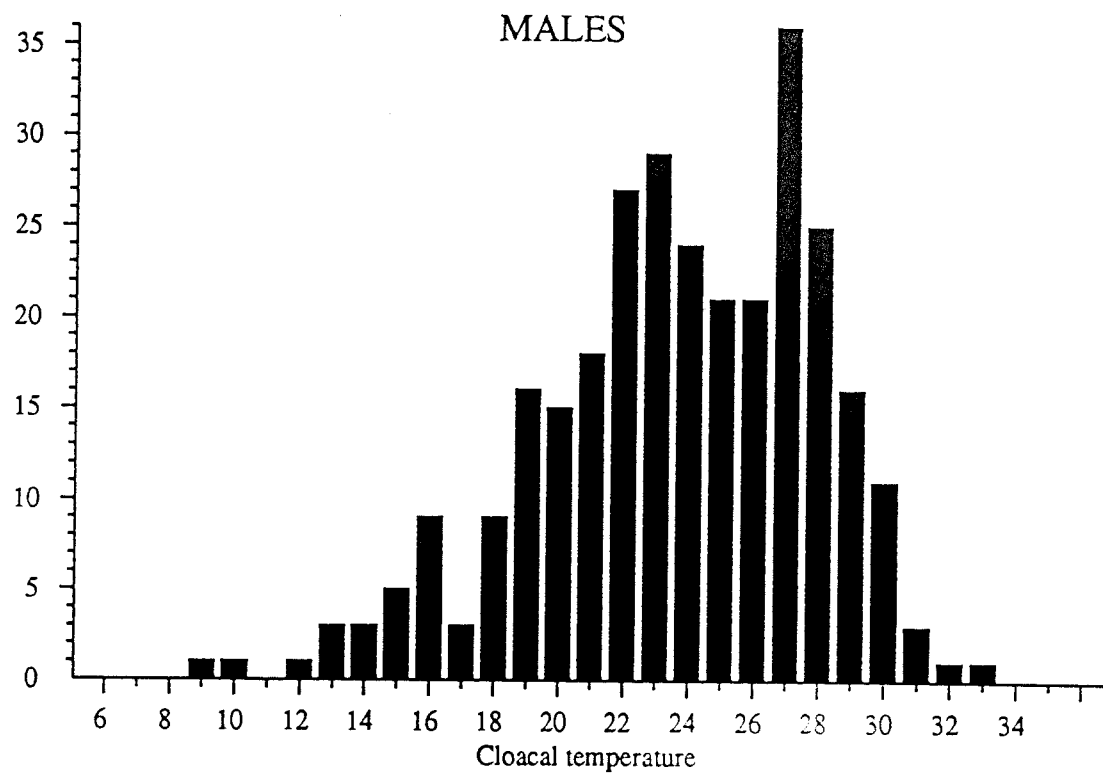


Fig. 7.2 Distribution of differences between cloacal and air temperatures for males and females.

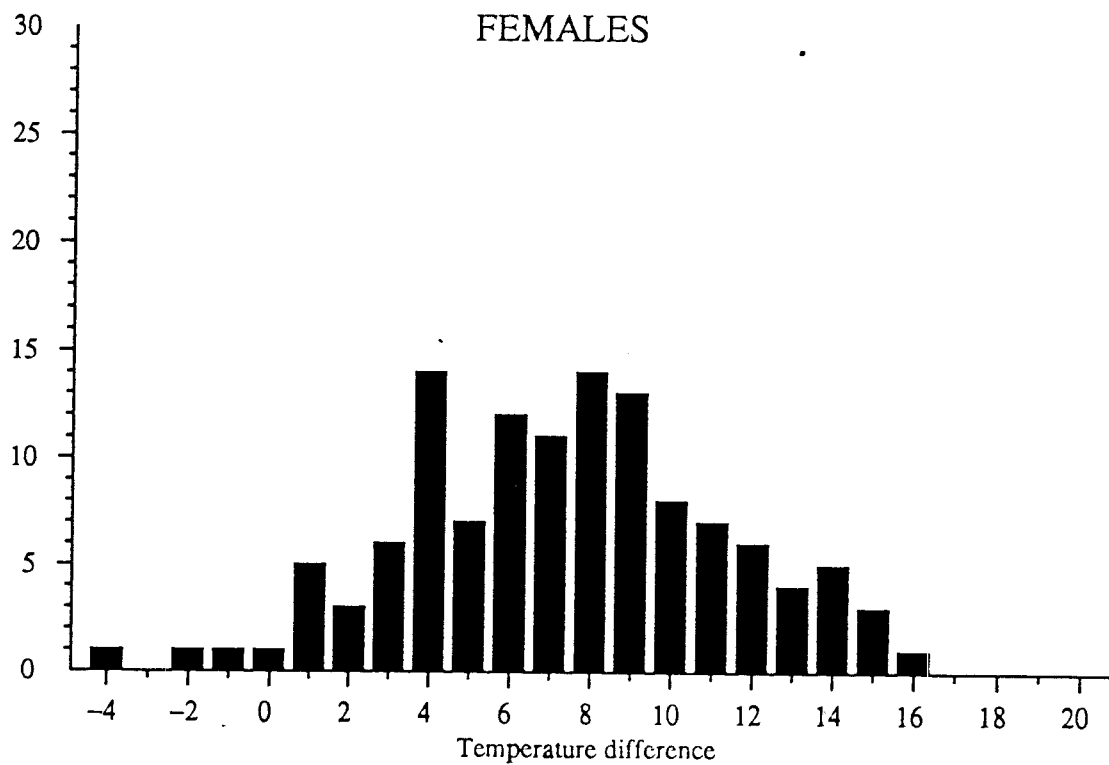
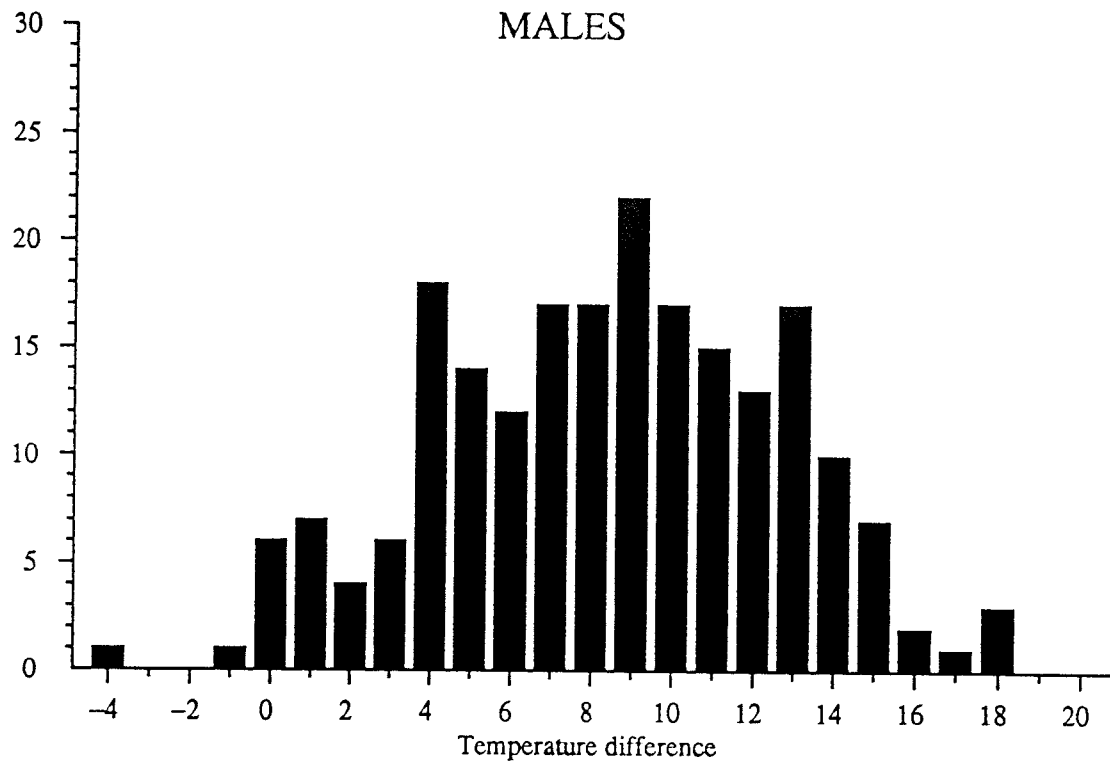


Fig. 7.3 Relationship between cloacal and air temperatures for males and females.

Upper line is linear regression line, lower shows equality of temperatures.

