UNIVERSITY OF SOUTHAMPTON

Faculty of Science

Department of Biology

ECOLOGY OF THE SAND LIZARD (*LACERTA AGILIS* L.) IN SOUTHERN ENGLAND AND COMPARISONS WITH THE COMMON LIZARD (*LACERTA VIVIPARA* JACQUIN)

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ABSTRACT

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ECOLOGY OF THE SAND LIZARD (LACERTA AGILIS L.) IN SOUTHERN ENGLAND AND COMPARISONS WITH THE COMMON LIZARD (LACERTA VIVIPARA JACQUIN)

by Andrew Miles Nicholson

The ecology of the sand lizard (Lacerta agilis) and the sympatric common lizard (Lacerta vivipara) was studied at two sites in Dorset, England from 1975 to 1977. Lizards were caught in dry pitfall traps at one site and by hand at the other. Each individual caught was weighed, measured, and marked, before release.

Diet was studied by faecal analysis. Both species took invertebrate prey of a variety of types and sizes but there were several taxonomic differences in prey taken. L.agilis took larger and harder prey than L.vivipara. Relationships between prey length and snout-vent length were examined for both species.

Prey of L.agilis in spring was smaller, harder, and less diverse than in summer. Food consumption, measured by production of nitrogenous excreta, was lower in spring. Factors affecting production of nitrogenous and faecal excreta were investigated. Faecal excreta was unsuitable as a measure of food consumption for L.agilis because of its relationship with prey hardness.

Stomach capacity of *L.agilis* was much greater than normal daily levels of food consumption. Individuals appeared capable of exploiting locally and seasonally abundant prey by feeding at high rates.

Reproductive effort of *L.agilis* increased with age. Annual adult mortality was estimated as 28%. Densities at both sites were approximately 50 individuals hectare^{-1}.

Sub-adult *L.agilis* grew faster than sub-adult *L.vivipara*. Energy devoted to growth by different age classes of both species is compared.

Individuals of *L.agilis* had overlapping home ranges and did not defend territories. It is suggested that home range size is too large to allow resources to be defended.

Pitfall traps caught 7 times more *L.agilis* than *L.vivipara*. Rates of capture of *L.agilis* increased with increasing temperature and radiation whereas those of *L.vivipara* did not.

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CHAPTER 1

INTRODUCTION

The lizard family Lacertidae is the dominant family of lizards throughout Europe, and is also widespread in Asia and Africa. The Lacertidae are the Old World analogues of the New World Teiidae, having well-developed legs and long tail.

Two species from the family occur in the British Isles, Lacerta agilis L., known in England as the Sand Lizard, and the Common or Viviparous Lizard Lacerta vivipara Jacquin. These two species form part of an indigenous British reptile fauna of only six species; the remaining species are the slow-worm or legless lizard, Anguis fragilis L., the grass snake Natrix natrix Lacepede, the adder Vipera berus L., and the smooth snake Coronella austriaca Laurenti.

Both L.agilis and L.vivipara are widespread in Europe and Asia (Figure 1.1). L.agilis occurs throughout continental Europe but is absent from Mediterranean regions. In Britain, L.agilis is at the extreme north western edge of its range. Populations of L.agilis on the European continent occur in a wide variety of different, but usually dry, habitats including field edges and hedgerows, roadside embankments, rough grassland, heathland and woodland edges (Van de Bund 1964; Glandt 1976; Arnold & Burton 1978). There is some geographical variation between populations and five different sub-species are recognised by Mertens & Wermuth (1960). Spellerberg

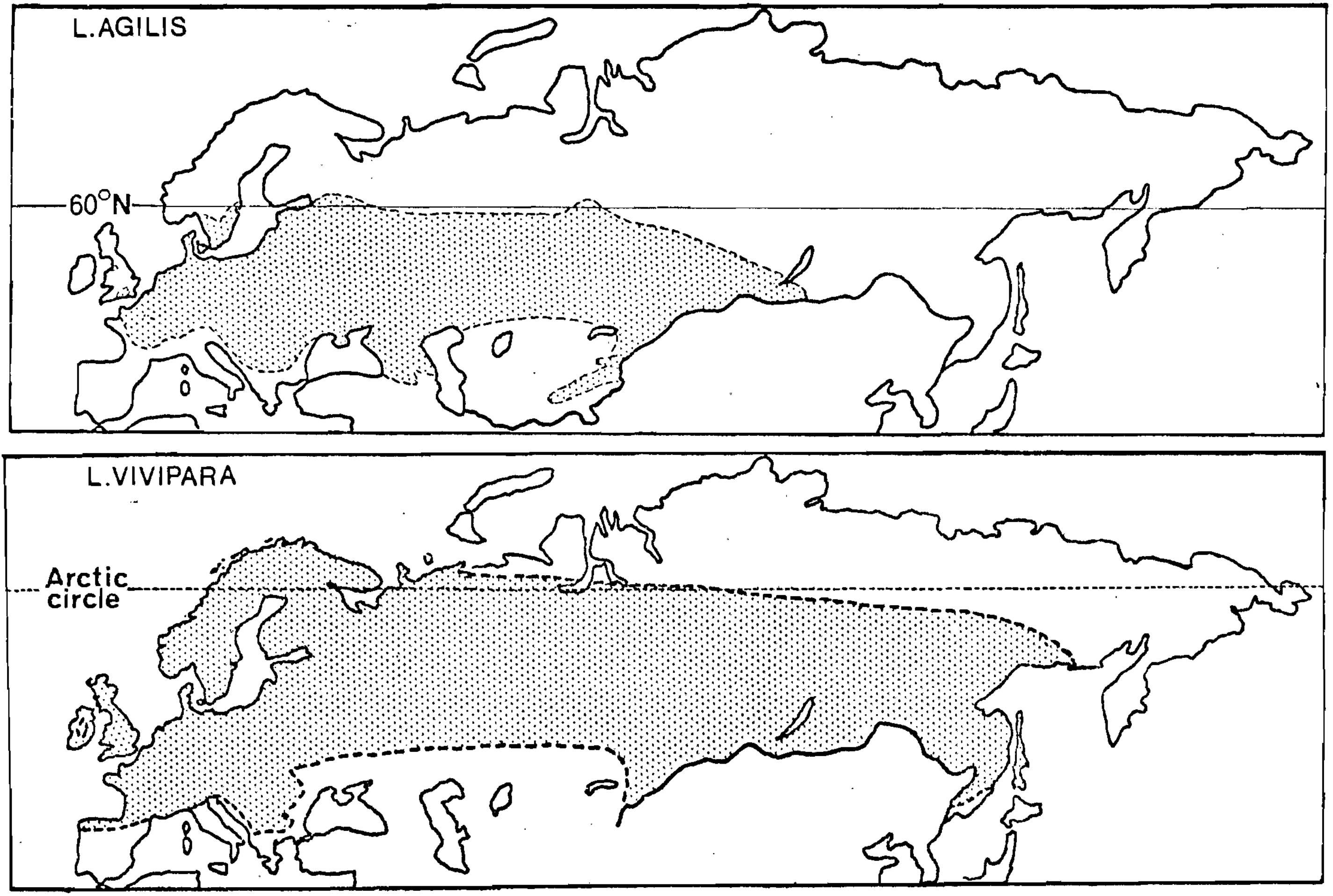

FIGURE 1.1 The distribution of Lacerta agilis and Lacerta vivipara. After Curry-Lindahl (1975) (Europe), and Bannikov, Darevsky & Ristamov (1971) (U.S.S.R.).

(1975) reports some evidence which suggests that British L.agilis may constitute a separate physiological race from Continental L.agilis.

L.vivipara is also widespread in Europe and, to the east, its range extends to the Pacific Coast of Asia. In the south of its range, the species is often montane and populations are largely confined to moist places, but, further north, it occurs in a greater variety of habitats (Arnold & Burton 1978). In northern Norway, the range of this species extends beyond the Arctic Circle. There is little geographical variation between populations and no sub-species are recognised, which is remarkable for such a widespread species.

Whereas L.vivipara is found throughout the British Isles, L.agilis is restricted to three areas. These are the Dorset heathlands and the heathlands of Surrey/Hampshire, both in southern England, and sand-dune coast of Lancashire in northern England (Figure 10.2). Spellerberg (1975) considers that the small population of L.agilis in Lancashire compared with the larger populations in southern England indicates that the range of L.agilis has at some time retreated. He further suggests that, after the last ice age, colonisation of the south coast of Britain, by means of the Pleistocene land connection, took place between 11,000 and 7500 BP. After this time, Britain became isolated from the continent. Forest deterioration and the spread of heath communities then allowed a northward spread of populations of L.agilis around 3000 BP, which was followed by a gradual reduction of populations in central England, caused by a deterioration in climate.

In recent years a further decline in the numbers of *L.agilis* in England has occurred. This decline has largely been caused by the loss of the natural habitat of the species, through such human activities as agricultural reclamation, urbanisation and commercial forestry. The collection of lizards for the pet trade may also have been an important factor. Since 1975, however, *L.agilis* has been listed in Schedule One of the Conservation of Wild Creatures and Wild Plants Act, 1975, and so is protected from collection.

The decline in the numbers of *L.agilis* has, for practical reasons, been documented less thoroughly than the destruction of habitat. However, Smith (1951) notes the disappearance of *L.agilis* from the coasts of Flint and Cheshire, and also a reduction in the numbers of *L.agilis* in Lancashire. Prestt, Cooke & Corbett (1974) note a dramatic decline in the numbers of *L.agilis* in Lancashire between the 1930s and 1974. Much of this loss is attributable to habitat destruction. Some 600 hectares of suitable habitat (20% of the total) have been lost in Lancashire since 1953 (Jackson 1978). Prestt *et al* (1974) also record a drastic reduction in the number of colonies of *L.agilis* in one area of the Surrey/Hampshire heathlands and Spellerberg (1975) notes the disappearance of *L.agilis* from the New Forest. In Dorset the loss of the habitat of *L.agilis* - the heathlands of the Poole Basin - has been documented by both Moore (1962) and Webb & Haskins (1979).

The heathlands of the Poole Basin are one of several examples of lowland heathland found in southern England. These dwarf scrub communities, dominated by ericaceous plants, are associated with light, sandy soils; in Dorset these soils are the tertiary deposits of the Bagshot Beds. Dry heathland in Dorset is dominated by Calluna vulgaris (L.) with scattered Erica cinerea L. and Ulex minor Roth. or U.gallii Planch.; wet heathland is dominated by Erica tetralix L. and peatland by the grass Molinia caerulea (L.) with Sphagnum mosses. It is with dry heathland that populations of L.agilis are normally associated and L.vivipara occurs together with L.agilis on most of the Dorset heaths (pers. obs.).

Open heathland and scrub was first formed in the Poole Basin in the early Bronze age (3600 BP); by the late Bronze age (2950 BP) open heathland had become entirely dominant and few changes occurred until the nineteenth century (Haskins 1978).

Today, only 15% of the heathland area which existed in the late eighteenth century remains and the heathlands are very fragmented (Webb & Haskins 1979). Agricultural reclamation, urbanisation, and commercial forestry have been the major causes of these losses. Heathland in the Poole Basin continues to be developed or reclaimed and many populations of L.agilis remain endangered. Spellerberg (1975) has stressed the need for detailed ecological research on Britain's threatened reptile species, for it is important to obtain ecological data on these species so that remaining populations can be effectively managed.

Heathland communities have been the subject of much previous ecological work (see Gimingham 1972). In Dorset, several invertebrate groups including spiders (Merrett 1967, 1968 & 1969) and ants (Brian 1964) have been studied in detail on heathland, as well as predators of invertebrates such as the Dartford Warbler (Sylvia undata) (Bibby 1977) and other predators such as the snakes V.berus (Prestt 1971) and C.austriaca (Spellerberg & Phelps 1977). Knowledge of the ecology of invertebrate predators such as L.agilis and L.vivipara thus contributes to our understanding of the heathland community.

Populations of L.agilis in England are at the north western limit of the range of the species, and furthermore, they experience an oceanic climate very different from the continental climate which prevails over most of the range. Populations in England have also been isolated from those on the continent for approximately 7500 years so it is possible that genetic differences have become established (see Spellerberg 1975). There is therefore considerable interest in the comparison between populations of L.agilis in England and the continent.

Most previous studies of lizard communities have been of tropical or desert lizards with many different lizard species (e.g. Schoener 1968b; Pianka 1969). In Britain, lizard communities consist of, at the most, three species. Of these the slow-worm (Anguis fragilis) is thigmothermic (Spellerberg 1976) and very different in its ecology from L.agilis and L.vivipara, and so unlikely to be a potential competitor of either species. L.agilis and L.vivipara, however, are potential competitors, and it is of particular interest to see how these conditions (only two potential lizard competitors existing in a cool, oceanic climate) affect the nature of the interaction between the two species.

There are therefore several reasons why ecological research on L.agilis is particularly valuable, but despite this, little detailed work has been published. This is not because the ecology of L.agilis has only recently begun to be investigated, for in 1943, Liberman & Pokrovskaja in the U.S.S.R. examined thermoregulatory behaviour and the development of the eggs in some depth. More recently, in the field of thermoregulation, Spellerberg (1974, 1975, 1976) has measured voluntary and critical minimum temperatures for L.agilis in the laboratory. Recent work in the U.S.S.R. includes that of Tertyshnikov (1970) on home range ecology and that of Rashkevitch & Semenikhina (1974) on diet. Feeding ecology has been particularly neglected, the latter study probably being the most detailed investigation of diet so far published.

In contrast, there has been a greater amount of work on the ecology of L.vivipara, particularly concerning feeding ecology. The diet has been examined in Finland (Itiames & Koskela 1971; Koponen & Heitakangas 1972) and England (Avery 1966). Avery has also investigated food consumption (Avery 1971), its relationship with stomach volume and the rate of digestion (Avery 1973), storage lipids (Avery 1974), longevity (Avery 1975a), and clutch size and reproductive effort (Avery 1975b). Glandt (1976) has compared the habitat preferences of L.agilis and L.vivipara in Germany.

Feeding is clearly of crucial importance to any animal and it is the feeding ecology of L.agilis that forms the central aspect of this work. Furthermore, data on the food requirements of individuals are important from the point of view of conservation and management. Feeding ecology is also of importance in the context of the predatory role of *L.agilis* in the heathland community, and the partitioning of resources between *L.agilis* and *L.vivipara* is of particular interest, as mentioned above. The comparison between *L.agilis* and *L.vivipara* is a theme which runs throughout the work and although the study of *L.agilis* was the primary objective, comparative data on *L.vivipara* were collected wherever possible.

Although the central aspect of the work concerned the feeding ecology of *L.agilis* (chapters 4 and 5) it is not possible to understand feeding ecology in isolation from other aspects of the ecology. For example, the dispersion of individuals in the habitat is closely linked with the density and distribution of food resources. Thus, for *L.agilis*, the home range size and the degree of overlap between home ranges (see chapter 9) may be related to the availability of food resources; home range size and the degree of overlap may in turn affect the availability of food resources. Several additional aspects of the ecology of *L.agilis* were therefore considered (chapters 6-10), both because of their relationship with feeding ecology and because of their intrinsic interest.

In chapter 4, a detailed analysis of the diet of *L.agilis* is presented. The prey of *L.agilis* is examined on different sites and at different times of year, prey size and prey hardness and their relationship to lizard size are considered. Comparisons are made with the prey of *L.vivipara* in terms of prey taxonomy, prey size and prey hardness. Prey selection of *L.agilis* is discussed in detail.

The food consumption studies on L.agilis in chapter 5 are based on the ideas and methods used by Avery (1971, 1978) to measure the food consumption of L.vivipara and Podarcis muralis/sicula. The food consumption of L.agilis at different times of year are compared, and the relationship between food consumption and stomach volume examined. The importance of these investigations is that they throw light on the factors which limit the rate of food consumption of individuals, which are clearly of fundamental interest. Finally in chapter 5, the relationship between food consumption and prey selection of L.agilis and L.vivipara is discussed.

The energy obtained from food consumption is allocated predominantly between three areas, reproduction, growth and maintenance (metabolic expenditure, including that on activity). The proportion of the total energy budget that is devoted to each of these areas depends on several factors including the availability of resources and demographic factors such as life expectancy. In chapter 6 the amount of energy devoted to reproduction by female L.agilis is estimated. Other aspects of the reproductive ecology of L.agilis are also considered. Estimates of the density of two populations of L.agilis and of the longevity of adults of L.agilis are made and the life history strategies of L.agilis and L.vivipara are discussed.