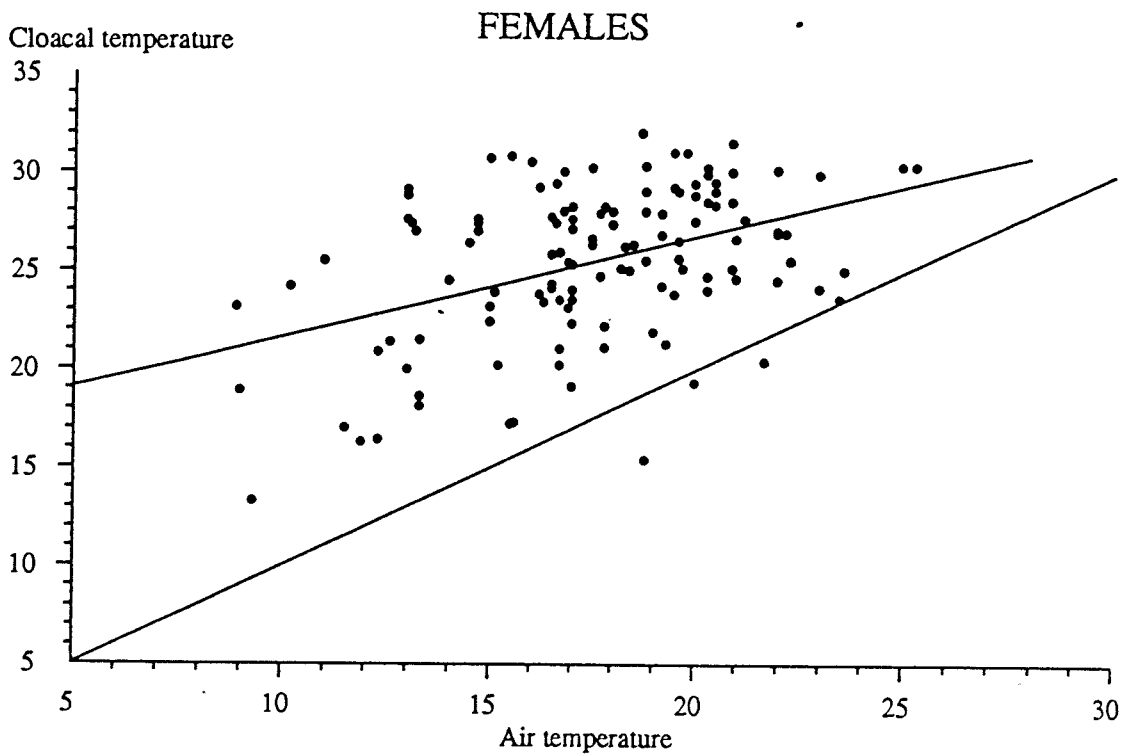
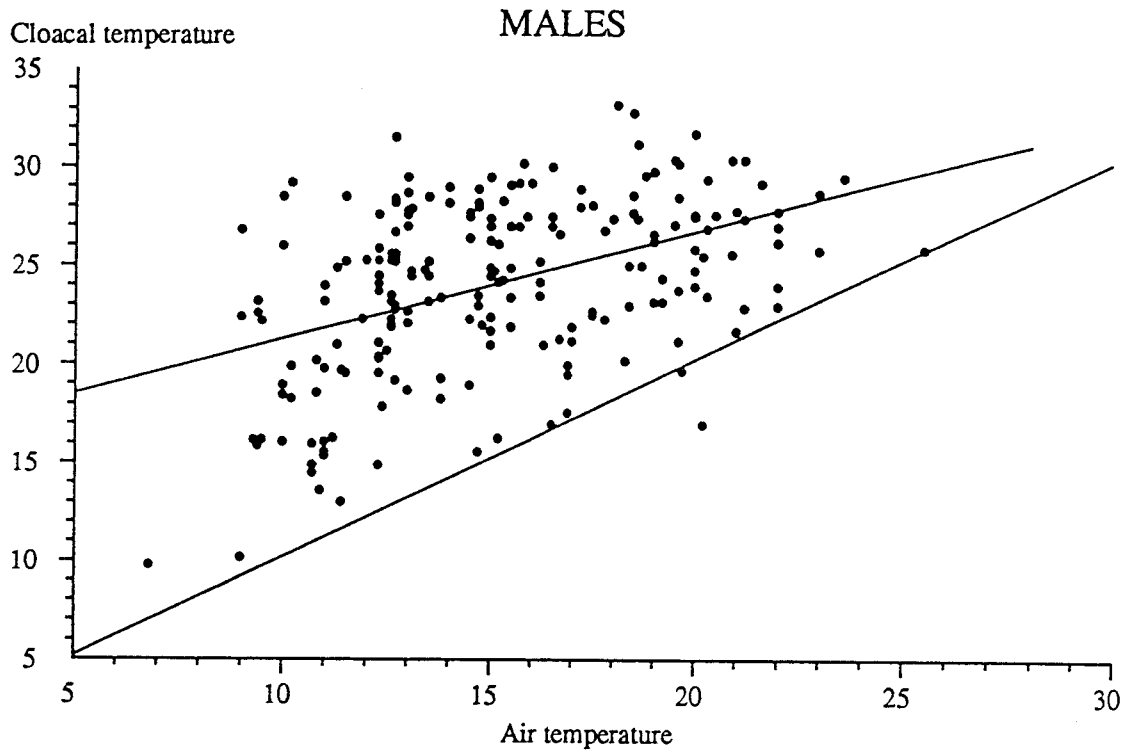




Table 7.1. Medians and interquartiles of cloacal temperatures, and means and standard deviations of differences from air temperatures, of males and females by month.

#### CLOACAL TEMPERATURES

	MALES				FEMALES			
	N	MED	LQ	UQ	N	MED	LQ	UQ
=====								
MAR	7	19.7	15.9	23.2	2	19.7	-	-
APR	69	23.4	19.4	27.5	16	23.7	19.1	27.0
MAY	118	24.9	22.0	27.6	37	26.6	20.9	28.0
JUN	57	25.8	22.0	28.3	43	25.9	23.6	29.2
JUL	26	25.2	22.3	27.5	28	27.6	24.1	29.2
AUG	14	25.7	23.5	27.4	24	25.9	24.1	27.8
SEP	8	21.4	19.9	22.9	12	24.3	21.6	25.3
OCT	0	-	-	-	9	18.1	17.5	18.6

#### DIFFERENCES

	MALES			FEMALES		
	N	MEAN	SD	N	MEAN	SD
=====						
MAR	7	9.1	4.44	2	9.4	-
APR	49	9.7	4.71	11	7.7	5.42
MAY	92	10.1	3.62	26	9.9	4.64
JUN	28	8.0	3.86	27	8.8	3.41
JUL	15	5.6	3.99	20	7.8	2.33
AUG	13	5.6	2.91	22	6.1	3.05
SEP	6	3.7	2.31	11	5.6	2.67
OCT	0	-	-	5	5.0	2.66

Table 7.2. Medians and interquartiles of cloacal temperatures, and means and standard deviations of differences from air temperatures, of males and females by hour.

#### CLOACAL TEMPERATURES

MALES					FEMALES			
HOUR	N	MED	LQ	UQ	N	MED	LQ	UQ
=====								
10	35	22.3	20.0	24.5	18	23.7	21.0	26.3
11	58	24.8	22.0	27.8	41	25.0	22.9	27.6
12	84	26.0	22.3	28.0	45	27.0	23.8	29.0
13	16	25.6	22.9	27.9	5	30.7	27.9	30.8
14	7	22.5	22.3	27.0	9	18.6	17.8	24.0
15	32	25.0	22.7	27.4	22	24.8	23.0	26.6
16	32	24.6	21.1	27.7	16	27.5	22.2	29.5
17	27	23.4	19.3	27.0	10	24.3	20.1	28.8
18	8	22.9	20.3	26.2	3	26.9	-	-

#### DIFFERENCES

HOUR	MALES			FEMALES		
	N	MEAN	SD	N	MEAN	SD
10	30	7.6	4.42	14	6.5	3.88
11	44	8.0	4.19	36	7.7	3.78
12	51	9.9	4.39	28	8.8	4.10
13	12	10.6	3.01	4	12.5	3.83
14	4	7.4	4.09	5	8.3	4.25
15	23	10.0	3.68	14	6.4	3.57
16	20	9.3	4.49	12	8.2	4.05
17	20	8.6	4.38	8	7.8	3.27
18	6	8.1	4.24	2	7.1	-

Table 7.3. Medians and interquartiles of cloacal temperatures, and means and standard deviations of differences from air temperatures, of males and females by octel.

#### CLOACAL TEMPERATURES

MALES					FEMALES			
OCTEL	N	MED	LQ	UQ	N	MED	LQ	UQ
=====								
0	28	27.2	22.6	28.4	15	26.9	23.6	30.1
1	20	26.1	24.0	27.8	7	24.5	22.4	28.0
2	23	27.0	22.8	29.0	8	26.4	20.4	27.9
3	25	27.6	23.0	28.7	14	26.3	23.0	30.0
4	18	23.8	21.5	28.1	15	25.1	23.2	30.0
5	34	25.0	22.2	27.5	30	25.8	21.5	28.5
6	53	24.5	23.2	27.3	25	27.0	22.9	28.5
7	68	23.2	20.6	26.7	34	25.0	23.4	27.6
8	30	20.5	17.6	23.1	21	23.8	21.1	27.1

#### DIFFERENCES

MALES				FEMALES		
OCTEL	N	MEAN	SD	N	MEAN	SD
=====						
0	23	8.7	5.59	12	5.9	4.02
1	18	7.9	3.65	7	7.9	4.23
2	15	12.9	3.47	6	10.1	7.15
3	11	9.1	4.90	6	8.0	4.77
4	8	9.5	4.77	10	8.0	3.61
5	30	9.6	4.80	23	8.9	3.96
6	39	8.7	4.01	18	7.6	3.90
7	48	9.1	3.61	23	7.7	2.32
8	18	5.4	3.16	18	7.6	3.99

Table 7.4. Medians and interquartiles of cloacal temperatures, and means and standard deviations of differences from air temperatures, of males and females by percent of tin in sun.

CLOACAL TEMPERATURES								
MALES					FEMALES			
LEVEL	N	MED	LQ	UQ	N	MED	LQ	UQ
=====								
1	34	21.2	18.3	23.5	28	23.0	20.0	25.2
2	15	25.9	23.0	27.9	8	28.2	25.7	30.1
3	27	24.8	22.0	28.5	12	27.3	25.6	29.5
4	90	26.0	22.3	28.3	35	26.6	22.4	28.1
DIFFERENCES								
MALES					FEMALES			
	N	MEAN	SD		N	MEAN	SD	
=====								
1	21	5.1	3.82		20	3.8	3.15	
2	10	8.1	1.87		5	8.2	3.89	
3	21	10.1	3.61		11	8.8	4.76	
4	63	10.1	3.66		21	9.6	3.11	

Table 7.5. "Maximum tolerated temperatures" of three male slow-worms.

NUMBER	SEX	SVL	MAXIMUM			TIME (MINS)
			START CLOACAL TEMPERATURE	TOLERATED TEMPERATURE	INCREASE	
=====						
SB8	M	168	24.7	35.3	10.6	28
SB8	M	168	25.6	35.5	9.9	25
SB8	M	168	25.3	35.0	9.7	17
SB8	M	168	28.6	36.4	7.8	16
SB9	M	180	24.7	37.0	12.3	31
SB9	M	180	23.5	34.4	10.9	28
SB9	M	180	23.7	35.9	12.2	22
SK1	M	146	27.6	37.8	10.2	26
SK1	M	146	25.3	35.0	9.7	25
AVERAGE			25.5	35.8	10.3	24

## CHAPTER 8. CLIMATE AND THE DISTRIBUTION OF THE SLOW-WORM

### 8.1 INTRODUCTION

Reptile are ectotherms, and are therefore intimately dependent on the weather and climate for their distribution and day to day activity. There has been a great deal of research, both theoretical and practical, on the influences of weather and microclimate on the behaviour, distribution and population biology of a number of species (Porter et al. 1973; Porter and Tracy 1983). These studies are wider in their scope than those which just study the thermoregulatory behaviour of an individual species, since they also take into account the effects of other environmental factors, such as precipitation and sunshine.

There has, however, been very little work on the correlations between climate and distribution on a wider geographical scale for individual species. A number of studies have looked at the possible influences of climate and other variables on the changes in faunal composition and community structure of reptiles over large geographical areas, such as Texas (Rogers 1976; Owen 1989). These areas usually have political rather than climatic or geographical boundaries. Caughley et al. (1987) used a discriminant function analysis with twelve climate variables to try and explain the differences in distribution of three species of large kangaroos, Macropus, in Australia.

There has been no study using any of these approaches on a European reptile species, faunal assemblage or community. For individual species this may in part be due to the poor understanding of their distributions. In Chapter 1 it was hinted that data on the slow-worm had been collected for certain parts of its distribution in order to produce Figs. 1.1, 1.2, and 1.3. The area that

was investigated most intensively was the Iberian Peninsula, so that it has become possible to make a reasonably accurate statement of the distribution of the slow-worm in that region. With the knowledge of the distribution of the slow-worm and the use of a coherent geographical area which has a distributional limit within it, it may be possible to see which climate variables correlate best with the distribution of the species. It is clear from Fig. 1.1 that the slow-worm is far from uniformly distributed over the peninsula. Given the nature of the distribution data available, and the large geographical area, it was considered that analysis by multivariate discriminant functions was most appropriate, using the presence or absence as the classifying factor.

## 8.2 DISTRIBUTION OF THE SLOW-WORM IN THE IBERIAN PENINSULA

The Iberian Peninsula consists of Spain, Portugal, Andorra and Gibraltar. The Balearic Islands are included in the geographical definition of the peninsula, but the Atlantic Island provinces of Spain and Portugal, such as the Canaries, Azores, Cape Verdes and Madeira, are not.

It was found necessary to collect detailed distribution data because the maps given in recent faunal works are contradictory, vague and incomplete (Salvador 1974, 1985; Barbadillo 1986; Andrada 1980). There have been several recent surveys of provinces or larger areas, but these do not cover the whole of the distribution of the slow-worm and in some cases they are not precise enough for present purposes.

Data on the distribution of the slow-worm came from a variety of sources. Requests were sent to all major Natural History museums in Europe for data on localities of capture of their specimens of the slow-worm. Many minor museums in the peninsula and some large North American ones were also approached. The majority replied, but not



all were able to supply relevant data. An extensive search of the literature was made and some private individuals gave data. There were also a small number of personal observations.

The precision of the locality data varied considerably. Modern authors and collectors are much more aware of the need for accuracy than earlier workers. One problem is that in Spain and Portugal nearly all the provinces and districts take their names from that of the capital city. If, as is often the case, a locality is cited as "Burgos" or "Huesca" (Bosca 1877), does it refer to the province as a whole, or an observation within or close to the city? The point is important because the apparent limit of the distribution of the slow-worm can often be found in such provinces, and a true locality in the capital city could represent a range extension. Therefore, unless the citation is modern and has supplementary information (such as size of animal or habitat), it is not used.

The results of the collection of this data are shown in Fig. 8.1. There are 469 valid localities in the peninsula that were used to prepare the map. It is not possible to show every locality on a map of this scale, but the number within a province are shown. Depicting the range boundary is a compromise between showing sufficient detail and making assumptions about the distribution in areas of few localities. Individual localities are shown where they are probably outside the general area of distribution. It is not possible here to give a complete discussion of the data and its validity.

### 8.3 CLIMATE STATIONS AND VARIABLES

The Iberian Peninsula has a very wide range of climates. The northern coastal region has a mild and humid oceanic climate. The interior of the peninsula has a continental climate with hot dry summers and cold winters.



The peninsula is very mountainous, which affects the climate markedly. Mediterranean coastal areas have the typical climate associated with that region, with hot dry summers and mild, wet winters. However, these climates are often drier than those of other European countries at similar latitudes in the Mediterranean. The climate of the extreme south-east of Spain, in Almeria province, is the driest in Europe. The hottest part of the peninsula (and of Europe) is the basin of the Rio Guadalquivir, inland from the Mediterranean coast. A full description of the climate is given by Lines Escardo (1970).

There are a great many climate variables that could be used in this analysis. Many will be highly inter-correlated and will therefore contribute little. The choice of variables is to some extent subjective, but it is reasonable to choose a fairly small number that nevertheless take into account the range of climate factors. The major factors considered in this analysis are temperature, precipitation and sunshine. Seven variables were chosen to represent the climate at a station plus one topographical variable. Only stations that had data for all eight variables were used since discriminant function analysis does not handle missing data very well. There were 51 stations with complete data spread over the whole peninsula. The data were obtained from Lines Escardo (1970) and Meteorological Office (1972). The variables chosen were: the altitude of the climate station in meters above the mean sea level at Alicante (ALT); the average daily maximum temperature in degrees C. of the warmest month (TMAX); the average daily minimum temperature of the coldest month (TMIN); the total annual precipitation in mm (PREC); the proportion of the annual precipitation falling in summer (i.e., June to August) (SUM); Conrad's Continentality coefficient (CONT) (Conrad 1946), defined as:

$$(1.7 * (TMAX - TMIN) / \sin(L + 10)) - 14$$

where L is the latitude in degrees; Emburger's pluviocity coefficient (EMB), defined as:

$$(2000 \times \text{PREC}) / (TMAX - TMIN) (TMAX + TMIN);$$

and the annual total of hours of sunshine (SUN). The data for all stations are shown in Table 8.1. The continentality coefficient is an empirically derived measure of the variability of a climate. It was designed so that the most continental climate known had a coefficient of 100 and the least one of 0 (Conrad 1946). Allowance is made for the effect of latitude. Climates with a high coefficient of continentality tend to be drier and have mean annual temperatures below the latitudinal average. The pluviocity coefficient is a measure of the biological effectiveness of rainfall and, as can be seen from the formula above, takes the absolutes and the range of temperature into account (Bagnouls and Gaussen (1957)).

Each climate station was placed in one of three categories: 1, the slow-worm is definitely present in the area around the station (n = 13); 2, it is uncertain whether the slow-worm is present (n = 7); 3, the slow-worm is definitely absent in the area around the climate station (n = 31). These categories were determined from Fig. 8.1. All category 1 stations are within the definite range of the slow-worm, all category 3 stations are outside the definite range, and all category 2 stations are close to the range or to isolated localities. The positions and categories of the stations are shown in Fig 8.2. and Table 8.1.

#### 8.4 ANALYSIS

Discriminant analysis calculates a single linear function that best separates discrete populations of data

on a multivariate axis, by minimising the linear distance between members of one population while maximising the separation of the predefined populations. The analysis requires that each case (i.e., climate station) be pre-classified by the factor that is of interest (i.e., the presence or absence of the slow-worm) and that this classification is entered into the analysis. Discriminant analysis allows for cases where it could not be stated definitely that the slow-worm was present or absent to be excluded at first for later classification.