In chapter 7 data on the growth of L.agilis and L.vivipara are presented and the amount of energy devoted to growth by different age classes of both species is compared.

The home range ecology of L.agilis is examined in chapter 8. It was not possible to obtain any data on the home range ecology of L.vivipara. The social structure of L.agilis populations and the relationship with home range ecology is also examined.

In chapter 9 a further component of metabolic expenditure, activity, is examined by means of the results from pitfall trapping. In particular the activity of L.agilis and L.vivipara is examined in relation to temperature and levels of radiation. Having seen how these variables may affect the activity of individual lizards, the relationship between climate and the distribution of L.agilis is investigated in chapter 10.

The discussion in Chapter 11 concentrates primarily on the comparison between L.agilis and L.vivipara and ideas for further work are considered.

CHAPTER 2

THE STUDY AREAS

2.1 The Soldiers Road study area

The Soldiers Road study area is an area of heathland on the north-western boundary of Hartland Moor National Nature Reserve. The Reserve consists of approximately 300 hectares of dry heathland and valley bog in south-east Dorset, England (Lat. 51°40'N, Long. 2° W). It was once part of an extensive area of heathland covering Dorset and south-west Hampshire but is now surrounded on three sides by agricultural land, and on one side by pine plantations.

The study area consisted of approximately 0.5 hectares of dry heathland (Figure 2.1). The area was dominated by heather (Calluna vulgaris (L.)) which formed an almost continuous canopy of varying height (mean about 0.6 metres). The canopy was broken in places by paths, and by bare ground made by rabbits (Oryctolagus cuniculus L.). Apart from Calluna the most common plants were species of heaths (Erica ciliaris L., Erica tetralix and Erica cinerea), dwarf gorse (Ulex minor), and purple moor grass (Molinia caerulea). There were some clumps of common gorse (Ulex europaeus L.) and a few small birch saplings (Betula sp.). The site was burnt in 1956 so the heather was approximately 20 years old at the time of the study. The site was again burnt in August 1976, along with the greater part of the Reserve.

The study area was sheltered by higher ground on three sides. The gorse and birch thickets and a hedge

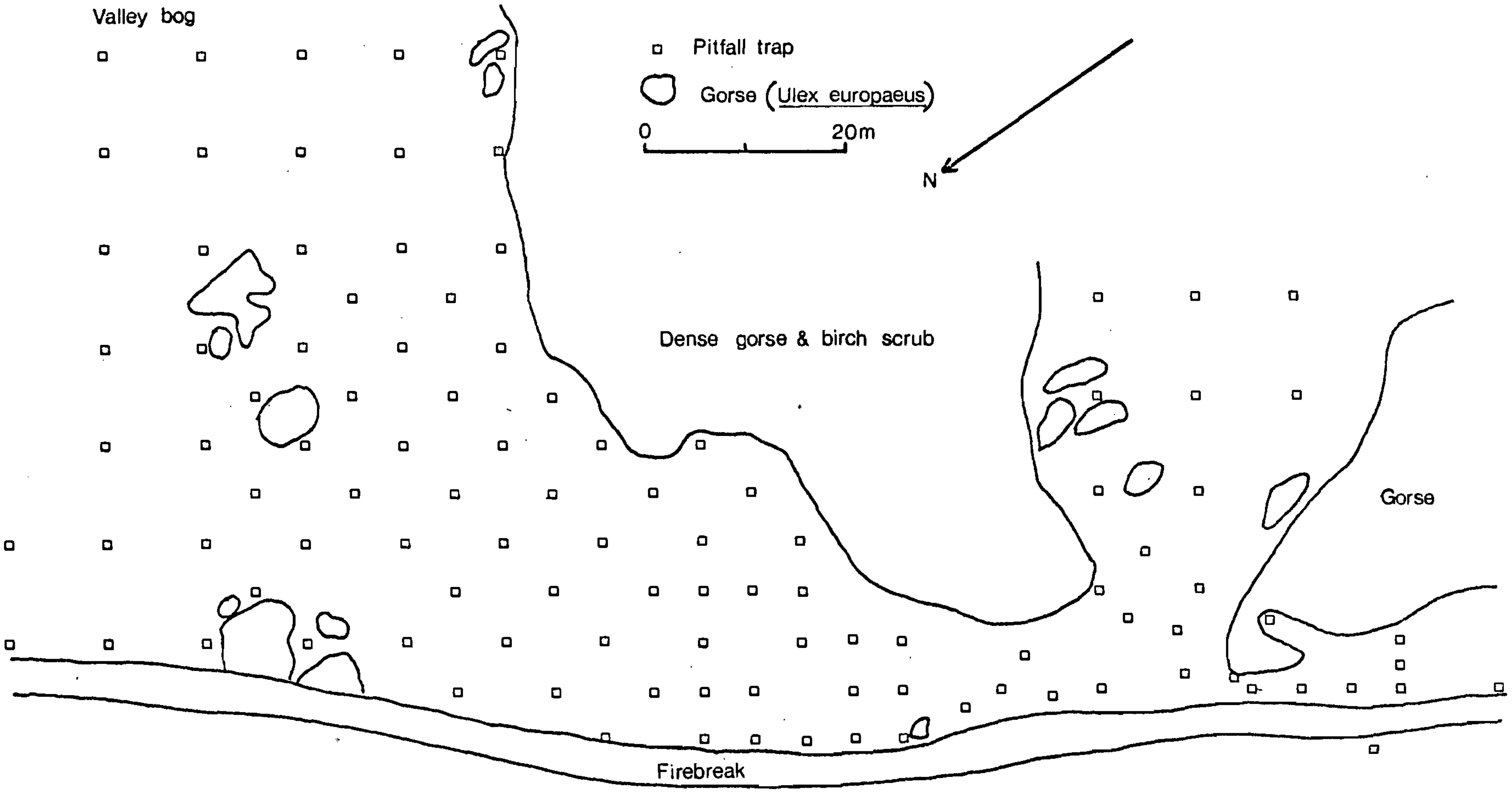

FIGURE 2.1 The Soldiers Road study area.

along the road also provided some shelter. The central area had a slight southern aspect and the north-eastern part sloped down to a valley bog, and so had a slight easterly aspect. At the northern edge there was a series of shallow gulleys approximately 1 metre deep. The rest of the area was relatively flat. The soil was acid, sandy and well-drained.

Besides L. agilis and L. vivipara, the slow worm Anguis fragilis was found in the study area, as were two species of snake, the adder (Vipera berus) and smooth snake (Coronella austriaca).

2.2 The Railway study area

The second site studied was situated north of Corfe Castle, Dorset (about 3 km south of the Soldiers Road site) on a railway line that had been disused since 1970 (Figure 2.2). Before this date, the embankments were burnt frequently.

Although the track itself is still largely uncolonised by vegetation, the embankments have been overgrown with birch (Betula sp.), sallow (Salix sp.), gorse (Ulex europaeus), hawthorn (Crataegus monogyna Jacq.), brambles (Rubus sp.) and bracken (Pteridium aquilinum (L.)) amongst other species. To the north is an area of bog which is dominated by rushes (Juncus sp.), with thickets of birch, gorse and sallow. This bog merges into deciduous woodland on its northern edge. The site is largely surrounded by agricultural land except to the south-west, where there is a disused clay working, now overgrown with heathland species.

This section of the railway runs approximately east-west, providing sheltered, south-facing embankments. At the eastern end of the site the embankments are approximately 3 metres above the level of the track. For the rest of the site, however, they are no more than 1 metre high and at the western end they are virtually level with the track. To the north of the track there is an old tramway which, owing to its use by cattle, is largely bare. From this the ground drops steeply to the bog, providing a shaded, north-facing slope.

The central part of the site consisted of an old siding on the northern side of the track, where rails and sleepers were still in position. This was covered mainly with coarse grasses. The disused tramway was raised approximately 1 metre above this siding, providing a south-facing wall.

It can be seen that this is an artificial site, consisting of a wide variety of habitats within a small area.

Besides L.agilis and L.vivipara, A.fragilis was also occasionally found on the study area. Adders (Vipera berus) were abundant on the study area and grass snakes (Natrix natrix) were seen occasionally.

In 1977 the study area at the Railway was extended to include a further large area to the west of the original site (see Figure 6.4). A large part of this area had been burnt in about 1971 and consisted partly of areas dominated by bracken (Pteridium aquilinum) and partly of areas dominated by gorse (Ulex europaeus) and the grass Agrostis setacea Curt., with some Erica cinerea.

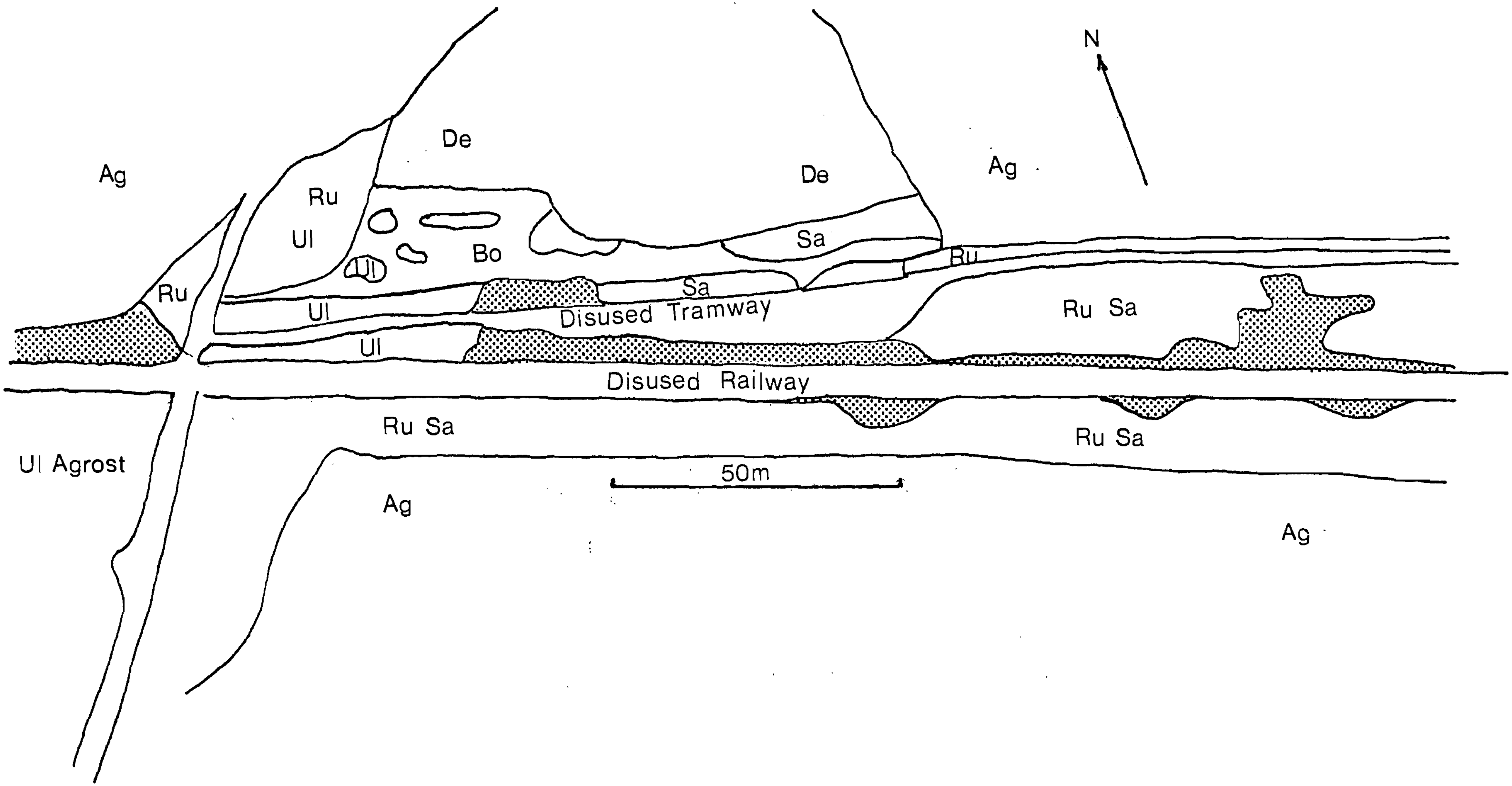

FIGURE 2.2 The Railway study area. De., deciduous woodland; Ag., agricultural land; Bo., Bog; Sa., *Salix*; Ru., *Rubus*; Ul., *Ulex europaeus*; Ul. Agrost., *U. europaeus* and *Agrostis setacea*. Stippled areas, coarse grass.

To the west the ground sloped down to a small pond. This slope and surrounding area was dominated by mature Calluna with scattered pines (Pinus sp.). The extended area was used for the collection of lizards for the food consumption study (chapter 5).

2.3 Studland Heath

This site was used only for the collection of lizards for the food consumption studies in the spring of 1977 (chapter 5). The site consisted of about 5 hectares of mature dry heath similar to that at Soldiers Road and dominated by Calluna with Erica cinerea, Ulex minor, and scattered Ulex europaeus.

CHAPTER 3

GENERAL METHODS

3.1 Pitfall trapping

Pitfall trapping was used as a method for catching lizards only at the Soldiers Road study area. In an initial trial to determine the suitability of the method, twenty traps were positioned at random in June 1975. After the success of this trial further traps were set out on a five metre grid, a total of sixty-six traps being in operation in 1975.

Each trap consisted of a 16 oz glass jar, 150 mm high with a diameter at the neck of 50 mm and at the base of 70 mm. This relatively thin neck prevented the lizards escaping; individual lizards were often placed in these jars after capture by hand and none was ever observed to escape.

Trapping continued until the 14 September 1975. The traps were checked every evening and normally each lizard caught was kept overnight and released by the same trap the next morning, although occasionally, individuals were released the same evening. The traps were kept dry and were emptied of water after heavy rain.

Pitfall trapping continued at Soldiers Road in the spring of 1976 but a few changes were made. Some plastic jars of a similar size and shape were used in addition to the glass jars and drainage holes were made in their bases. The number of traps was thus increased to 109 and they were placed over a wider area, with the distance between traps increased. They were placed on a 7 metre grid over the central part of the site and on a 10 metre grid on the outskirts.

3.2 Other methods of capture

The other methods of catching lizards consisted of searching for individuals by slowly walking around the site and the capture of lizards by hand or by noose. Searching and hand or noose capture was rarely attempted at Soldiers Road.

The noose was the method normally used to catch the larger individuals. The nooses were made from thin canes with fine nylon line (2 lb breaking strength) attached. This was a successful method of catching most lizards seen although individuals became "shy" of the noose after having been caught several times. Juveniles of Lacerta agilis and juveniles and sub-adults of Lacerta vivipara were too small to be caught with a noose and so were captured by hand.

3.3 Examination and measurement of lizards

After capture each lizard was placed in a cloth bag and the place that the individual was first sighted was recorded. The following measurements were then taken. Each individual was weighed in a small plastic bag of known weight, using a 10 g Pesola spring balance, graduated at 0.2 g intervals or, for heavier individuals, a 30 g balance, graduated at 1 g intervals. Snout-vent length, tail length and head width were measured with a steel rule graduated in mm. Broken and regenerated tails were noted and the distance between the break and the vent measured.

Each individual was permanently marked by toe-clipping. Tips of two toes were clipped, but never two toes on the same foot, giving a possible 150 combinations. Where natural loss of toes could be used for identification, toes were not clipped.

From 1976 onwards the dorsal pattern of each individual L.agilis was recorded by drawing (Figure 3.1). Each individual of L.agilis has a unique and distinctive pattern of dorsal markings, and the recording of these patterns provided a check on toe-clip identifications, as well as enabling many individuals to be recognised in the field without capture.

Lizards were retained for up to 1 hour at the site in order to obtain faecal samples (see chapter 4).

3.4 Statistical Methods

Unless otherwise stated, all regressions were fitted by the method of least squares, comparisons of means were made using t tests and the level of significance used is 5%. Natural logarithms were used for all logarithmic transformations.

3.5 Temperature and radiation data

Data for temperature and net solar radiation used in chapters 5 and 9 was from an Epyslon Automatic Climatological Monitoring Station on Hartland Moor N.N.R., courtesy of the Institute of Hydrology.