A set of discriminant function coefficients, one per variable plus a constant, is calculated, from which the discriminant function value for each case is calculated. Sets of discriminant classification coefficients plus constants are also calculated, one for each pre-classified category included in the analysis. There is one classification coefficient for each variable plus a constant in each set. For each case the value of each variable is multiplied by the corresponding classification function coefficient and these values are summed for each set, producing a classification function value that applies to each predetermined category. The category with the largest of the values is also that with the greatest probability, so the analysis classifies the case into that category. The greater the difference between the classification function values, the higher the probability of the case being correctly classified. Thus it is possible to classify cases not included in the analysis by calculating the classification function values to find the largest, even though these cases contributed nothing to the original analysis. The relative importance of each variable can be shown by calculating a correlation coefficient between the "real" values of a variable and the discriminant function values. A scatter diagram with

one fewer axes than predetermined categories can be drawn.

Discriminant analysis works best with normally distributed variables. In this analysis, two variables (ALT and EMB) were distributed significantly non-normal and were transformed to their natural logarithms, which succeeded in correcting the situation.

Only two predetermined categories were entered into the original analysis, presence and absence. Those cases (i.e., climate stations) where it was unknown if the slow-worm was present or not were initially excluded. Including them in the original analysis would have created a third category into which the analysis could have placed climate stations. This would not aid one of the purposes of the procedure, namely to classify as clearly as possible those stations where the distribution of the slow-worm is unknown as present or absent. The present analysis is the simplest possible, with only two categories, which means that the scatter diagram of discriminant function values has only a single axis.

### 8.5 RESULTS

Averages and standard deviations of the eight variables are given for each category in Table 8.2. There are clear differences between categories 1 and 3 for six of the eight variables, with four, TMAX, PREC, EMB and SUN, being highly significantly different. The averages of TMIN are almost identical and there is also no difference between the averages of ALT, due to the large variances. Climate stations where the slow-worm is present have lower maximum temperatures, higher precipitation and fewer sunshine hours.

The averages for category 2 are often intermediate between those for categories 1 and 3. Those for TMAX and SUN are approximately mid-way between the other two, those for PREC, CONT and EMB are close to category 3. Only the average for SUM is close to that for category 1. Category

2 averages for TMIN and ALT are very different from those of the other two categories. These stations tend to be on the inland plateau of the peninsula and are at higher altitudes with cooler winters than the others.

The significance of a discriminant function analysis is determined from a chi-squared test on the eigenvalue, with the same number of degrees of freedom as there are variables. Initial analysis indicated that the chi-squared value for the eight variables was 61.473 ( $p \ll 0.00001$ , 8 d.f.). This indicates that the analysis has managed to classify the cases with a very high degree of separation.

The discriminant and classification function coefficients for the eight variables are given in Table 8.3. The correlation coefficients for the relationship of the discriminant function coefficients and the values of each variable are also given. Three of the variables (PREC, EMB and SUN) have  $r > 0.8$ . The effect of these variables is not cumulative, since they are strongly correlated with each other ( $p$  for all combinations  $\ll 0.0001$ ). However, excluding any of them reduced the effectiveness of the analysis by reducing the chi-squared value and introducing mis-classifications. Each of them adds "information" to the analysis.

Fig. 8.3 shows a histogram of the discriminant function values for each climate station by the pre-classified category. The arrows show the discriminant function value at which there is an equal probability of the case being classified as 1 or 3. The analysis also calculates a "centroid" for each predetermined category; this is the mean of the discriminant function values for the category, and the further apart the centroids are, the greater the separating power of the analysis. For category 1 the centroid was 3.033 and for category 3 it was -1.272.

The two-letter codes of cases close to the line, and all category 2 cases, are shown. The analysis has classified all but one of the category 1 and 3 cases

exactly as they were pre-classified. The exception is Cabo Bagur (CB), preclassified as slow-worm present, which falls almost exactly on the dividing line between categories 1 and 3, but is just classified as category 3. Some other stations, such as Tortosa, (TT) and Barcelona, (BR) are also close to the dividing line. These places tend to be close to the distribution limits of the slow-worm.

The analysis has classified all seven unknown stations as being outside the distribution of the slow-worm. Two, Avila and Zaragoza, are close to the centroid of category 3, as would be expected for these hot, dry stations. Both were included in category 2 because of nearby localities that were considered reliable. Four stations, although their values are similar to each other, are widely scattered geographically and have reliable locality records nearby. Burgos (BU) is the category 2 station closest to being classified as category 1. The province of Burgos has been well surveyed by Barbadillo (1983), who found many localities in the mountains to the north and east of Burgos, but so far none in the city itself.

The resolving power of individual variables is illustrated by Fig. 8.4, where the four variables with the highest correlation with the discriminant function values are shown as scatter diagrams in two pairs. It should be noted that the category 2 stations tend to clump with those of category 3.

## 8.6 DISCUSSION

As far as is known, discriminant functions have not been used in the analysis of problems of the distribution of reptiles before. A number of factors must be discussed before the validity of the method can be decided. This is especially important in the present case since there are such clear-cut results.

The choice of climate variables is important. It is theoretically possible to use a very great number of variables, limited only by available data, but, since so many would be highly correlated, adding variables would not necessarily produce more reliable results. There is a happy medium, which may become clearer as more analyses are done. For the moment, choosing a small number of variables that express the basic factors of a climate seems reasonable.

The criteria used to pre-classify the climate stations are also important. These criteria must be reasonable and not biased by expectations of the outcome of the analysis. In the present case it could be argued that some climate stations should have been classified differently; Lerida, Tortosa and Braganca being possibilities. However, changing the classification of a small number of cases would not markedly alter the conclusions drawn from the analysis. A "jack-knife" procedure would also be unlikely to change matters.

All statistical procedures are influenced by sample sizes and the accuracy of the data. An analysis of this type should have climate stations that cover the geographical area and the range of climates as comprehensively as possible, and this is equally true of distribution data. Fig. 8.1 shows that there are many more localities in some parts of the peninsula than others. Records are particularly few in Portugal, which may reflect genuine scarcity of the slow-worm, since the area has been relatively well surveyed (Malkmus 1982). More data are always desirable, but not always forthcoming. Better distribution data would have meant a more precise description of range boundaries, and more stations may lead to a better understanding of the influence of the climate variables.

There are many factors other than climate that influence the distribution of an organism, at both micro-

and macro- scales. It is not assumed by the present analysis that climate is the only factor that has an effect on the distribution of the slow-worm, nor do the results "prove" that a particular combination of climate variables is the cause of that distribution. Caughley et al. showed that the distribution of kangaroos, Macropus spp., could be explained quite well by climate variables. There were areas of Australia that lacked a particular species of kangaroo but, according to the analysis, could support it. The conclusion was that climate could "allow some understanding" of the distribution of kangaroos, but there were other factors involved. Thus, if in the present study the discriminant function classification was unclear, it would be quite reasonable to conclude that other factors had strong influences on the distribution. Since the classification is clear, it should be concluded only that the combination of chosen climate variables correlates well with the known distribution.

Neither climate nor the distribution of an organism are static over space and time. Rapid changes in either could produce a less clear-cut result, since the two are not in equilibrium. The time-scale in the case of the slow-worm is about a century, i.e., roughly since recording of climate and distribution began. A small-scale change in climate, leading to perhaps local extinction or range expansion, would probably have very little affect on the results.

This method is dependent on there being a range boundary in the area under consideration. A climate station can only be classified as present, absent or unknown, since there are insufficient data to classify by population density or other more sophisticated criteria. It should be possible to analyse other parts of the slow-worm's range by a similar method. Climate should have a strong affect on the northern limits of the range of a temperate reptile species. One area that could give



interesting results is the northern range boundary in Scandinavia. There are reasonable or good surveys of Norway, Sweden and Finland available in the literature (Appendix 1), and climate data are available. An analysis would show which factors are important in the north, as opposed to those in the south. Perhaps not surprisingly, sunshine and temperature have previously been the factors used to explain the distribution limits of north temperate species. Jackson (1978) argued that low amounts of sun in May explained the distribution of Lacerta agilis on the Lancashire coast, and Terhivuo (1981) showed that the northern limits of the slow-worm in Finland correlated well with the 1300 day-degree isocline.

All of the above considerations should be borne in mind when interpreting the results. The results confirm the subjective impressions outlined in Chapter 1. the slow-worm is found, in the south of its range at least, in cooler, wetter areas with moderate sunshine levels. The minimum temperature of the coldest month is probably not important, perhaps because they have little effect on an individual, providing that it is deep enough in its shelter to avoid lethal temperatures.

Figures are numbers of localities in a province or area  
and dots are isolated localities.

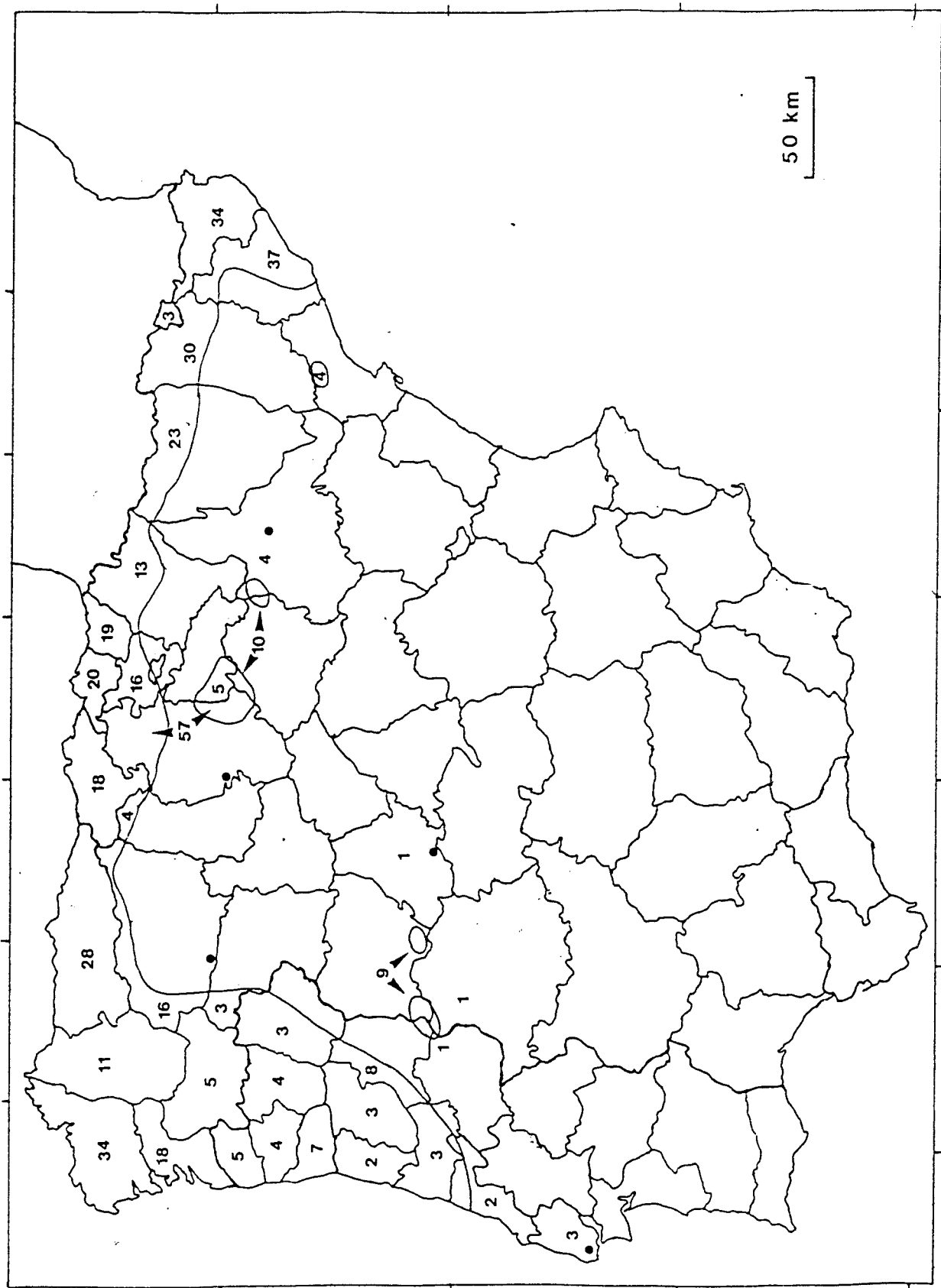


Fig. 8.2 (Overleaf) Climate stations and codes used in the discriminant function analysis.

The symbols indicate the category of climate station as follows: closed circle = category 1, slow-worm definitely present; cross = category 2, unknown whether slow-worm present, station to be classified after initial analysis, open circle = category 3, slow-worm definitely absent.

STATION	CODE	STATION	CODE
=====			
Alicante	AC	Jaen	JA
Almeria	AL	La Coruña	LC
Avila	AV	Leon	LE
Badajoz	BA	Lerida	LD
Barcelona	BR	Lisbon	LI
Bilbao	BI	Los Llanos	LL
Braganca	BC	Madrid	MD
Burgos	BU	Malaga	MA
Cabo Bagur	CB	Megalco	MG
Cabo Carveiro	CV	Moura	MO
Caceres	CC	Murcia	MU
Cadiz	CA	Pamplona	PM
Campo Maior	CM	Pontevedra	PO
Categena	CT	Porto	PT
Castelo Branco	CS	Praia de Roca	PR
Ciudad Real	CR	Sagres	SG
Coimbra	CI	Salamanca	SA
Cordoba	CO	Santander	SD
Cuenca	CU	Sevilla	SE
Evora	EV	Soria	SO
Faro	FA	Toledo	TO
Figueira de Castelo		Tortosa	TT
Rodrigo	FG	Valladolid	VA
Finisterre	FN	Valencia	VL
Giraltar	GB	Zaragoza	ZG
Gijon	GJ		
Granada	GR		

Fig. 8.2 Climate stations and codes used in the discriminant function analysis.

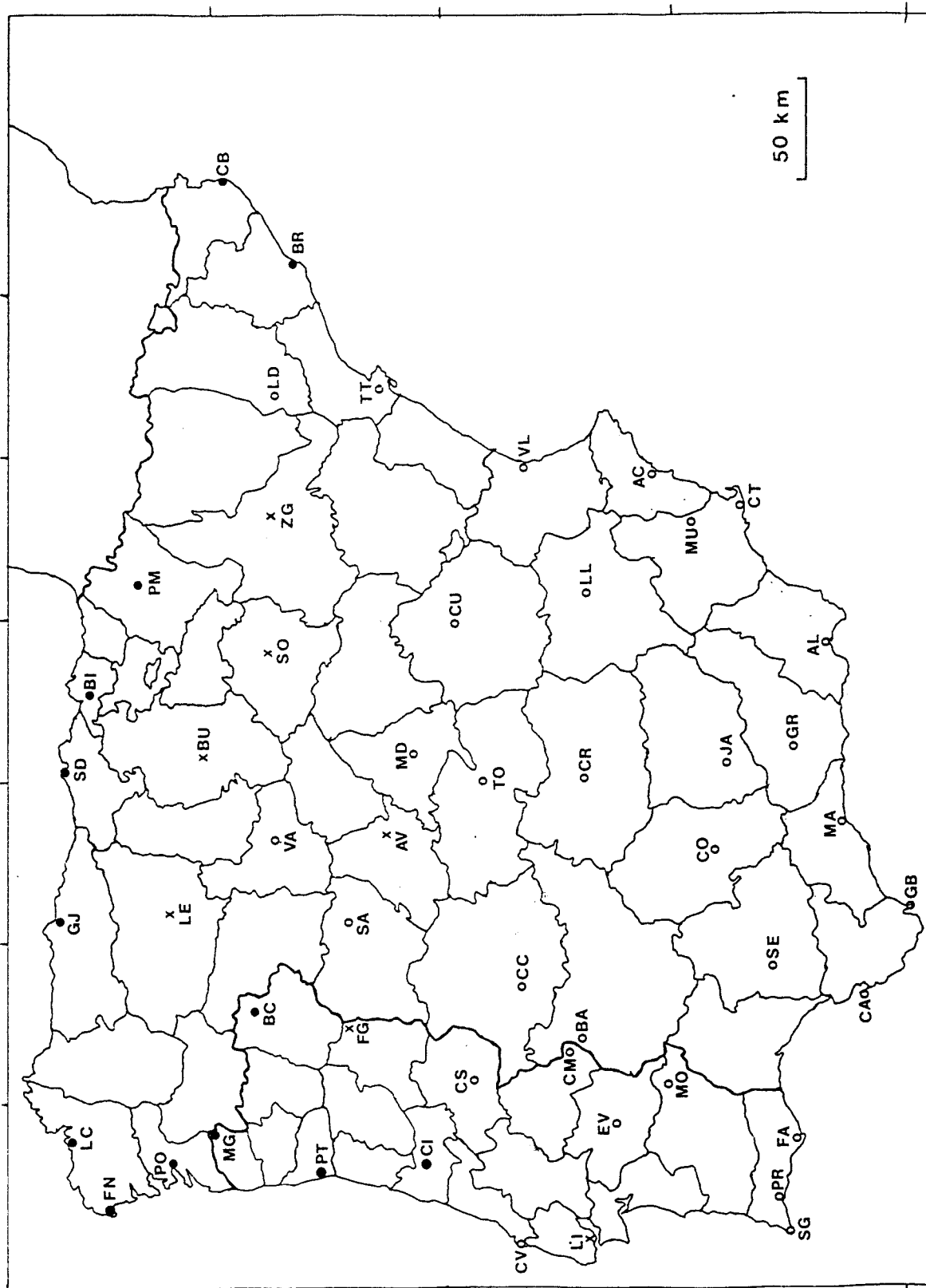


Fig. 8.3 Discriminant function values (DFV) for the three categories of climate station.

The arrows indicate the DFV where the probabilities of the station being classified as 1 or 3 are equal. Note that in category 1, CB was just classified as category 3, while BC was retained in category 1.