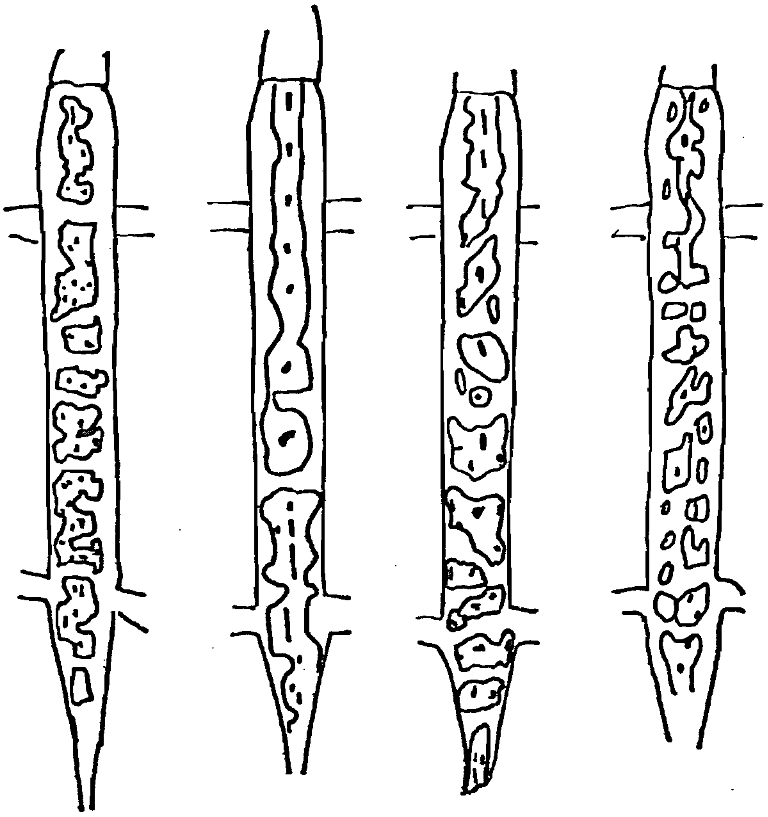

FIGURE 3.1 Use of the dorsal markings for the identification of individual <u>L.agilis</u>. Four field sketches of different individuals; the enclosed areas represent dark brown markings on a lighter background, and the black spots represent white spots on this dark background.

CHAPTER 4

GENERAL FEEDING ECOLOGY

4.1 Introduction

Although a few species of lizard are herbivorous, most are carnivorous; in particular small lizards (under 20 g) are almost exclusively carnivorous (Pough 1973) eating predominantly invertebrates. The first determinations of the diet of some of these small lizards by stomach content analysis suggested that the majority of these species were unspecialised predators taking a great variety of different invertebrates (e.g. Burt 1928; Blair & Blair 1941; Knowlton 1942, on various New World species; Krasavtsev 1936; Broadley 1958; Avery 1962, on species of Lacertidae). Many authors have since examined the diet of small lizards in more detail, considering such aspects of feeding ecology as seasonal variation in prey (Kennedy 1956; Asplund 1964; Bostic 1966; Sexton, Bauman & Ortleb 1972), prey size and its relation to lizard size (Rand 1967; Jackson & Telford 1975; Rose 1976) and diet as one aspect of the comparative ecology of different populations (Pianka 1970; Parker & Pianka 1975). The majority of these studies have been of New World species and together with many other investigations of the feeding ecology of lizards, they have confirmed that most small lizards are unspecialised predators of invertebrates although some species specialise on ants (Knowlton & Nye 1946) and termites (Bostic 1966).

The study of the feeding ecology of lizards has also been diversified into several different but related areas. The rate of food consumption of different lizard species has been measured both in the field and in the laboratory and related to other aspects of the energetics of the species (e.g. Johnson 1966; Avery 1971, 1978; Kitchell & Windell 1972; review by Turner, Medica & Kowalewsky 1976). This aspect of the feeding ecology of Lacerta agilis and Lacerta vivipara is considered in the following chapter.

The relationship between feeding ecology and territorial and aggressive behaviour is a subject to which much less attention has been given. Recently however, papers by Simon (1975) and Stamps (1977) have considered this aspect of the biology of the iguanid lizards Sceloporus jarrovi and Anolis aeneus.

Perhaps the most intensively investigated and rewarding field of study has been that concerning the partitioning of food resources between sympatric, and often congeneric, lizard species. Notable amongst this type of study, following the early work of Milstead (1957), have been the investigations by Schoener (1968b, 1970) and Schoener & Gorman (1969) of species of tropical iguanid lizards of the genus Anolis on Caribbean islands, and work by Pianka (1969) and Pianka & Pianka (1976) on different groups of congeneric lizards in the Australian Desert. These and other studies have established that although each species of lizard may itself be an unspecialised predator, taking many different types of invertebrates, there are nevertheless often consistent dietary differences between even very similar congeners. Such differences have normally been found in both prey size and prey taxonomy and they demonstrate that the mechanism of prey selection of each species is more complex than the unspecialised nature of its feeding habits might suggest.

Food is one of several resources that are partitioned between sympatric lizard species and the degree of partitioning of food may be related to the degree of partitioning of other resources. For example, Schoener (1968b) showed that species pairs of Anolis with a high overlap value for food tended to have a low overlap value for microhabitat. On the other hand, differences in microhabitat may lead to exposure to different prey and thus accentuate dietary differences. Pianka (1974), using data from a variety of different countries and habitats, has shown that the average degree of overlap between lizard species along several resource dimensions is inversely related to the number of lizard species in the community. Thus the factors affecting the degree of partitioning of food resources between species are diverse and complex.

There have been comparatively few studies of feeding ecology in the Lacertidae, and few of L.agilis in particular. The diet and feeding ecology of the Japanese lacertid Takydromus tachydromoides has been examined in detail by Jackson & Telford (1975), and Avery (1966) and Itiames & Koskela (1971) have investigated the diet of L.vivipara in England and Finland. The diet of L.agilis has been examined in the U.S.S.R. by Krasavtsev (1936) and Rashkevitch & Semenikhina (1974) but there has been no published work of any detail on the diet of L.agilis in England and the Russian work has gone little further than listing prey taxonomically.

None of the studies on the Lacertidae mentioned above have compared the feeding ecology of two or more sympatric species. L.agilis and L.vivipara are sympatric over large parts of their range in Europe and Asia (Figure 1.1). In Britain the distribution of L.agilis is restricted (Figure 10.2) whilst L.vivipara is widespread. L.vivipara has been recorded from most of the sites in Dorset where L.agilis is found (pers. obs.) and was common on the study sites. The majority of previous studies of the feeding ecology of sympatric species have been made on tropical or desert lizards making this study of two species in a cool temperate climate of additional interest.

In this chapter, the taxonomy of the prey taken by L.agilis is first examined in detail and the main trends of seasonal variation in diet are identified. Comparison is then made between the diet of L.agilis and the results from a less detailed study of the diet of L.vivipara. The size of the prey taken by both species is examined and related to the different sizes of lizards within the populations. Finally, three additional aspects of the feeding ecology of L.agilis and L.vivipara arising from the initial consideration of prey taxonomy and prey size are examined. These are prey hardness, variation between individual faecal samples of L.agilis and what this reveals about prey selection, and the prey of L.agilis and L.vivipara in relation to possible differences in microhabitat preferences between the species.

4.2 Materials and Methods

(i) Faecal analysis

Previous investigations into the diet of lizards have almost exclusively used the method of stomach content analysis involving the killing of many individuals. This was not possible in this study of L.agilis both because other aspects of the ecology of the population were being studied simultaneously and because the species is listed in schedule one of the Conservation of Wild Creatures and Wild Plants Act, 1975. The alternative of faecal analysis was therefore used which although largely untried on lizards has been used successfully for birds (Gibb 1956; Bibby 1977).

Lizards were captured both in glass pitfall traps and by hand. They were either retained for up to one hour on the site before being released or they were brought back to the laboratory. The procedure for keeping the lizards in the laboratory is described in the following chapter. Although faecal samples were often obtained soon after catching a lizard it was obviously more reliable to retain the animal for longer. Lizards caught in pitfall traps were usually retained overnight and released the next morning. Lizards were only retained for longer periods than this in 1977, in connection with the work on food consumption described in the following chapter.

The sites and sampling periods during which faecal samples were collected are shown in Table 4.1. Sampling was continuous in 1975 and 1976 although faecal samples were obtained irregularly, but was not continuous in 1977. For ease of analysis, the year has been divided into three sampling periods and in some cases two years' data have been combined.

The faecal samples were preserved in 70% alcohol for subsequent examination. They were dissected under a microscope and potentially identifiable fragments were removed for examination and measurement. Table 4.2 shows

TABLE 4.1 SITES, SAMPLING PERIODS AND HABITATS FOR THE COLLECTION OF FAECAL SAMPLES

	Site	Sampling period	Habitat
(a)	Soldiers Road	April & May 1976	Dry heathland
(b)	Railway	April & May 1976	Grass & scrub
(c)	Railway*	April & May 1977	Grass, scrub & dry heathland
(d)	Studland	May 1977	Dry heathland
(e)	Soldiers Road	1st June - 15th July 1975 & 1976	Dry heathland
(f)	Railway	1st June - 15th July 1975 & 1976	Grass & scrub
(g)	Soldiers Road	16th July - 15th August 1975	Dry heathland
(h)	Soldiers Road	16th July - 15th August 1976	Dry heathland
(i)	Railway	16th July - 15th September 1975 & 1976	Grass & scrub
(j)	Railway*	15th July - 15th August 1977	Grass, scrub & dry heathland
(k)	Railway*	September 1977	Grass, scrub & dry heathland
(l)	Railway	September & October 1977 (juveniles)	Dry heathland
(m)	Railway & Soldiers Road	May & June, 1976 & 1977 (young sub-adults)	Dry heathland & grass/scrub

* Note the difference in habitats between the Railway 1975/1976 samples and the Railway 1977 samples.

TABLE 4.2 PARTS FOUND IN THE FAECAL SAMPLES. THE TABLE LISTS THE TYPE OF REMAINS FROM COMMON PREY GROUPS AND THE PARTS COUNTED WHEN MORE THAN ONE PREY ITEM FROM A GROUP WAS PRESENT

PREY GROUP	Parts found in faecal samples	Parts counted when assessing numbers
COLEOPTERA		
Carabidae	Elytra, pronotum, head, legs, abdominal sternites & tergites, genitalia.	Elytra, heads & pronota.
ARANEAE	Chelicerae, carapace, sternum, legs, genitalia.	Chelicerae and carapaces.
OPILIONES	Chelicerae, legs, ocularium.	Chelicerae.
HYMENOPTERA		
Ichneumonidae	Wings, head, pronotum, legs, abdominal sternites & tergites.	Wings, heads & pronota.
Formicidae	Head, pronotum, petiole, legs, wings*, abdominal sternites & tergites.	Heads & pronota.
LEPIDOPTERA		
Larvae	Mandibles, head capsule.	Mandibles & head capsules.
Adults	Wing scales, head*, pronotum*, genitalia*.	Presence or absence of wing scales noted: heads.
DIPTERA	Wings, head*.	Wings & heads.
ORTHOPTERA		
Acrididae	Legs, genitalia.	Hind legs & genitalia.
HETEROPTERA		
Pentatomidae	Head, pronotum, fore & hind wings, legs, abdominal sternites & tergites.	Heads, pronota & fore wings.
ISOPODA	Mandibles & maxillae, head, legs.	Mandibles, maxillae & heads.

* Often absent although other parts present.

the remains of each type of prey which were found in the samples.

Identification of remains was carried out by comparison with reference material collected on the sites using both pitfall traps and a D-vac suction net, and by reference to keys. Once particular remains had been identified these were kept and subsequently referred to when similar remains were found.

Prey items were generally identified down to order and sometimes further, depending firstly on what was possible given the remains, and secondly on the frequency of the prey order in the diet. No attempt was generally made to identify the rarer prey groups any further than order.

The minimum numbers of prey items needed to account for the remains were recorded. For example, if six beetle legs were found one item was recorded unless it could definitely be established that the remains came from more than one animal.

Where the prey of *L.agilis* is related to the age class of individuals the definitions of age classes are as follows:

Juveniles - Individuals caught before their first winter (September and October 1977 in this case).

Young sub-adults - Individuals caught in the spring following their first winter (before 12th June, snout-vent length 37-45 mm).

Sub-adults - Strictly, individuals caught at any time during the year following their first winter, but in this chapter their age is always defined more precisely by the time at which the sample was taken.

Adults - Individuals that have experienced two winters.

(ii) Prey size

The length of each prey item identified in the faecal samples was estimated in two ways. The most usual method was to measure fragments of prey, such as elytra length for beetles or wing length for Diptera, using a calibrated graticule in the microscope eyepiece. Relationships between the length of these fragments and the length of complete prey items were then obtained from measurements on the reference material (appendix II). The second method was only applicable when identification had been made down to species level. The mean length of specimens of that species was used, obtained either from measurements on the reference material or from keys.

The largest lepidopteran larvae in the reference material were approximately 50 mm in length. The measurements of the mandibles of larvae in the faeces indicated that the lizards had taken larvae larger than this. In the calculation of mean prey sizes these larvae were taken as being 50 mm long.

For the display of prey length frequency distributions prey was classed into 1 mm length categories, items over 30 mm in length being placed in one class.

Overlap between different prey length frequency distributions was computed as the sum of the percent frequency shared for all prey lengths by the two populations being compared (Holmes & Pitelka 1968).

(iii) Prey hardness

The hardness of each prey item identified in the faecal samples was not measured directly. Instead each prey item was classed into one of three prey hardness groups according to its taxonomy. The classification of the prey was based on a subjective assessment of the thickness of the integument of each prey group, mainly from observations of the remains of these groups in the faecal samples. The classification was as follows starting with the softest category.

I	Araneae, Opiliones, larvae, lepidopteran adults, Diptera, Acrididae, Homoptera, Dictyoptera, Chilopoda.
II	Hymenoptera (except Apoidea), most Heteroptera, Coleoptera (Cantharidae, Coccinellidae, Calomicrus), Dermaptera.
III	Coleoptera (Carabidae, Curculionidae, Staphylinidae and most other families), Apoidae, Heteroptera (Pentatomidae and Alydidae), Isopoda, Tettigoniidae.

Overlap between prey hardness distributions was measured in the same way as for prey length.

4.3 The prey of Lacerta agilis

(i) Adults and sub-adults

In the following section the results from the taxonomic analysis of faecal samples taken from individuals of *L. agilis* are presented. Each prey item was classed into one of thirty-four different taxonomic categories. Table 4.3 shows the number and percentage by number of prey items identified in each of these prey categories for adult and sub-adult individuals for different sites and sampling periods. Prey species identified are listed in Appendix I. The more important and interesting species are also mentioned in the text. Authorities are given in Appendix I.

With reference to Table 4.1 showing the sites and sampling period for collection of faecal samples, it should be noted that in 1975 and 1976 samples were taken at the Railway only from lizards in a grass/scrub habitat. Comparison of the prey from these samples with those from Soldiers Road therefore compares the diets of two populations in two contrasting habitats and this comparison is shown in Figure 4.1. However, in 1977 collection of lizards at the Railway was over a wider area which included areas dominated by bracken (*Pteridium aquilinum*) and heather (*Calluna vulgaris*) (Table 4.1). Therefore these samples are not representative of any one habitat type, as are the other samples.

The most numerous prey order found in the faecal samples was Coleoptera. Weevils (Curculionidae) were particularly common but they occurred in large numbers only in the samples from heathland sites. At these sites they were much more abundant in the spring samples than in other samples (Table 4.3 and Figure 4.1). The most common species of weevil taken was *Strophosomus sus*. The larger weevil *Phyllobius pyri* was also common in the spring faecal samples.

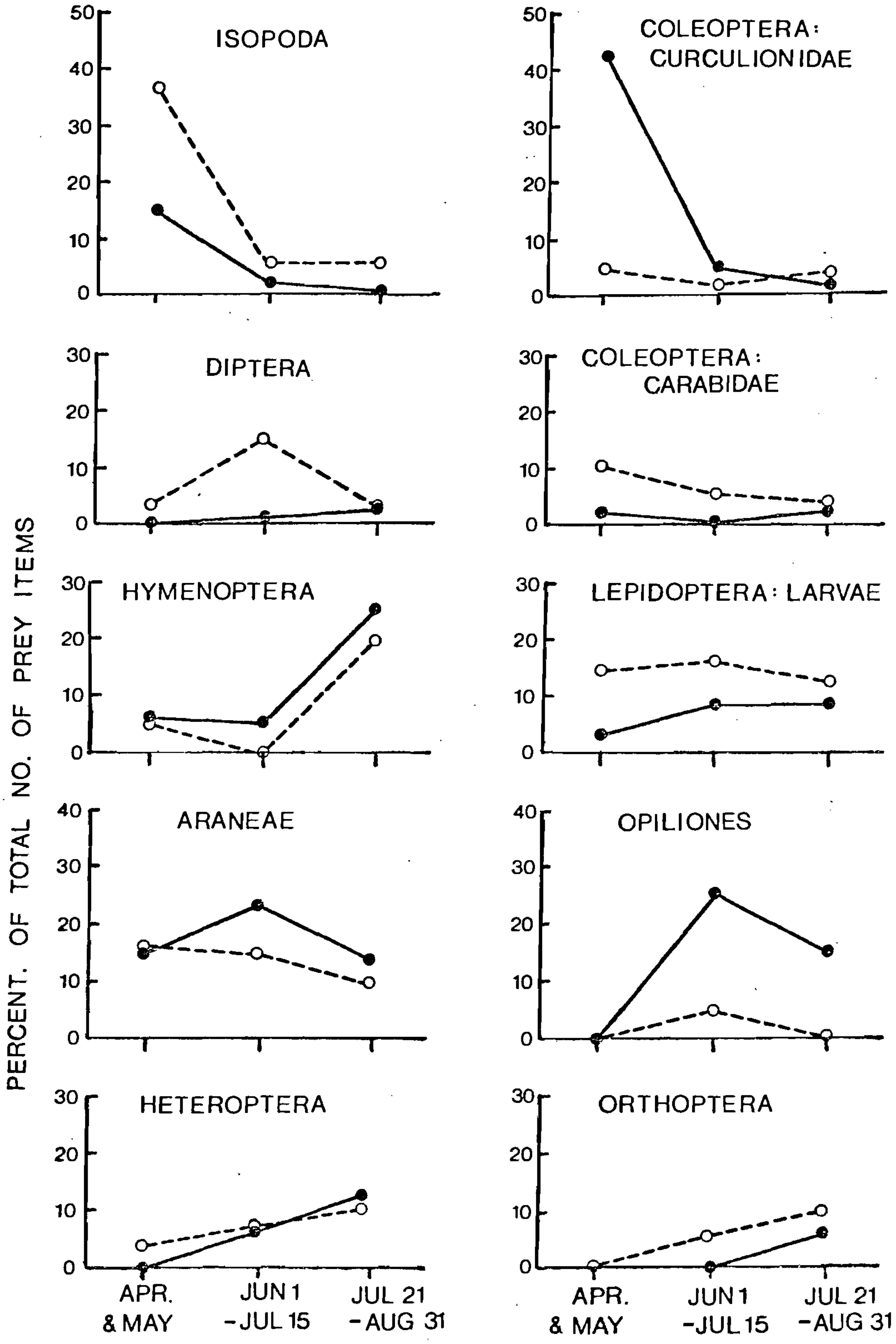

FIGURE 4.1 Seasonal variation in the prey of L.agilis in two contrasting habitats. Dotted line Railway site (grass/scrub), solid line Soldiers Road (heathland). Combined data for 1975 and 1976.

TABLE 4.3 THE PREY OF L. agilis. THE TABLE SHOWS THE NUMBER OF PREY ITEMS IN DIFFERENT TAXONOMIC CATEGORIES IDENTIFIED FROM THE FAECAL SAMPLES. LETTERS REFER TO SAMPLING PERIODS LISTED IN TABLE 4.1. FIGURES IN PARENTHESIS ARE PERCENTAGE OCCURRENCES (BY NUMBER) IN EACH SAMPLE PERIOD

	SPRING SAMPLES				EARLY SUMMER SAMPLES		LATE SUMMER SAMPLES					
	(a)	(b)	(c)	(d)	(e)	(f)	(g)	(h)	(i)	(j)	(k)	TOTAL
COLEOPTERA												
TOTAL	29 (54)	11 (17)	17 (29)	50 (46)	10 (10)	9 (17)	27 (13)	2 (3)	10 (14)	145 (26)	20 (15)	330 (22.6)
CARABIDAE	1 (2)	7 (11)	2 (3)	4 (4)		3 (6)	9 (4)		3 (4)	15 (3)	10 (8)	54 (3.7)
CURCULIONIDAE	23 (43)	1 (2)	11 (19)	40 (37)	5 (5)	3 (6)	3 (1)	2 (3)	1 (1)	68 (12)	4 (3)	151 (11.0)
STAPHYLINIDAE			1 (2)			1 (2)	1 (0.5)		2 (3)	20 (4)	2 (2)	27 (1.8)
OTHERS	5 (9)	3 (5)	3 (5)	6 (6)	5 (5)	2 (4)	14 (6)		4 (5)	42 (8)	4 (3)	88 (6.0)
ARANEAE	8 (15)	11 (17)	16 (27)	16 (15)	23 (24)	8 (15)	28 (13)	4 (7)	7 (10)	99 (18)	17 (13)	237 (16.2)
OPILIONES					25 (26)	3 (6)	38 (18)	4 (7)	1 (1)	15 (3)	1 (1)	87 (6.0)
HYMENOPTERA												
TOTAL	3 (6)	4 (6)	5 (8)	9 (8)	5 (5)		57 (26)	12 (21)	14 (20)	61 (11)	31 (24)	201 (13.8)
ICHNEUMONIDAE	1 (2)	1 (2)	1 (2)	4 (4)	1 (1)		7 (3)		5 (7)	18 (3)		38 (2.6)
APOIDEA		1 (2)	1 (2)		2 (2)			4 (7)	2 (3)	22 (4)	20 (16)	52 (3.6)
SYMPHYTA	1 (2)	1 (2)	1 (2)	2 (2)						3 (0.5)		8 (0.5)
FORMICIDAE		1 (2)	1 (2)	2 (2)			44 (20)	5 (10)	3 (4)	7 (1)	9 (7)	73 (5.0)
OTHERS	1 (2)		1 (2)	1 (1)	2 (2)		6 (3)	2 (3)	4 (5)	11 (2)	2 (2)	30 (2.1)
LEPIDOPTERA												
TOTAL	3 (6)	10 (15)	2 (3)	6 (6)	12 (12)	10 (19)	16 (7)	13 (22)	13 (19)	69 (13)	7 (5)	161 (11.0)
LARVAE	2 (4)	10 (15)	2 (3)	6 (6)	9 (9)	9 (17)	11 (5)	13 (22)	9 (13)	51 (9)	5 (4)	127 (8.7)
ADULTS	1 (2)				3 (3)	1 (2)	5 (2)		4 (6)	18 (3)	2 (2)	34 (2.3)
DIPTERA		2 (3)	1 (2)	8 (7)	1 (1)	8 (15)	6 (3)	1 (2)	2 (3)	52 (9)	35 (27)	116 (7.9)
ORTHOPTERA												
TOTAL						3 (6)	6 (3)	10 (17)	7 (10)	24 (4)		50 (3.4)
ACRIDIDAE						3 (6)	5 (2)	10 (17)	6 (9)	16 (3)		40 (2.7)
TETRIGIDAE										8 (1)		8 (0.5)
TETTIGONIIDAE							1 (0.5)		1 (1)			2 (0.1)
HETEROPTERA												
TOTAL		3 (5)	2 (3)	3 (3)	6 (6)	4 (7)	25 (12)	11 (19)	8 (11)	20 (4)	6 (5)	88 (6.0)
PENTATOMIDAE & ALYDIDAE			1 (2)		4 (4)	1 (2)	17 (8)	9 (16)		2 (0.4)	2 (2)	36 (2.5)
NABIDAE			1 (2)	2 (2)	1 (1)	2 (4)	2 (1)	2 (3)	4 (6)	5 (1)	4 (3)	23 (1.6)
OTHERS		3 (5)		1 (1)	1 (1)	1 (2)	6 (3)		4 (6)	13 (2)		29 (2.0)
HOMOPTERA												
TOTAL	3 (6)		1 (2)		3 (3)	2 (4)	4 (2)		1 (1)	15 (3)	2 (2)	31 (2.1)
APHIDAE	2 (4)				2 (2)	2 (4)				5 (1)	1 (1)	12 (0.8)
AUCHENORRHYNCHA	1 (2)		1 (2)		1 (1)		4 (2)		1 (1)	10 (2)	1 (1)	19 (1.3)
UNIDENTIFIED LARVAE					1 (1)		2 (1)	1 (2)		14 (3)	2 (2)	20 (1.4)
ISOPODA	8 (15)	24 (36)	15 (25)	16 (15)	2 (2)	3 (6)	1 (0.5)		4 (6)	19 (3)	1 (1)	93 (6.4)
DERMAPTERA				1 (1)			1 (0.5)		1 (1)	2 (0.4)		5 (0.3)
DICTYOPTERA					2 (2)	2 (4)	2 (1)			6 (1)	4 (3)	16 (1.1)
CHILOPODA		1 (2)			5 (5)	2 (4)	3 (1)			1 (0.2)		12 (0.8)
ODONATA										2 (0.4)	1 (1)	3 (0.2)
PSOCIDAE										3 (0.5)		3 (0.2)
TRICHOPTERA					1 (1)				1 (1)			2 (0.1)
MECOPTERA					1 (1)							1 (0.1)
NEUROPTERA										1 (0.2)		1 (0.1)
MOLLUSCA									1 (1)			1 (0.1)
JUVENILE LIZARD										2 (0.4)	1 (1)	3 (0.2)
TOTAL	54	66	59	109	97	54	216	58	70	550	128	1461
Number of faecal samples	99	11	9	14	13	8	27	11	13	39	8	162

Ground beetles (Carabidae) were less frequent in the faeces than weevils. Most common were species of Amara (6-8.5 mm) and the larger Pterostichus (9-14 mm). Remains of two individuals of the much larger beetle Carabus problematicus (20-30 mm) were also found.

The majority of the staphylinid beetles taken were of one species, Staphylinus compressus (14.5 mm). Staphylinids smaller than this were not found. Other notable species of Coleoptera found were the small chrysomelid, Calomicrus circumfusus (4 mm) which was common in some of the July-August 1977 samples at the Railway, click beetles (Elateridae) which were commonest in the spring samples but generally rare, and a species of sailor beetle (Cantharidae) which was frequent in the July-August 1975 sample from Soldiers Road. Ladybird beetles (Coccinellidae) were notable for their rarity in the faecal samples.

A species list of the spiders identified from the faecal samples is given in Appendix I. A total of thirty-one species of spider taken by L.agilis were identified. Most common were the wolf spiders (Lycosidae), and, in particular, species of Pardosa. There was comparatively little seasonal variation in the proportion of spiders in the diet (Table 4.3, Figure 4.1), although different species were important at different times of year. The proportion of spiders in the diet at different sites was also similar.

In contrast to spiders, there is a marked seasonal variation in the occurrence of harvestmen in the diet. Harvestmen were absent from the spring samples but occurred frequently at other times of year. They were also more common at Soldiers Road than at the Railway (Table 4.3, Figure 4.1).

A similar trend in the seasonal occurrence of Hymenoptera is also apparent (Figure 4.1). The high proportion of Hymenoptera in the late summer samples at both sites was caused by different hymenopteran groups at each site. At Soldiers Road the reason was the large number of queen ants taken, whereas at the Railway a variety of different groups were responsible.

The daily occurrence of ant queens in the faecal samples from Soldiers Road during July/August 1975 is shown in Figure 4.2. Between 28 July and 3 August ant queens constituted 33% of the prey identified. This corresponded to the period when the sexual stages of the ant species were observed to swarm and illustrates the ability of individuals of *L. agilis* to adapt rapidly to new food sources.

The majority of the ant queens were species of *Lasius* but remains of some *Formica* queens and some queens of the turf ant, *Tetramorium caespitum* were also found. In contrast to the large numbers of queen ants found, only four workers and no male ants were found in the faeces. Three of these workers were *Tetramorium caespitum* and it may be relevant that workers of this species, unlike workers of *Formica* or *Lasius*, contain no formic acid (M.V. Brian pers. comm.).

Of the other hymenopteran groups distinguished, sawflies were rare in samples, ichneumon flies being much more important (Table 4.3). Bees were also

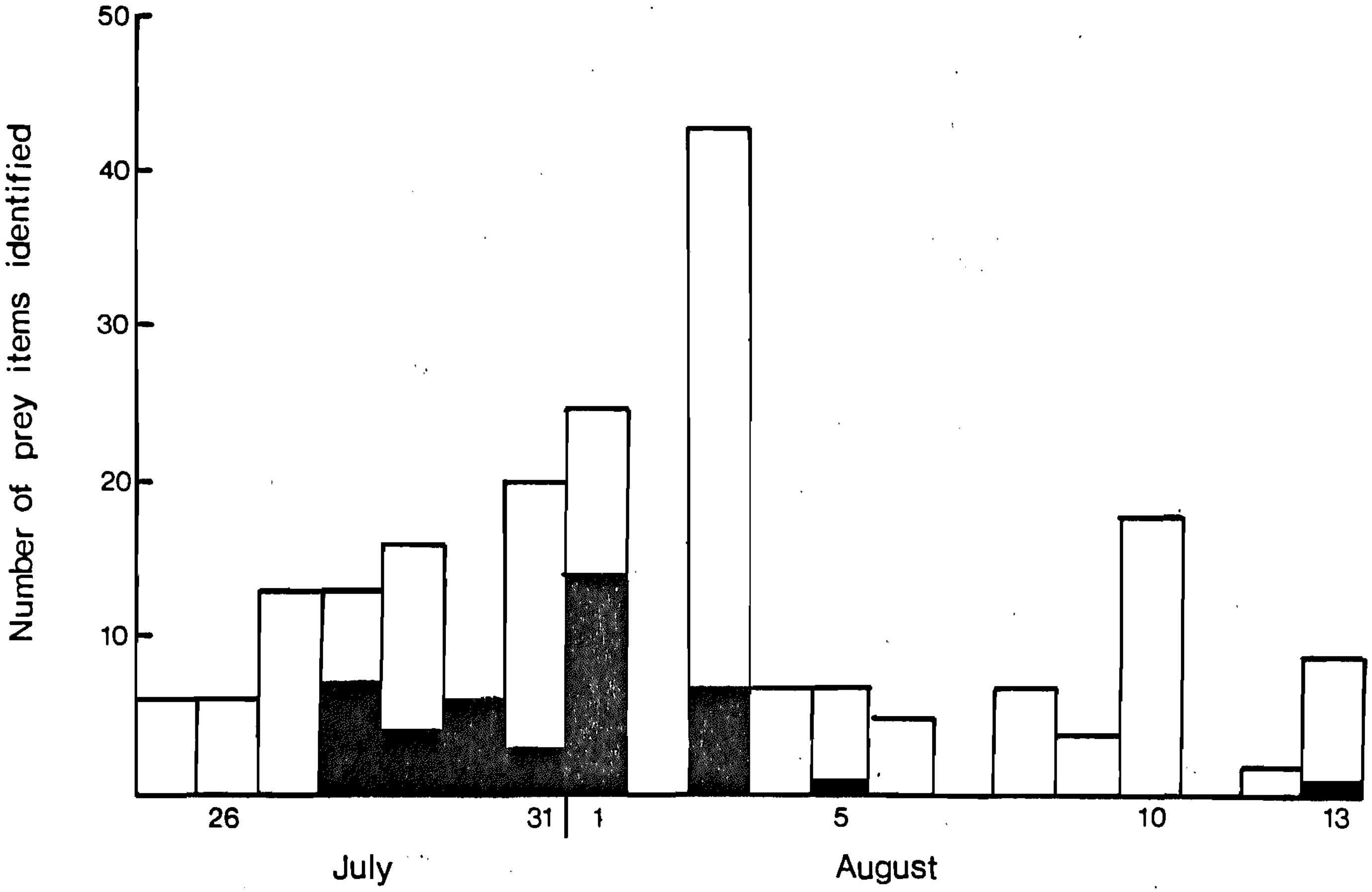

FIGURE 4.2 The occurrence of ant queens in the diet of L.agilis at Soldiers Road in July and August 1975. Shaded bars represent the number of ant queens identified, unshaded bars other identified prey.

important; many of the bees taken were large bumble bees (Bombus sp.). Particularly high numbers of bees were found in the September 1977 samples. At this time the Calluna at the site was flowering which attracted large numbers of bees to the area.