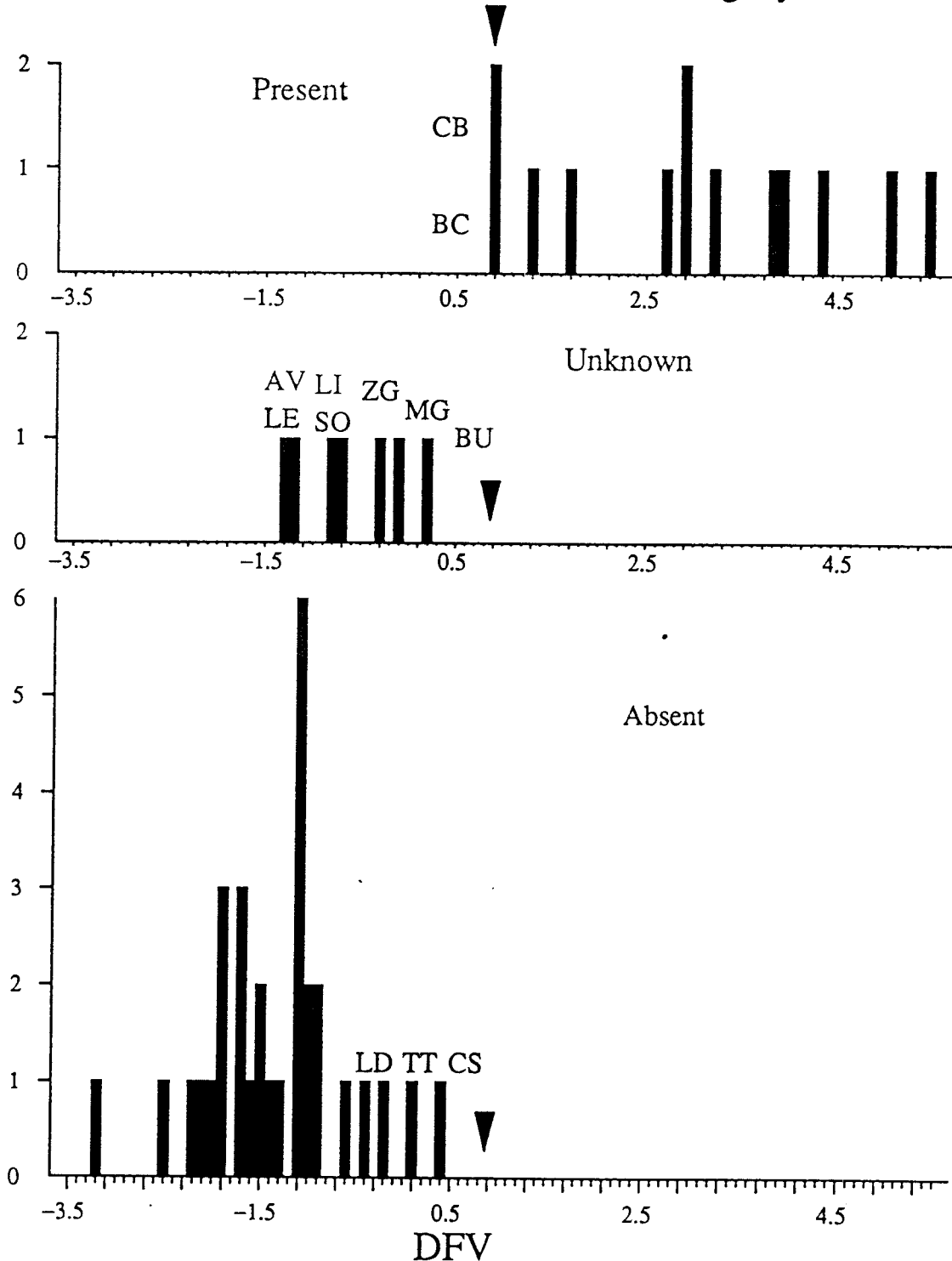


Fig 8.4 Scatter plots of the climate stations using two pairs of the most discriminating variables.

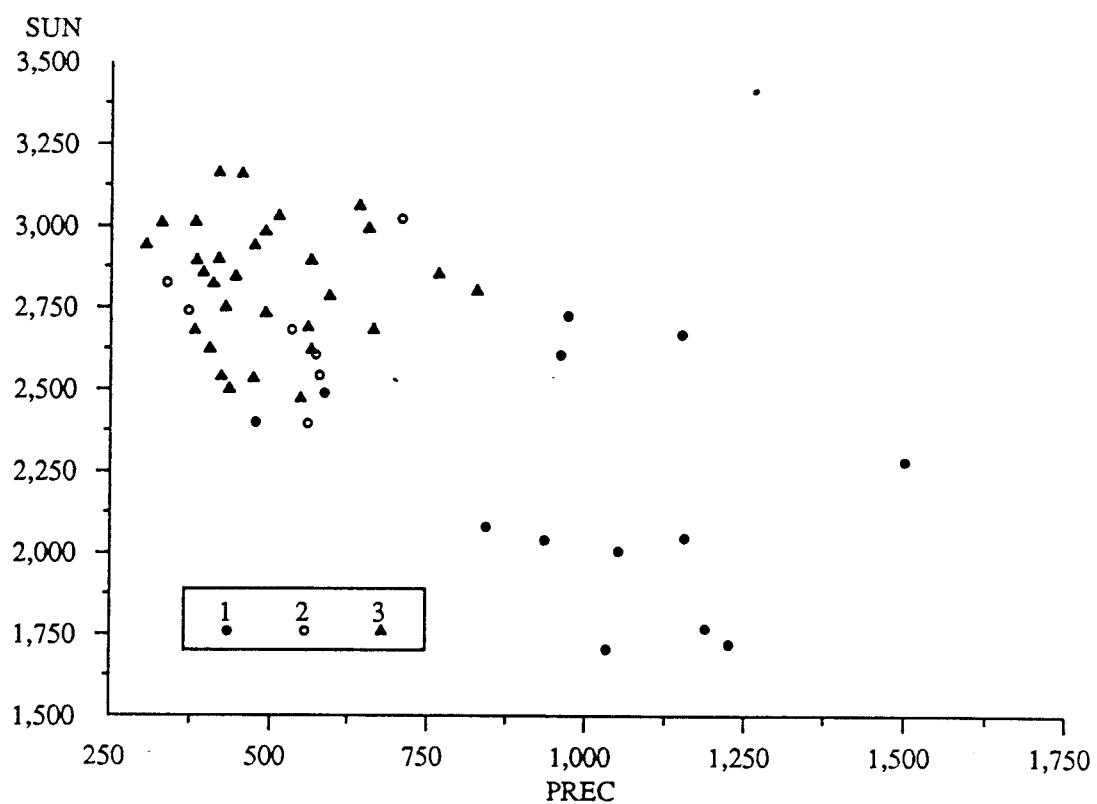
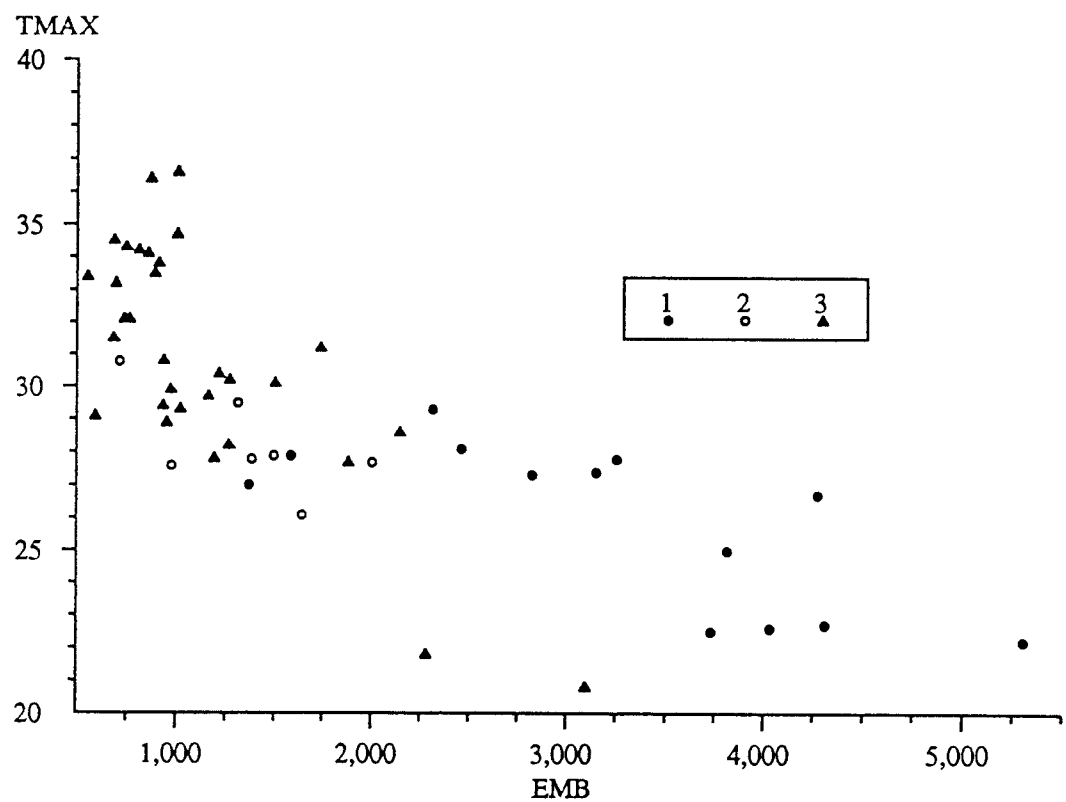


Table 8.1 Climate data for 51 Iberian stations.

For definition of variables see text. Categories under AF column are as follows: 1 = slow-worm present; 2 = presence of slow-worm unknown; 3 = slow-worm absent.