There was comparatively little seasonal variation in the proportion of lepidopteran larvae in the diet although the spring samples at Soldiers Road and Studland contained fewer larvae (Figure 4.1 and Table 4.3). Lepidopteran larvae were less common in the Soldiers Road samples than in the samples from the Railway site (Figure 4.1). Lepidopteran adults (probably mostly moths) were generally uncommon but found more regularly in the summer than the spring samples (Table 4.3).

During most sampling periods Diptera were only rarely found in the faecal samples. However, they were common in a few sampling periods, notably in September 1977 (Table 4.3). The majority of the flies eaten at this time appeared to be hover-flies (Syrphidae). These may have been attracted to the area by the flowering of the Calluna, as was suggested in the case of bees which were also taken frequently during this sampling period.

The majority of the Orthoptera taken were grasshoppers (Acrididae) although a few groundhoppers and bush-crickets were also taken (Table 4.3). The proportion of Orthoptera in the diet increased during the year and they were more frequently taken at the Railway site than at Soldiers Road (Figure 4.1).

There was a similar increase in the proportion of

Heteroptera in the diet during the year at both sites (Figure 4.1). Heteropteran bugs from the families Pentatomidae and Alydidae consisted of the two large shieldbugs Picromerus bidens (12-13.5 mm) and Rhacognathus punctatus (7-9 mm) together with Alydus calcaratus (11-12 mm), a species restricted primarily to heathland (Southwood & Leston 1966). The predatory bug Nabis ericetorium (6-8 mm), also a well known heathland species, was taken regularly. These four large predatory bugs constituted over 50% of the heteropterans eaten. In comparison with heteropteran bugs, homopterans were rarely taken.

Woodlice were an important prey group, especially in the spring when they were common in samples from all sites, but particularly at the Railway site (Figure 4.1, Table 4.3).

No other prey category apart from those already mentioned constituted more than 1.4% of the diet and together they accounted for only 46% of the total number of prey items identified. Each group, therefore, is taken too rarely to have much significance in the biology of L.agilis. Unidentified larvae (Table 4.3) were probably mostly coleopterans. Notable prey items found were juvenile lizards (one certainly L.vivipara, two either L.vivipara or L.agilis) and large damselflies (> 30 mm).

(ii) Juveniles and young sub-adults

Few faecal samples from juveniles and young sub-adults were collected. The results from those which were analysed are shown in Table 4.4. Diptera and Araneae are the dominant groups in the diet of juveniles.

TABLE 4.4 THE PREY OF JUVENILE AND YOUNG SUB-ADULT L.agilis. FIGURES IN PARENTHESES ARE PERCENTAGES (BY NUMBER)

	JUVENILES	YOUNG SUB-ADULTS
Coleoptera		2 (7)
Araneae	10 (26)	13 (46)
Opiliones	2 (5)	-
Hymenoptera	-	1 (4)
Lepidoptera larvae	2 (5)	4 (14)
Diptera	15 (39)	3 (11)
Orthoptera	-	1 (4)
Heteroptera	2 (5)	-
Homoptera	4 (11)	1 (4)
Unidentified larvae	1 (3)	-
Isopoda	1 (3)	-
Chilopoda	-	1 (4)
Psocidae	1 (3)	-
TOTAL	38	26

(iii) Distasteful items

The only clear example of a distasteful prey type was worker ants. These were only very occasionally found in the faecal samples. Many observations were made both in the field and in captivity of individual lizards ignoring worker ants. Presumably they are not eaten because of their formic acid content. Queen ants, which do not contain formic acid, were taken.

Millipedes were also not eaten. Possibly they may also be distasteful. Lizards in captivity would not eat millipedes.

(iv) Seasonal and inter-site variation in prey

The most important trends in the seasonal and inter-site variation in the prey of L.agilis can now be summarised. At both the two heathland sites (Soldiers Road and Studland) the dominant prey group in the spring was weevils. Spiders and woodlice were also important. In the grass/scrub Railway habitat woodlice replace weevils as the dominant spring prey group. In the spring 1977 Railway samples taken from a larger area, including a heather dominated area, woodlice and weevils occurred in almost equal proportions.

From early June onwards, a greater range of prey seems to become available, and new prey groups, such as Opiliones, Hymenoptera, Orthoptera and Heteroptera, become important. Weevils and woodlice generally decline in importance but the proportions of spiders and larvae remain relatively constant throughout the year.

In the summer samples, it is more difficult to distinguish differences between the Railway and Soldiers

Road. Opiliones, Araneae and Hymenoptera appear more important at Soldiers Road, Carabidae, larvae, Isopoda and Orthoptera more important at the Railway (Figure 4.1). Large numbers of Diptera and bees were found in the September sample. This may have been caused by the flowering of the Calluna.

In the spring the pattern seems reasonably clear with woodlice or weevils being dominant depending on the habitat and spiders and larvae also being common. In the summer, however, a much greater variety of prey groups are potentially important, the particular groups which are taken most frequently probably varying greatly between sites and between years.

4.4 The prey of L.vivipara

The faecal samples which were analysed to provide a sample of the prey of L.vivipara were taken from lizards caught at the same sites as L.agilis. A total of 180 prey items were identified. Prey categories were distinguished in the same way as was done for L.agilis but no attempt was made to investigate seasonal or inter-site variation in prey.

The percentage by number of each prey group in the diet is shown in Figure 4.3 where it is compared with a similar histogram for L.agilis. Spiders were the dominant prey group (43.7%). Other important groups were larvae (13.2%), Diptera (11.5%) and Opiliones (9.8%). Species of spider identified from the faecal samples are listed in Appendix I. The most important were spiders of the genera Pardosa, Xysticus and Zora.

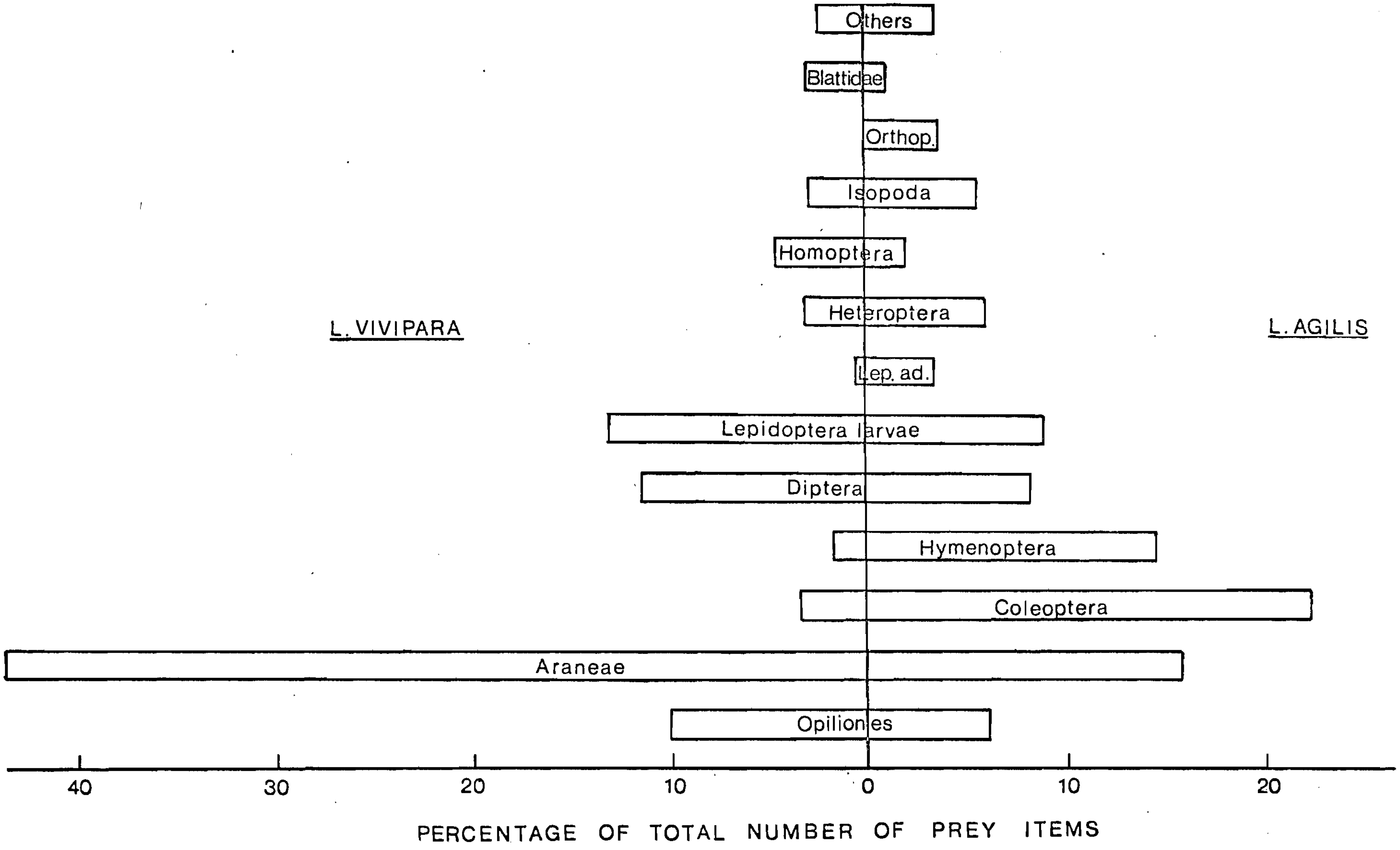

FIGURE 4.3 Comparison of the prey of L.agilis and L.vivipara (combined data for different sites and years).

There are several evident differences between the prey of L.vivipara and L.agilis (Figure 4.3). In particular, Coleoptera and Hymenoptera were important prey for L.agilis but not for L.vivipara. Araneae, larvae, Opiliones and Diptera were all taken by both species but more frequently by L.vivipara. Many of the species of spider identified were eaten by both species in particular species of Zora, Xysticus and Pardosa.

4.5 Prey size

(i) L.agilis

Frequency distributions of prey length for L.agilis for four different sampling periods are shown in Figure 4.4. The samples include adult and sub-adult lizards but not juveniles or young sub-adults.

The prey size distributions in Figure 4.4 show several consistent features. There is considerable variation in the length of prey eaten which varied from 3 to over 30 mm long, some items even being over 50 mm long. There was a definite lower limit to the size of prey taken, prey under 2 mm long not being taken and prey between 2 and 3 mm being taken only rarely. Peak abundances in these distributions occurred between 3 and 10 mm.

Prey length distributions at the different sites reflect differences in the types of food available. For example the peak at 9-10 mm at Soldiers Road (Figure 4.4) was caused by the queen ants in the diet. Despite these differences the mean prey length for each L.agilis distribution in Figure 4.4 is similar. Owing to the large

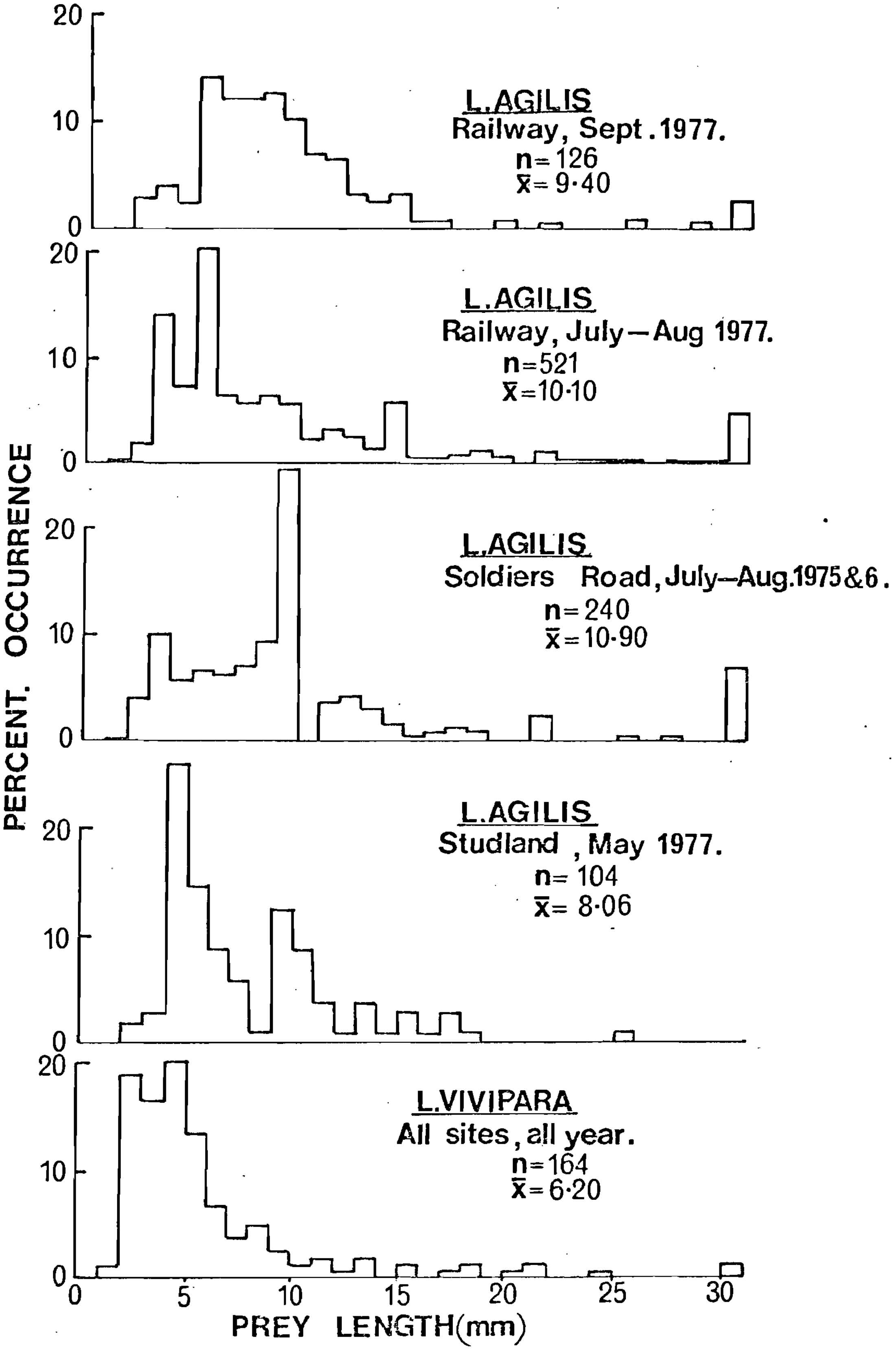

FIGURE 4.4 Frequency distributions of prey length for L.agilis at three sites and at different times of year, and comparison with L.vivipara.

sample sizes, the mean prey lengths could be compared using t-tests despite the deviation of each distribution from normality. The differences in mean prey length between the L. agilis distributions in Figure 4.4 were not significant.

Mean prey length for further sampling periods is shown in Table 5.9. This again shows the similarity in mean prey size for samples taken from different sites and at different times of year, although mean prey size for the spring samples is slightly less than for samples taken later in the year. Table 4.5 gives the mean length and the length of the smallest item taken by adults and sub-adults from some selected prey groups.

Figure 4.5 compares frequency distributions of prey length for males and females during one sampling period. The two distributions have a very similar shape; the mean prey length for males is only slightly greater than that for females and the difference was not significant.

The relationship between prey size and body size for L. agilis will now be considered. Comparatively few items eaten by juvenile L. agilis were identified and measured. The mean prey length for these items (5.1 mm, n = 37) was less than the values of mean prey length for adult and sub-adult lizards (Figure 4.7) but the means were not compared statistically because of the small sample size for juveniles. The largest prey items found in the faeces of juveniles were two larvae 13 mm long, a spider 9.5 mm long, and a dipteran 8.5 mm long.