SITE	ALT	TMAX	TMIN	PREC	SUM	CONT	EMB	SUN	AF
=====									
Alicante	81	31.5	5.9	328	0.091	44.23	685	3009	3
Almeria	6	29.1	8.0	233	0.043	35.18	595	3031	3
Avila	1128	27.6	-1.9	371	0.187	42.50	979	2739	2
Badajoz	203	34.1	4.4	491	0.053	53.02	859	2982	3
Barcelona	93	27.9	6.3	587	0.193	32.98	1589	2487	1
Bilbao	17	27.8	4.4	1227	0.166	35.64	3257	1720	1
Braganca	720	28.1	0.0	973	0.075	46.77	2464	2724	1
Burgos	854	26.1	-0.6	560	0.191	40.76	1645	2394	2
Cabo Bagur	110	27.0	5.8	477	0.184	31.77	1372	2400	1
C. Carveiro	32	20.8	8.9	548	0.038	12.66	3101	2471	3
Caceres	460	33.5	4.1	492	0.067	51.74	890	2730	3
Cadiz	14	27.7	9.3	641	0.017	29.10	1883	3061	3
Campo Maior	280	33.8	4.4	512	0.049	52.21	912	3030	3
Cartagena	13	28.9	6.1	381	0.073	38.49	955	3010	3
Castelo									
Branco	390	31.2	4.7	828	0.042	44.97	1741	2800	3
Ciudad Real	628	34.5	0.7	409	0.078	62.15	687	2822	3
Coimbra	141	29.3	5.4	961	0.072	38.88	2317	2605	1
Cordoba	91	36.6	4.5	664	0.024	59.61	1007	2681	3
Cuenca	944	30.4	-2.0	560	0.170	48.96	1217	2688	3
Evora	309	30.1	5.7	656	0.037	41.33	1502	2990	3
Faro	36	28.2	9.0	453	0.015	30.62	1268	3158	3
Figueira de	587	29.5	1.1	572	0.089	48.23	1316	2606	2
Castelo Rodrigo									
Finisterre	146	22.5	7.4	843	0.116	18.19	3734	2079	1
Gibraltar	2	28.6	10.2	767	0.010	29.38	2149	2850	3
Gijon	29	22.7	6.0	1034	0.163	21.29	4315	1705	1
Granada	689	34.2	2.1	473	0.040	60.43	812	2532	3
Jaen	582	34.7	4.7	594	0.039	54.84	1005	2783	3
La Coruna	58	22.6	6.8	937	0.127	19.47	4034	2040	1

Table 8.1 (Continued).

SITE	ALT	TMAX	TMIN	PREC	SUM	CONT	EMB	SUN	AF
Leon	913	27.8	-1.3	534	0.135	42.72	1385	2682	2
Lerida	203	32.1	0.8	380	0.266	53.88	738	2679	3
Lisbon	77	27.7	7.8	708	0.032	31.02	2004	3022	2
Los Llanos	697	32.1	0.1	393	0.158	58.25	763	2855	3
Madrid	660	30.8	1.5	444	0.119	50.63	938	2843	3
Malaga	33	29.7	8.2	474	0.019	36.21	1163	2938	3
Megalco	235	27.4	4.2	1156	0.100	35.97	3154	2045	1
Moura	158	34.3	5.4	428	0.049	51.96	746	2750	3
Murcia	44	33.4	4.3	304	0.063	52.59	554	2941	3
Pamplona	466	27.3	0.6	1053	0.165	42.97	2827	2004	1
Pontevedra	24	26.7	3.3	1501	0.098	36.19	4276	2280	1
Porto	95	25.0	4.7	1151	0.076	30.32	3818	2667	1
Praia Rocha	19	27.8	8.7	417	0.023	30.31	1196	3160	3
Sagres	41	21.8	10.5	417	0.019	12.27	2285	2896	3
Salamanca	805	29.9	-0.1	435	0.129	51.22	973	2500	3
Santander	66	22.2	6.7	1189	0.169	18.79	5309	1767	1
Sevilla	9	36.4	5.5	564	0.025	57.36	871	2893	3
Soria	1080	27.9	-2.3	579	0.200	41.40	1498	2541	2
Toledo	539	33.2	1.6	383	0.117	56.08	697	2893	3
Tortosa	44	30.2	4.8	565	0.186	41.71	1271	2621	3
Valencia	13	29.3	5.6	422	0.142	39.00	1020	2538	3
Valladolid	695	29.4	0.0	404	0.153	49.73	935	2623	3
Zaragoza	237	30.8	2.2	337	0.208	48.00	714	2824	2



Table 8.2 Averages, standard deviations and t values for climate variables by category of station.  
t tests carried out on data transformed to logarithms for PREC, EMB and SUN.

	CATEGORY							
	PRESENT		ABSENT		t	p	UNKNOWN	
	MEAN	SD	MEAN	SD			MEAN	SD
=====	=====	=====	=====	=====	=====	=====	=====	=====
ALT	169.2	203.9	281.3	297.7	1.237	>0.1	696.6	380.2
TMAX	25.88	2.54	30.92	3.59	4.582	<0.001	28.20	1.4
TMIN	41.74	2.29	4.76	3.35	0.022	>0.95	0.71	3.26
PREC	1006	268	486	131	7.832	<0.0001	523	119
SUM	0.131	0.044	0.076	0.062	2.887	<0.01	0.148	0.061
CONT	31.38	9.44	44.84	12.99	3.347	<0.01	42.09	5.32
EMB	3267	1138	1142	564	8.030	<0.001	1363	393
SUN	2194	360	2830	190	7.612	<0.001	2687	188

Table 8.3 Discriminant function coefficients (DFC), correlation coefficients (r), significance (p) and Classification function coefficients (CFC) for the climate variables.

	DFC	r	p	CFC 1	CFC 2
=====					
ALT	0.46596	-0.022	> 0.2	-40.063	-41.893
TMAX	-0.48936	-0.643	< 0.001	65.976	67.880
TMIN	0.45169	-0.004	< 0.001	-14.676	-16.413
PREC	0.01505	0.893	< 0.0001	-1.3376	-1.3791
SUM	12.0927	0.462	< 0.01	738.87	691.84
CONT	0.06065	-0.511	< 0.01	5.6770	5.4428
EMB	-3.7567	0.864	< 0.0001	1007.7	1021.8
SUN	-0.00092	-0.852	< 0.0001	0.1901	0.1942
CONST	29.508			-4443.9	-4552.6

## CHAPTER 9 SOME MISCELLANEOUS CONSIDERATIONS

### 9.1 INTRODUCTION

The preceding chapters have given the results of the work on the population ecology, reproduction, temperature relations and related topics. There were a number of other aspects of this work where data obtained were less complete or found from sources other than field work. While these data may not be as well documented as that already discussed, it is of some interest and relevance and may show the direction of future work. It may also show the difficulties of working with a species that is often difficult to observe undisturbed. A very brief outline is given below of some of these topics.

### 9.2 WHAT DO SLOW-WORMS EAT?

Many works state that slow-worms prey on a variety of invertebrates, but that slugs and worms are preferred. Beetles, woodlice and snails are also eaten (Smith 1964; Poivre 1975). Bruno et al. (1973) reported spiders, beetles and pseudoscorpions in gut contents from Italy, and Bas Lopez (1982) has reported a millipede, woodlice and fly larvae as prey in Spain. Apart from these reports there has been no study of the diet of the slow-worm. One method that has proved useful in the study of the diets of reptiles is faecal analysis, where undigested parts of invertebrate (and vertebrate) prey can often be identified to species, or at least family, and estimates made of number, diversity, weight and volume eaten. If the major items in the diet of slow-worms are indeed slugs and worms, what parts could pass through in a state suitable to be analysed? For slugs the only possible part is the radula and for earthworms it is the chaetae. One radula would indicate one slug, but it is not easy to estimate

the numbers, size or species of earthworms from a collection of setae (Sims pers.comm. 1980)

The cloacal fluid and faecal material of a number of slow-worms was looked at under low and high power microscopes. No identifiable prey item was found. Nematodes (probably Oswaldocruzia filiformis (Baylis 1964)) and small pieces of partially digested plant material were frequently seen. This was presumed to be from the gut of the slow-worm's prey. On a few occasions a slow-worm regurgitated a recently ingested prey item. In all cases the item was either small slug of the genera Arion or Deroceras (such as A. hortensis, A. sylvaticus or D. caruanae), or an earthworm, probably a small Lumbricus spp. or an Eiseniella spp.

There is no obvious way to proceed. Laboratory food preference experiments using tongue flick frequency may be of some use, but the data obtained must be treated with caution (Carr and Gregory 1976). Regurgitation can yield identifiable remains if done soon enough after ingestion as shown for the adder (Kjaerkegaard 1981), but is a rather invasive technique, since it involves keeping the animal for at least ten days at a temperature of 8 deg. C. There is also no evidence that cooling induces regurgitation in the slow-worm as it did in the adder.

### 9.3 WHAT EATS SLOW-WORMS?

There are very few direct observations of predation on the slow-worm. Husband (1967) noted an attack by a song thrush in Hampshire, but the slow-worm was not eaten and the observer concluded that it was viewed by the bird as a threat, not as prey. Smith (1964) commented that the predators on juveniles "are innumerable", but there is no direct field evidence.