Similarly, few items eaten by young sub-adults L. agilis were measured but it was clear that they also

TABLE 4.5 THE PREY SIZE OF ITEMS EATEN BY *L.agilis* FROM SELECTED PREY GROUPS FOR THREE SAMPLING PERIODS. (a) SOLDIERS ROAD 15TH JULY - 15TH AUGUST 1975 & 1976, (b) RAILWAY 15TH JULY - 15TH AUGUST 1977, (c) RAILWAY SEPTEMBER 1977. THE LENGTH OF THE SMALLEST ITEM (I) AND THE MEAN PREY LENGTH (II) ARE SHOWN. FIGURES IN PARENTHESES ARE THE SAMPLE SIZES

	Sampling period					
	(a)		(b)		(c)	
	(I) Smallest item (mm)	(II) Mean prey length (mm)	(I) Smallest item (mm)	(II) Mean prey length (mm)	(I) Smallest item (mm)	(II) Mean prey length (mm)
Ichneumonidae	4.0	6.2 (7)	4.0	8.5 (18)	-	-
Apoidea	9.8	12.8 (3)	5.9	11.7 (22)	6.2	10.8 (20)
Diptera	3.0	6.6 (7)	3.4	8.5 (47)	4.5	8.9 (35)
Lepidoptera larvae	3.9	36.9 (23)	4.4	27.3 (50)	9.9	23.1 (5)
Heteroptera	3.8	9.6 (35)	3.8	6.9 (18)	6.9	8.0 (5)

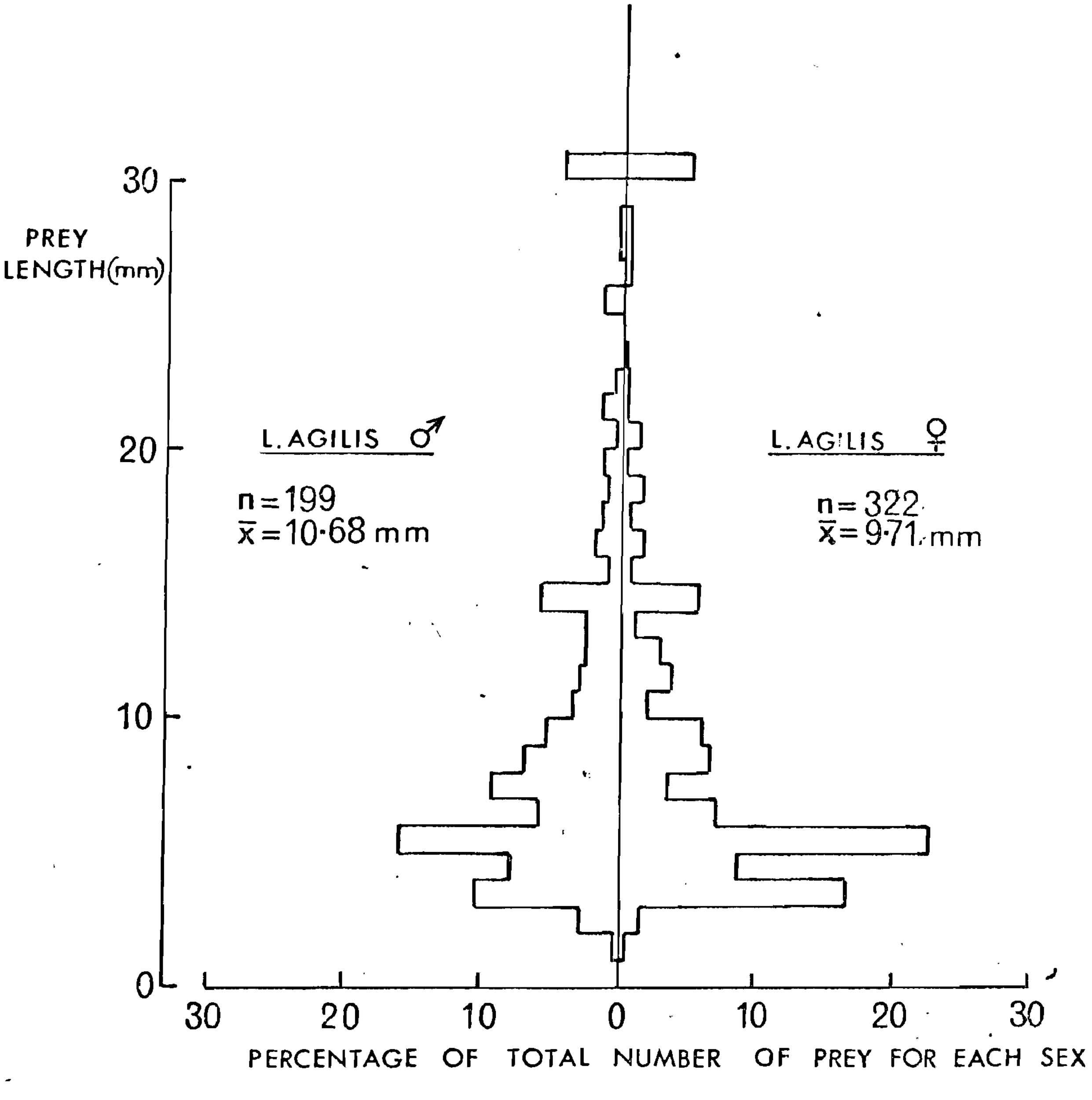

FIGURE 4.5 Frequency distributions of prey length (<u>L.agilis</u>). Comparison of males and females, Railway site, July - August 1977.

take smaller prey than adults. Mean prey length for young sub-adults was 6.4 mm (n = 31), only slightly greater than the value for juveniles. The largest item eaten was a larva 25 mm long.

Because of the similarity in mean prey length, the juvenile and young sub-adult samples were combined. Figure 4.6 compares the prey length frequency distribution of this combined sample with a sample of older sub-adults (caught between 15 July and 15 August). There are several differences. Prey 2-3 mm long is much commoner in the juvenile/young sub-adult sample, the peak at 4-5 mm is lower than that of the sub-adult sample and prey over 10 mm was rarer.

Sizes of the spiders eaten by juveniles and young sub-adults are shown in Table 4.7 so comparison can be made with the sizes eaten by adults (Table 4.6). Although the sample size for juveniles and young sub-adults was small they appear to take more spiders in the range 0-4 mm than adults. Juveniles are capable of taking large spiders (the largest found being 9.5 mm). The mean length of spiders eaten by juveniles was lower than that for adults.

The mean length of the Diptera eaten by juveniles was 4.8 mm (n = 15) compared with 8.9 mm for adults (Railway, September 1977 sample).

Frequency distributions of prey length for adults and sub-adults from the same sample are compared in Figure 4.7. The difference between the mean prey lengths is not significant and in general the two distributions are similar.

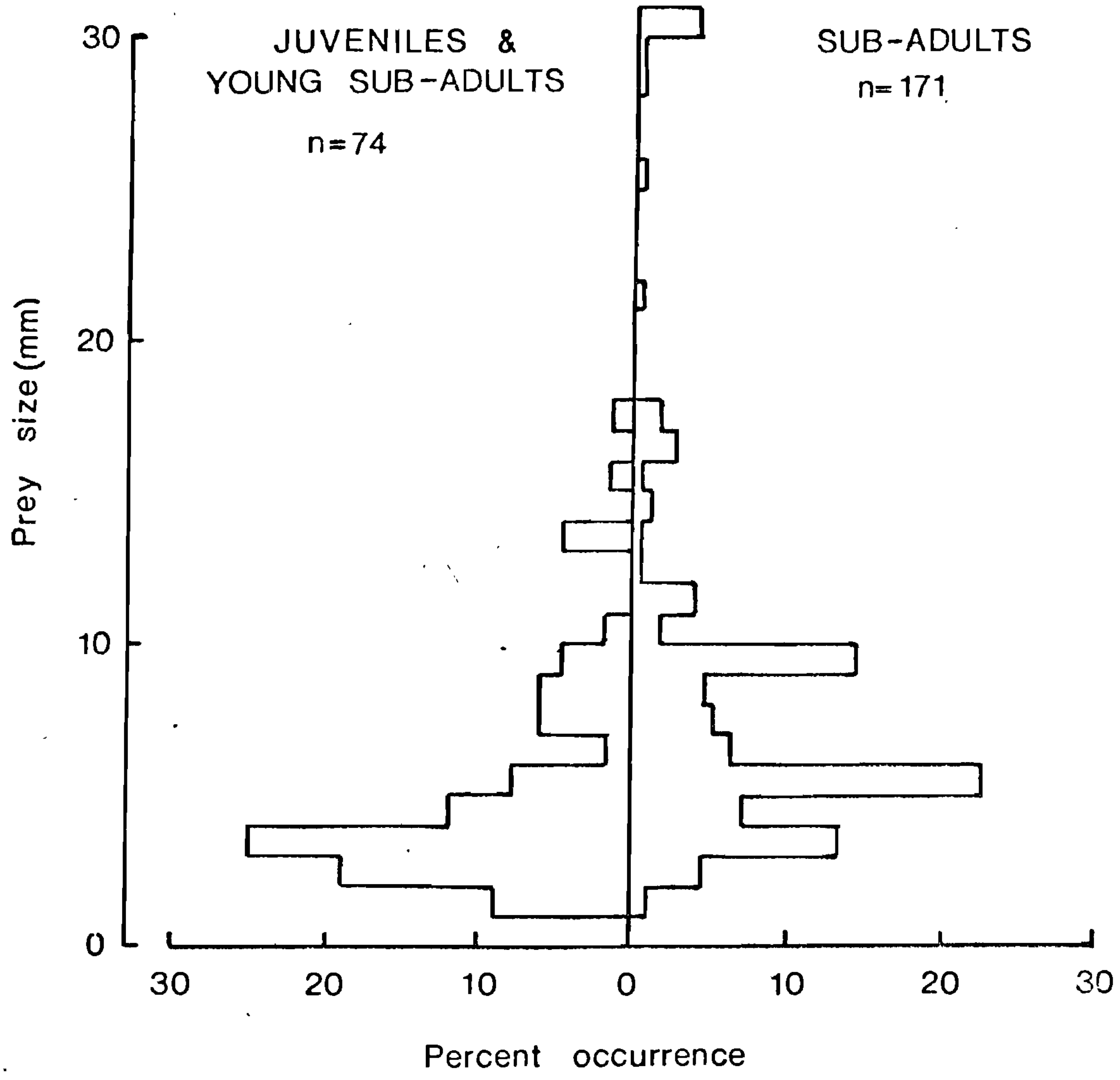

FIGURE 4.6 Frequency distributions of prey length (L.agilis). Comparison combined juvenile and young sub-adults samples with combined late summer samples of sub-adults.

TABLE 4.6 LENGTH OF SPIDERS EATEN BY L.agilis AT DIFFERENT SITES AND TIMES OF YEAR AND COMPARISON WITH L.vivipara. SITES AND SAMPLING PERIODS ARE (a) SOLDIERS ROAD APRIL, MAY 1976 AND STUDLAND MAY 1977, (b) RAILWAY APRIL, MAY 1976 AND 1977, (c) SOLDIERS ROAD MID-JULY - MID-AUGUST 1975 AND 1976, (d) RAILWAY JULY, AUGUST AND SEPTEMBER 1977, (e) L.vivipara, COMBINED DATA. FIGURES IN PARENTHESES ARE PERCENTAGES

	L.agilis				L.vivipara
	(a) Heathland spring	(b) Railway spring	(c) Heathland late summer	(d) Railway late summer	(e) All sites, all year
Under 2 mm	-	-	-	1 (0.9)	1 (1)
2-3 mm	1 (5)	2 (9)	1 (4)	8 (7)	9 (12)
3-4 mm	2 (11)	-	7 (27)	38 (33)	10 (14)
4-6 mm	10 (53)	10 (45)	13 (50)	51 (45)	38 (52)
Over 6 mm	6 (32)	10 (45)	5 (19)	16 (14)	15 (21)
TOTAL	19	22	26	114	73
Mean length mm	5.1	7.5	5.1	4.8	4.9

TABLE 4.7 LENGTH OF SPIDERS EATEN BY JUVENILE AND YOUNG SUB-ADULT *L.agilis*

	Juveniles	Young sub-adults
0-2 mm	2	-
2-3 mm	4	1
3-4 mm	1	6
4-6 mm	-	5
Over 6 mm	3	1
	n = 10	n = 13
	$\bar{x}$ = 4.2 mm	$\bar{x}$ = 4.1 mm

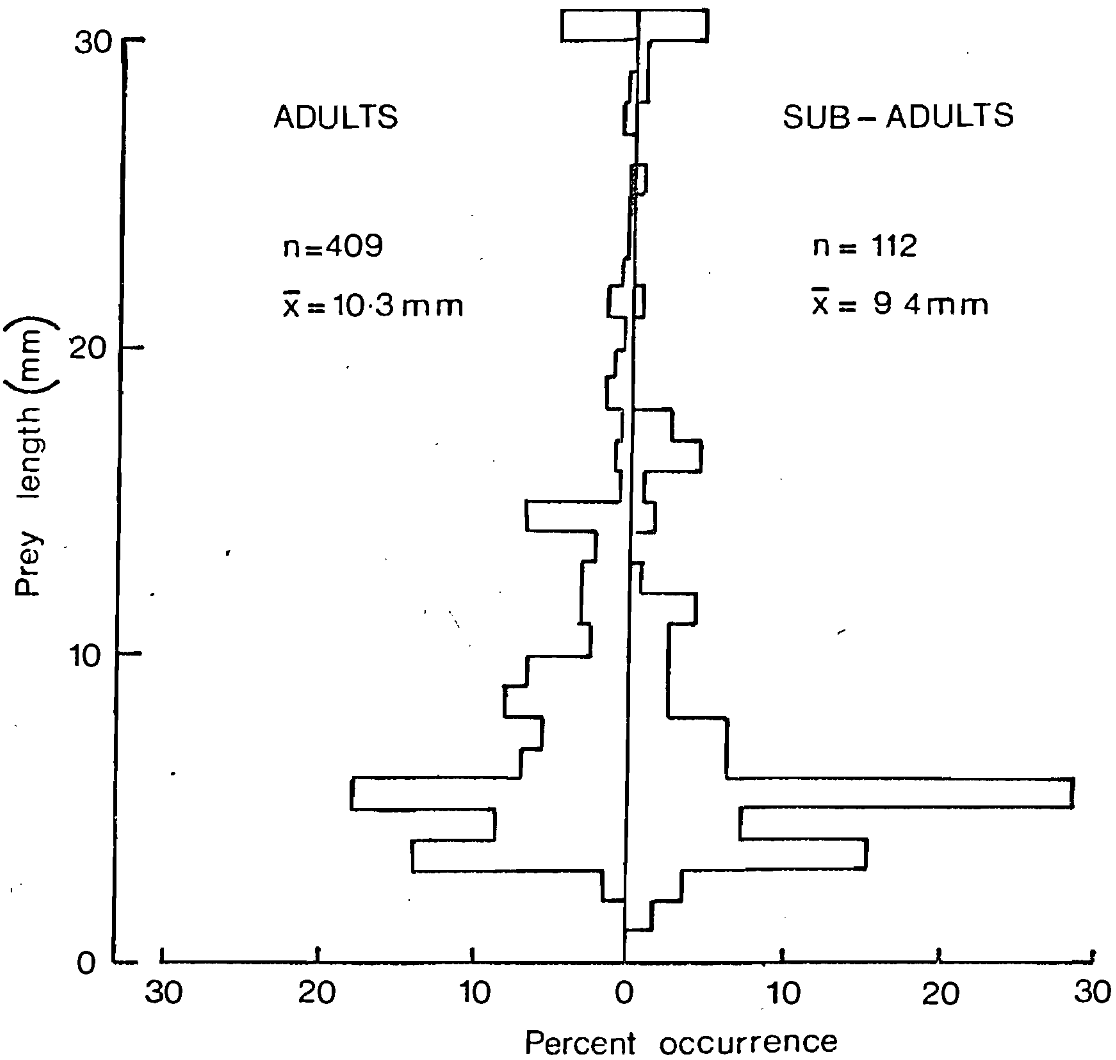

FIGURE 4.7 Frequency distributions of prey length (L.agilis). Comparison of adults and sub-adults, Railway site, July/August 1977.

To investigate the relationship between snout-vent length and prey length in more detail samples from different sites and years were combined and the mean prey length calculated for lizards in each S-V length group. There was an increase in mean prey length with S-V length but also, as the mean increased, there was a corresponding increase in the variance (Appendix IIIa). This effect is to be expected with the type of prey length distributions found, which are approximately log normal.

Because of the dependence of the variance on the mean the data were log transformed for formal statistical analysis. Mean prey length for the log data was then calculated for all individuals of a given snout-vent length. Data from different sites and years were again combined but some data for adults were not used because of the greater amount of data available for larger compared with smaller lizards. The results are shown in Figure 4.8 and Appendix IIIb.

The increase in mean prey length with snout-vent length is apparent but the relationship between the variance and mean has been eliminated. The data were subjected to an analysis of variance. Variations between snout-vent lengths were significant ($F_{32,980} = 4.83$, $p < 0.001$) but accounted for only 13.6% of the total variance in prey length. The majority of the total variance in prey length, therefore, is caused by variation in the length of prey eaten by individuals and between individuals of the same snout-vent length (note the large values for the variances in appendices).

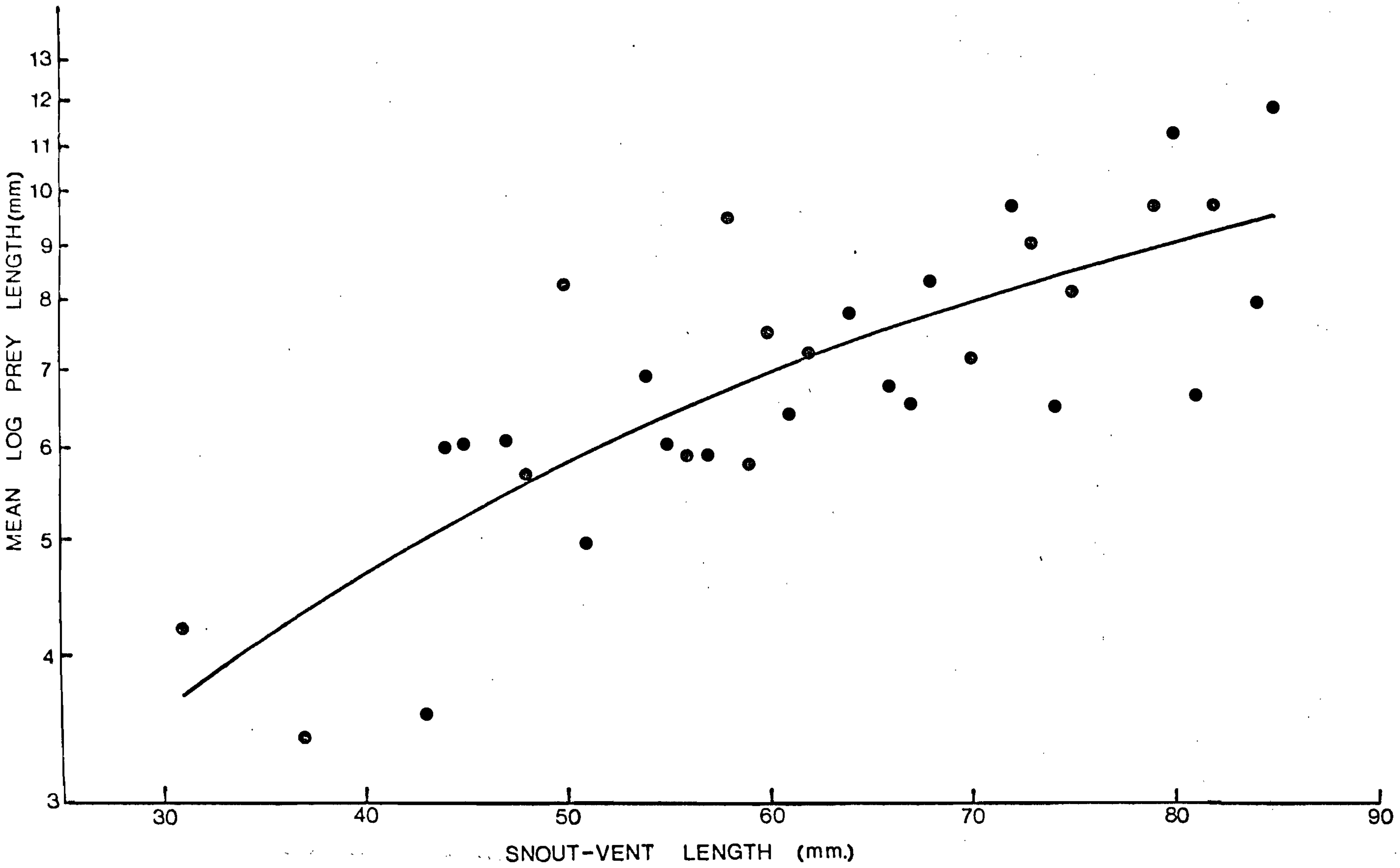

FIGURE 4.8 Regression of mean log prey size against snout-vent length for L.agilis. For further explanation see text (section 4.5(i)).

An asymptotic regression fitted by an iterative computer program through the points in Figure 4.8 gave the fit

$$P_L = 2.66 + 2.66\,(0.82^L) \qquad (n = 34,\ r = 0.80)$$

(where P_L = prey length and L = snout-vent length) which was highly significant ($p < 0.001$). Thus of the variations between snout-vent lengths (13.6% of total) 64% could be explained by this asymptotic regression.

A linear regression gave a slightly poorer fit to the data ($r = 0.79$).

(ii) L.vivipara

The frequency distribution of prey length for the total L.vivipara sample, undivided by sites or seasons, is shown in Figure 4.4 where it can be directly compared with the L.agilis distributions. Like L.agilis, L.vivipara takes prey of a broad range of sizes but there are several notable differences between the two species. Individuals of L.vivipara take many more of the smallest prey items than individuals of L.agilis, particularly items between 2 and 3 mm in length. The peak for the L.vivipara distribution at between 2 and 6 mm occurred at a smaller size than for the L.agilis distributions and far fewer items over 6 mm were taken.

The mean prey length for L.vivipara (Figure 4.4) was compared with the mean of each of the L.agilis distributions in Figure 4.4 using t tests. In each case the difference was significant ($p < 0.05$).

The sizes of the spiders taken by L.vivipara are shown in Table 4.6, and this size distribution is very similar to those for L.agilis. The mean lengths of the spiders eaten by the two species were not significantly different (5.2 mm *L.agilis*, 4.9 mm *L.vivipara*).

It was clearly shown for *L.agilis* that prey size was related to snout-vent length. Differences in prey size between the two species may therefore largely be related to differences in snout-vent length. The snout-vent length of the individuals of *L.vivipara* from which faecal samples were taken ranged between 38 and 69 mm, (i.e. ranging from a small sub-adult *L.agilis* to a small adult *L.agilis*). To investigate the effect of snout-vent length differences between the species on prey size the relationship between snout-vent length and prey size was analysed for *L.vivipara* in the same way as for *L.agilis*.

The mean prey length together with the variance and sample size for the log transformed data are shown in Appendix IIIc. Variations between snout-vent lengths were significant ($F_{16,133} = 2.96$, $p < 0.01$) and accounted for 26.2% of the total variance in prey size, approximately twice as much as for *L.agilis*. A linear regression gave the fit

$$P_L = 0.033L - 0.22 \quad (n = \textcircled{17},\ r = 0.86) \quad \text{(Figure 4.9)}$$

(where P_L = prey length and L = snout-vent length) which was highly significant ($p < 0.001$).

Thus despite the incompleteness of the data for *L.vivipara* compared with that for *L.agilis*, a strong relationship between snout-vent length and prey size can again be demonstrated.

Comparison of the two regression lines for *L.vivipara* and *L.agilis* (Figure 4.9) shows that for a given snout-vent length individuals of *L.vivipara* on

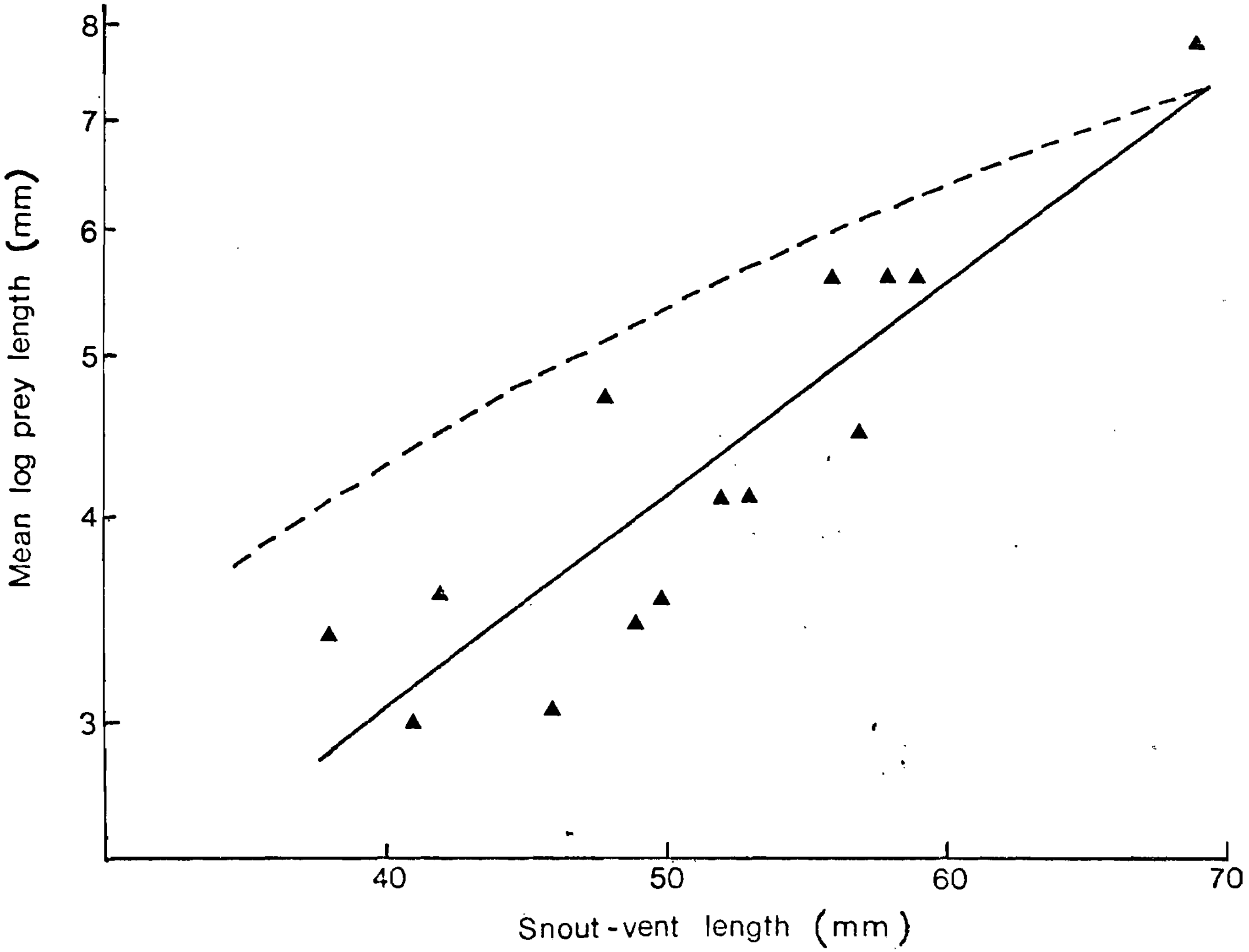

FIGURE 4.9 Regression of mean log prey size against snout-vent length for L.vivipara (triangles and solid line). The dotted line is the regression line for L.agilis as shown in Figure 4.8.

average select smaller prey than individuals of *L.agilis*. This difference narrows and eventually disappears, however, as the size of individuals increases, although this trend should perhaps be considered cautiously in view of the limited data available for *L.vivipara*.

This difference in prey size selection between individuals of the two species of the same snout-vent length may perhaps be partly explained by differences in head size. Figure 4.10 shows regressions of head width against snout-vent length for both sexes of each species. The four regression equations were

L.vivipara males $W = 0.008L + 0.11$ $(n=21,\ r=0.89)$ (4.1)
females $W = 0.004L + 0.24$ $(n=20,\ r=0.88)$ (4.2)
L.agilis males $W = 0.009L + 0.13$ $(n=89,\ r=0.95)$ (4.3)
females $W = 0.007L + 0.22$ $(n=67,\ r=0.97)$ (4.4)

where W is the head width in mm, L the snout-vent length in mm.

For both species males have relatively broader heads than females. The equations for *L.vivipara* males and *L.agilis* females are similar. Consequently if prey were selected on the basis of head width rather than snout-vent length it would be expected that individuals of *L.vivipara* would take smaller prey than individuals of *L.agilis* of the same snout-vent length.

The difference in relative head width seems sufficient to explain the difference in prey size; an individual of *L.vivipara* 60 mm in snout-vent length has on average the same head width as an individual of *L.agilis* 51 mm in length. Individuals of these two lengths also select prey of approximately the same mean

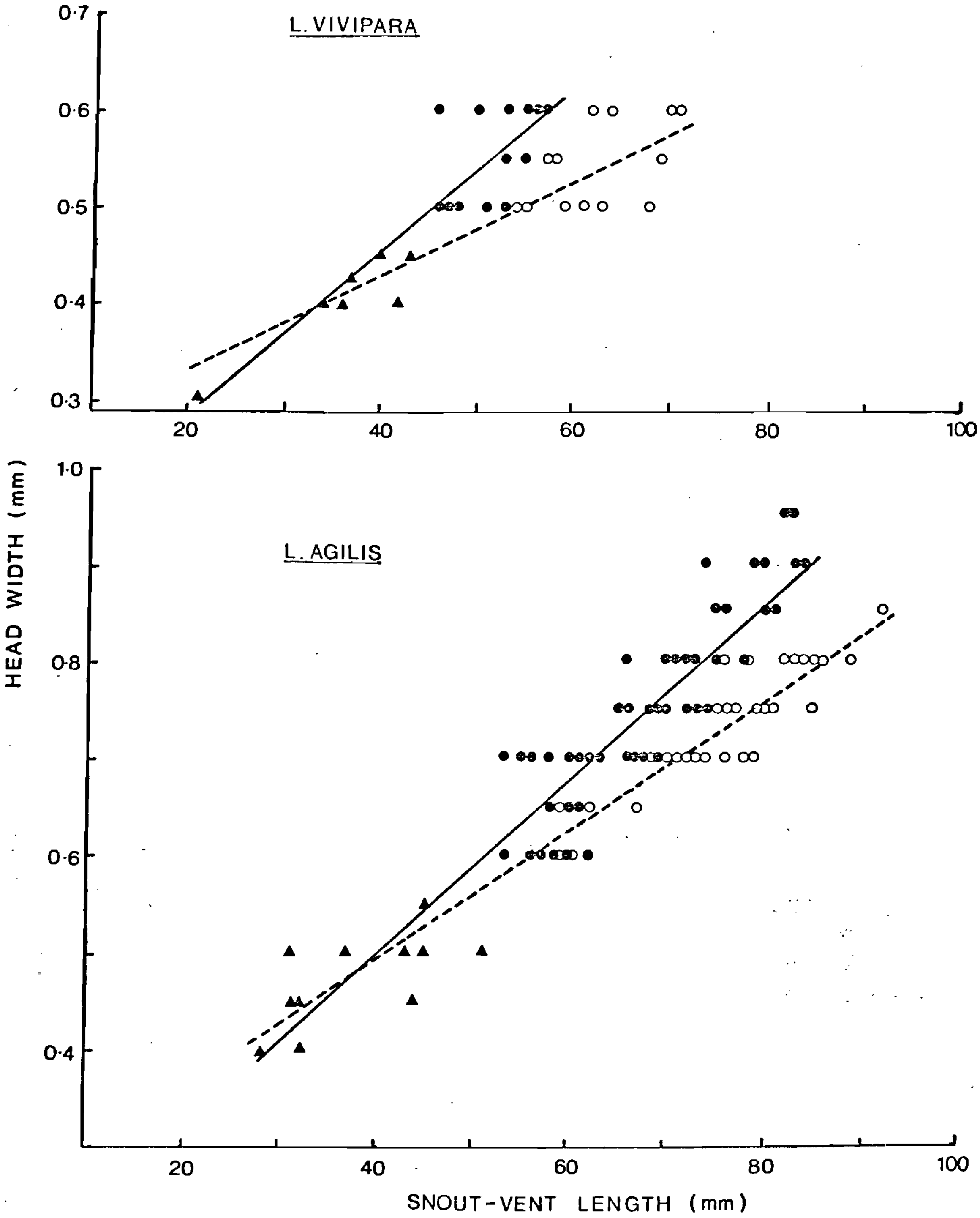

FIGURE 4.10 Regressions of head width against snout-vent length for L.vivipara (top) and L.agilis. Closed circles males, open circles females, triangles juveniles.

size (Figure 4.9). The difference in head width between the two species, however, remains relatively constant with increasing snout-vent length and so does not explain the narrowing of the prey size difference between the two species with increasing snout-vent length.

Overlap in prey length between different age classes of L.agilis and the combined L.vivipara sample is shown in Table 4.8. Overlap between the two species was greatest between juvenile L.agilis and L.vivipara and decreased as individuals of L.agilis increased in size.

4.6 Prey hardness

Prey hardness frequency distributions for L.agilis at different sites and times of year are shown in Figure 4.11. All the samples demonstrate that individuals of L.agilis commonly select prey from all of the three hardness categories although the differences in the distributions between samples reflect the different types of prey available.