The only case of predation noted in the present study was when a piece of very recently autotomised tail, about

40 mm long, from a sub-adult was offered to a song thrush at DC. The tail was eaten without hesitation.

There have been a very great number of studies on the diet of potential predators of the slow-worm. There have been no recorded cases of arthropods preying on slow-worms (McCormick and Polis 1982), but it is possible that some, such as larger carabid beetles, may do. Some amphibians may also be predators. There are no field data to show that they are, although Smith (1964) has recorded both frogs and toads readily eating juveniles in captivity.

Mammals can also be discounted here. Small european carnivores such as the stoat and weasel take mainly endothermic prey (Tapper 1976). The fox and the badger have wide diets, but both are extremely infrequently reported eating reptiles (MacDonald 1987; Richards 1977; Neal 1986). The hedgehog also has a wide diet, but there is no record of the slow-worm as a prey item (Yalden 1976; Dickman 1988), despite the popular belief that it is a formidable predator on adders. Shrews are very active small predators, but there is no record in the literature of the slow-worm as prey (Churchfield 1982; Rudge 1968).

The major predators are probably other reptiles and birds. There is no evidence that any of the larger european lizards eat slow-worms. There are, however, a large number of references to the diet of snakes that range from simple records of a regurgitated food item, such as Meek and Inskip (1981), to wider studies based on the contents of many stomachs (Beshkov and Dushkov 1981). These records involve several species of widespread european snake genera, such as Vipera, Natrix, Coronella, Coluber and Malpolon, but in none is the slow-worm a major prey item.

In birds the situation seems to be similar. A convenient source of summarised data is the series "Handbook of the Birds of the Western Palearctic" (Cramp and Simmons 1977 et seq.). Species from a wide selection

of families and genera have been recorded feeding on slow-worms, but most have very varied diets, implying that reptiles in general and slow-worms in particular are taken when available, rather than being selected. The only bird that specialises on reptiles in Europe is the short-toed eagle Circaetus gallicus. Smith (1964) was of the opinion that any bird species that regarded a slow-worm as edible as an earthworm was a significant predator. Although this may be true, available studies on thrush species do not bear it out.

This large amount of scattered data in the literature gives only the most superficial answers to the question at the start of this section. It is interesting to note that the slow-worm has many predators, but is difficult to see that any of them could have more than a slight effect on slow-worm populations. Chapter 3 has shown that a high proportion of adults have autotomised tails, presumably from attempts at predation. There is little indication from the available data that any known predator, or combination of predators, could have caused the high rate of autotomy. In some studies the low numbers of slow-worms found as prey may be due to their low population density, but this is not true of all. There may be other significant predator species, whose diets have not been studied, that could explain an apparent lack of predation.

#### 9.4 THE PATTERN AND COLORATION OF SLOW-WORMS

The range of pattern and colour in the slow-worm has briefly been described (Section 1.2). There is considerable size and sexual variation which may indicate that the functional significance of the pattern and colour is of interest. Can the pattern and colour, and their ontogenic changes, be viewed as cryptic, or disruptive, or as mimicry of the adder, as proposed by Smith (1974)? What is the significance of the bright yellow or gold dorsum of the newly-born juvenile and why does it change as the

animal grows? Why is there sexual dimorphism? The only aspect of the colour and pattern that has generated any continued interest is blue-spottedness in males, which has systematic implications as shown in Chapter 1. This interest has not produced many facts, much less an explanation for the great intra- and inter- individual variation that has been found (Simms 1970; Voipio 1962). It would be possible to speculate here on the functional significance of the various and varied colours and patterns, but there would be little point without experimental data.

Smith's (1974) argument that the dorsal pattern of female slow-worms mimics the zig-zag pattern of adders deserves some discussion. He argued that all neonate slow-worms have a zig-zag stripe along the back, and that some females retain this stripe as adults. This pattern is useful since females tend to bask more than other slow-worms while pregnant, making them more vulnerable to raptors. The adder and slow-worm tend to be pregnant and give birth at the same time of year. The female thus benefits from her similarity to the warning coloration of the adder.

Avery (1974) pointed out that similarity in the times of reproduction is much more likely to be due to the common physiological and climatic constraints of the adder and slow-worm than mimicry. Smith's (1974) argument, however, is mainly dependent on the idea that the coloration and pattern of the adder is aposematic, which he seemed happy to assume without evidence. Although it is obvious that the adder is potentially dangerous to predators, there are no data that shows that the zig-zag is a warning pattern or coloration. Smith in fact admitted that the pattern camouflages (disrupts is probably a better term) the adder in dead bracken. There was also no justification for assuming that the faint (if present at all) zig-zag of the female slow-worm has the same

functional relationship as the zig-zag of the adder, which (to a human observer) is much broader and more obvious. There is little knowledge of the searching images of actual or potential predators of the slow-worm. There is no clear validity for extrapolating from human perceptions.

Jackson et al. have shown that snake species that rely on speed for escaping from predators tend to have longitudinally striped patterns, while those, such as the adder, that rely less on this ability tend to be blotched or banded. The important factor seems to be the number of light-dark transitions passing across the visual field of the predator as the snake moves away. Note that the zig-zag pattern in many Vipera species is really a joined series of blotches; the zig-zag becomes a diamond pattern in other species. All presumed cases of mimicry by or of reptiles have been reviewed in detail by Pough (1988). There are many similarities of colour and pattern between viperids and harmless (usually colubrid) snake species, but it is possible to argue that the similarity in pattern is due to ancestral factors. Most of the presumed cases of mimicry between harmless elongate squamates and viperids show much greater similarity in size, pattern, coloration and behaviour than a faint or non-existent zig-zag and similarity of dates of birth of the species involved.

It is easy to think of alternative explanations for the colour and pattern of the slow-worm, and the differences between males and females and juveniles, but there is a complete lack of experimental evidence. What about, for instance, the clear golden yellow dorsal band of the neonate slow-worm, with or without the thin zig-zag. Might it not be cryptic in grassland in late summer, when they are born, when compared to dried grass stems? Their widths are very similar. Both sexes lose the great contrast in colour and pattern as they mature, though this more true of males than females.



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# APPENDIX 1. SUMMARY OF REFERENCES TO DATA ON THE DISTRIBUTION OF THE SLOW-WORM

COUNTRY	MAP TYPE	REFERENCES AND NOTES
=====		
Albania	Locality	Bruno (1989) Few widely distributed records.
Andorra	None	Martinez Rica (1983).
Austria	5' X 5'	Cabela and Tiedemann (1985). Grid is 9.2 X 9.3 km approx. Widely distributed to 2384 m
Belgium	4 X 4 km	Parent (1985); Sparreboom (1981) Widespread, commonest in south.
Bulgaria	Locality	Beshkov and Beron (1964); Beshkov (1966). Widespread to 2000 m
Channel Isles	10 X 10 km	Frazer (1983) Arnold (1973). Probably all main islands.
Czecho-slovakia	Locality	Lac (1967); Opatrny (1979). Widely distributed.
Denmark	5 X 5 km	Pers. comm. Widely distributed. All major and some small islands.
Eire	10 X 10 km	Lamnha (1979); McCarthy (1977). Single record, see section 1.4.
Finland	10 X 10 km	Terhivuo (1981) Common up to 63 °N. Seperate map for blue-spotted form.
France	20 (N-S) X 30 (E-W) km	Castenet (1978) Poor survey. Large areas have few records. Not on Corsica.
Germany (FRG)	10 X 10 km	Müller (1976). Widely distributed.
Germany (DDR)	None	Likely to be widely distributed.

COUNTRY	MAP TYPE	REFERENCES AND NOTES
=====		
Greece	None	Chondropoulos (1986). On larger Ionian islands, but mainland poorly known.
Hungary	Locality	Dely (1972, 1974). Widely distributed, but few records S & E of Tiszo River.
Iran	Locality	Schleich (1977). Mountains to S of Caspian Sea only.
Italy	None	Data poor. Islands, Sicily only.
Luxembourg	4 X 4 km	Sparreboom (1981). Widely distributed.
Netherlands	5 X 5 km	Bergmans and Zuijderwijk (1986). Centre and south, not islands.
Norway	50 X 50 km	Dolmen (1978). S & W coasts to 60 °N, coarse grid size.
Poland	None	Berger <u>et al.</u> (1969). Probably widely distributed.
Portugal	8 (N-S) X 16 (E-W) km	Malkmus (1982). Mostly in N, some small populations in S.
Roumania	Locality	Fuhn and Jancea (1961). Found widely, poor data for many areas.
Spain	Locality	Salvador (1985). Mainly in N and mountains, some good regional surveys.
Sweden	Locality	Gislen and Kauri (1959). To 64 °N, only near coast in N, not around Gulf of Bothnia.
Switzerland	Shading	Kramer and Stemmler (1986). Possible distribution shown.
Turkey	Locality	Baran <u>et al.</u> (1988). Black Sea coast to Caucasus.

COUNTRY	MAP TYPE	REFERENCES AND NOTES
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UK	10 X 10 km	Arnold (1973); Frazer (1983); Stafford (1989). See Section 1.4 and Fig. 1.4.
USSR	Locality	Bannikov <u>et al.</u> (1977). E to Tobol River, N to °63 , not Crimea. Caucasus populations isolated from rest of country.
Yugoslavia	Locality	Dzukic (1987). Widespread, rare in NE.