Figure 4.12 compares frequency distributions of prey hardness for different age/size classes of L.agilis. Juvenile lizards take prey predominantly from the softest category; progressively more prey is taken from the harder categories as the size of individuals increases.

In marked contrast to L.agilis, individuals of L.vivipara take prey almost exclusively from the softest category (Figure 4.11). Moreover there is no apparent tendency for larger individuals to take more prey from harder categories than smaller individuals. This is

TABLE 4.8 PERCENTAGE OVERLAP BETWEEN L.vivipara AND DIFFERENT AGE CLASSES OF L.agilis ALONG TWO RESOURCE DIMENSIONS, PREY SIZE AND PREY HARDNESS. FOR FURTHER EXPLANATION SEE TEXT.

PREY SIZE

		(I)	(II)	(III)	(IV)
(I)	L.vivipara				
(II)	L.agilis; juveniles & young sub-adults	78			
(III)	L.agilis; sub-adults	69	60		
(IV)	L.agilis; adults	64	57	84	

PREY HARDNESS

		(I)	(II)	(III)	(IV)
(I)	L.vivipara				
(II)	L.agilis; juveniles & young sub-adults	95			
(III)	L.agilis; sub-adults	76	71		
(IV)	L.agilis; adults	59	54	77	

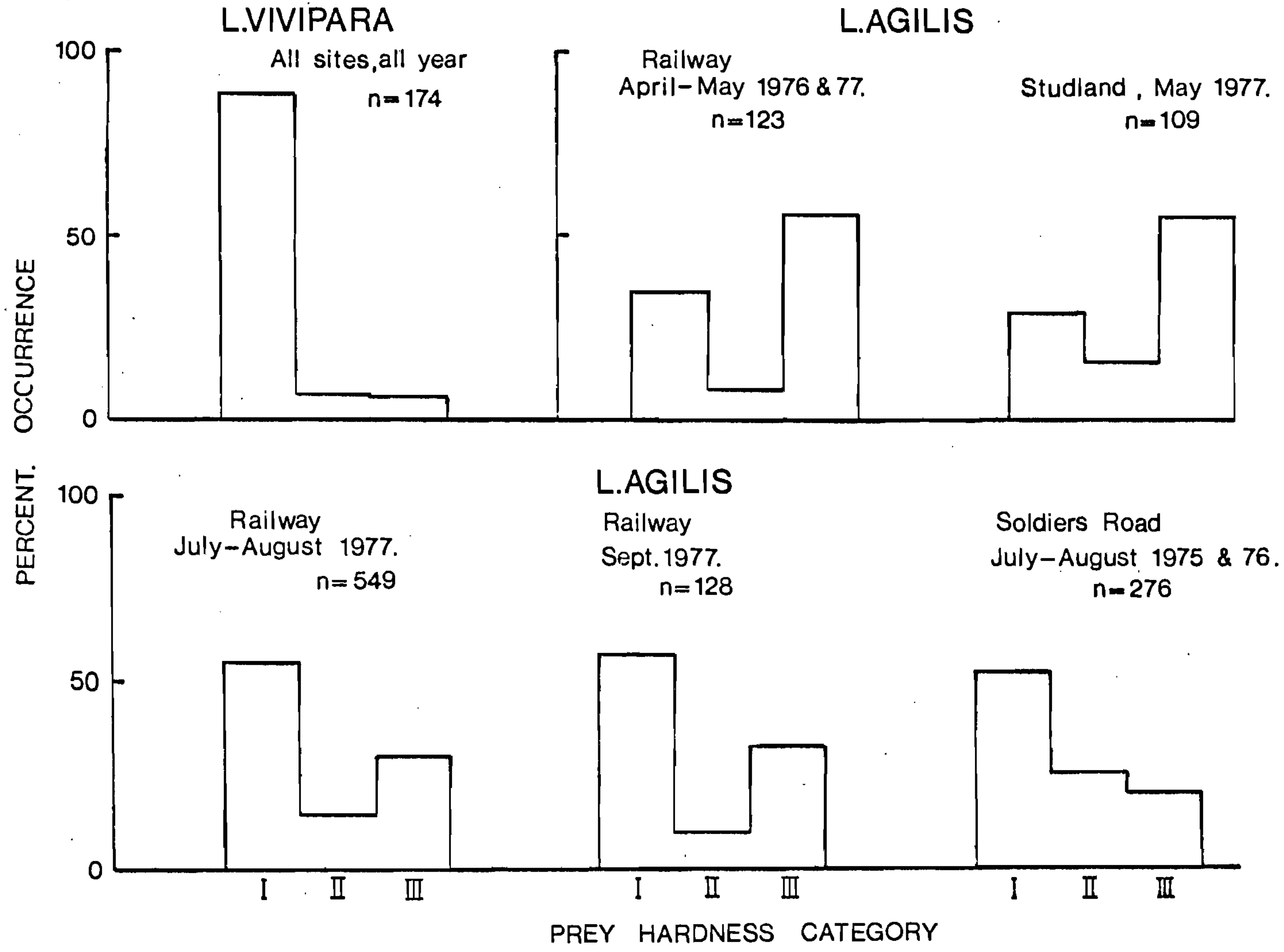

FIGURE 4.11 Frequency distributions of prey hardness categories for L.agilis at different sites and times of year and comparison with L.vivipara. For explanation of prey hardness categories see text (section 4.2(iii)).

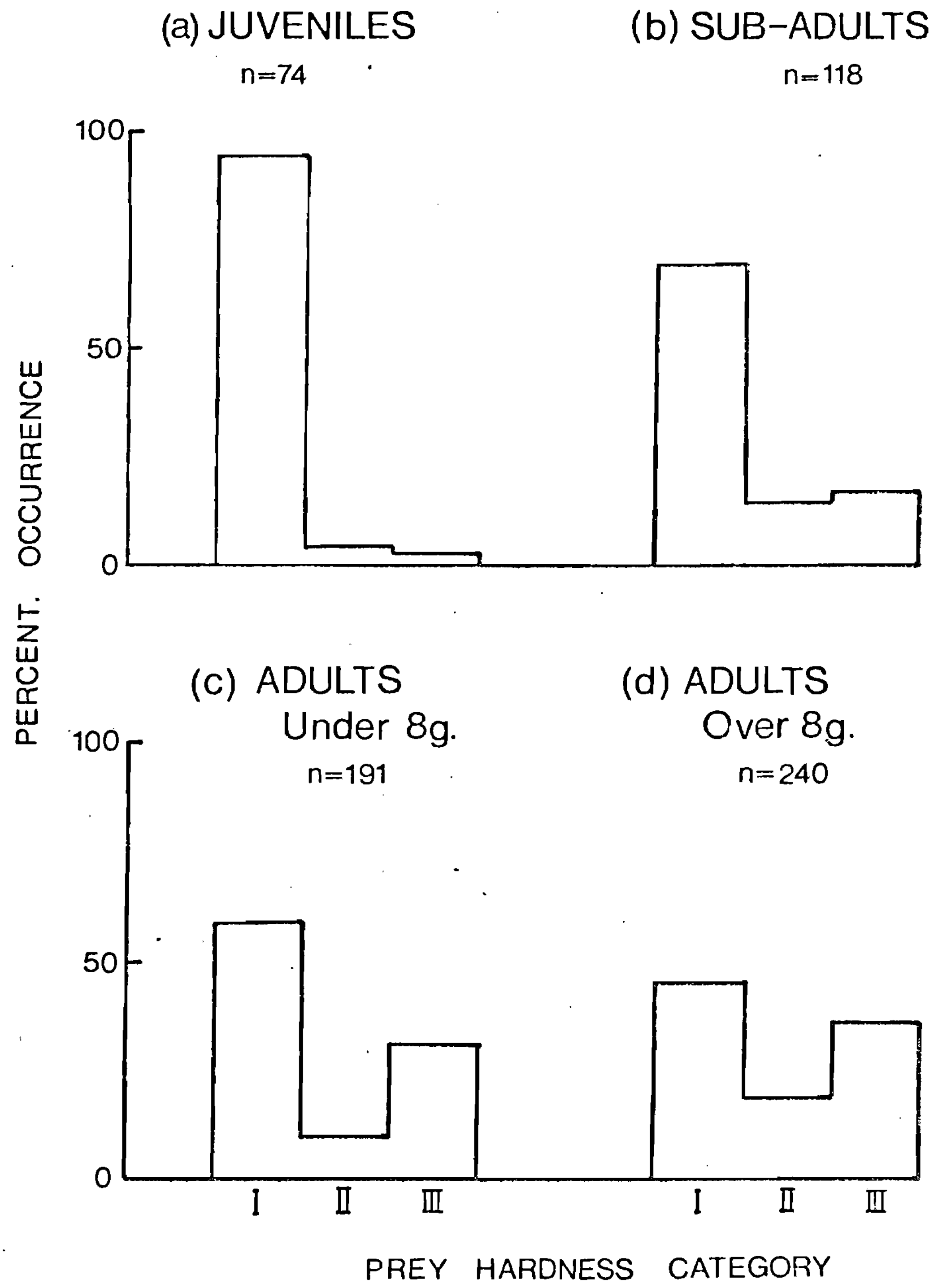

FIGURE 4.12 Frequency distributions of prey hardness for different size classes of L.agilis. (a) is the combined juvenile and young sub-adult sample, (b), (c) and (d) are sub-samples of the Railway site July/August 1977 sample.

demonstrated in Figure 4.13 where prey hardness frequency distributions of four different snout-vent length classes of *L.vivipara* are compared. Similar histograms for *L.agilis* in Figure 4.13 show a marked increase in the number of prey in categories II and III with increasing snout-vent length. It is also apparent that individuals of *L.agilis* take harder prey than individuals of *L.vivipara* of the same snout-vent length and this difference increases with increasing snout-vent length. The difference in relative head width between the species, such that an individual of *L.agilis* has the same head width as an individual of *L.vivipara* approximately 9 mm longer (equations 4.1 to 4.4) (P.58), is insufficient to explain the prey hardness difference in Figure 4.13.

As a result of the increase in the prey taken from categories II and III by individuals of *L.agilis* as they increase in size, the degree of overlap for prey hardness between the two species is greatest between *L.agilis* juveniles and *L.vivipara* (total sample) and is progressively smaller between *L.vivipara* and the larger size classes of *L.agilis* (Table 4.8).

The mean prey length for items taken by adult *L.agilis* from each prey hardness category is given below.

Group I $\bar{x} = 9.96$ mm $s = 10.2$ $n = 351$
II $\bar{x} = 7.57$ mm $s = 2.6$ $n = 190$
III $\bar{x} = 9.11$ mm $s = 3.9$ $n = 231$.

Thus it is not possible to explain the observed prey hardness differences in terms of prey size; prey size and prey hardness appear to be relatively independent.

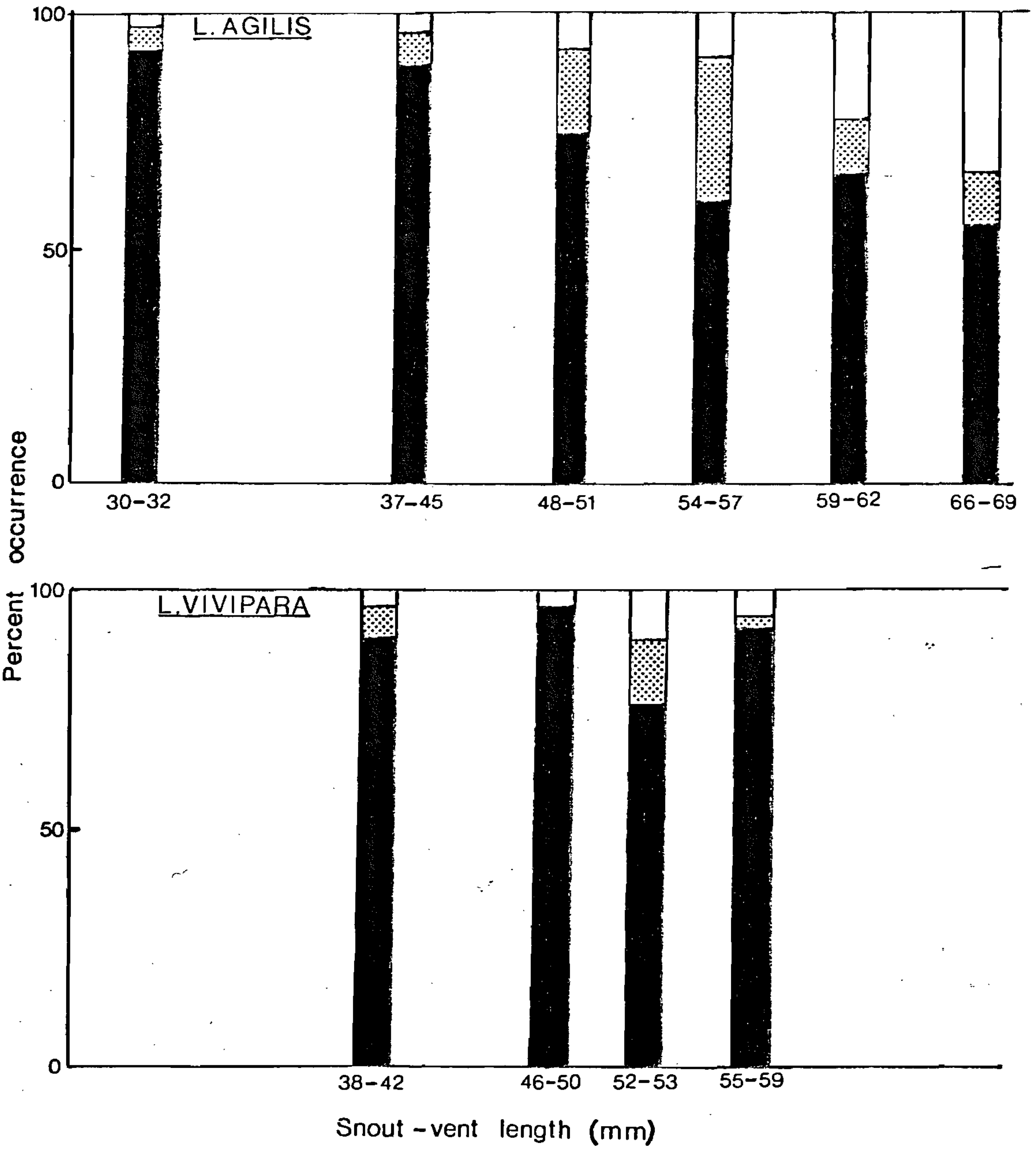

FIGURE 4.13 Frequency distributions of prey hardness for different snout-vent length classes of L.agilis and L.vivipara. Heavy shading category I; light shading category II; unshaded category III.

4.7 Variation between individual faecal samples (L.agilis)

(i) Differences in prey selection between individuals

The investigation pursued in this section was initiated by observations made on individual faecal samples. It was noticed that there was considerable variation between individual samples, even between those taken from different lizards within the same area on the same day. Moreover, some types of prey whilst uncommon in the diet as a whole and in the diet during the particular sampling period in question, sometimes occurred in surprisingly large numbers in individual samples. It can be seen that the individual samples listed in Appendix IV often contained several specimens of the same prey type and that these were not always common prey items in the diet generally. For example staphylinid beetles accounted for only 1.8% of the total number of prey items identified and only 3.6% of the prey during the July/August 1977 sampling period (Table 4.9). Yet one sample taken during this period contained seven staphylinids (out of 18 prey identified) and another five (out of 20). This and other examples of the same phenomenon are given in Table 4.9. The probabilities of these occurrences in the last column of Table 4.9 were calculated by assuming that the probability of the particular prey type (type i) being eaten is given by its proportion in the diet during the sample period. The probability of a certain number of items in any one sample being of type i is then given by the relevant term in the binomial expansion

$$P = \frac{n!}{n_i!\,(n-n_i)!}\, p_i^{\,n_i}\,(1-p_i)^{n-n_i}$$

TABLE 4.9 THE OCCURRENCE OF SOME PREY GROUPS WHICH ARE RARE IN THE DIET OF *L.agilis*, IN SELECTED INDIVIDUAL FAECAL SAMPLES

	Total number identified & percent occurrence			Occurrence in selected individual samples		Probability of this occurrence
Prey category	(all samples)	Sampling period	No. identified & % occurrence in sampling period	No. of items of particular prey type	Total number of prey items in sample	
Staphylinidae	27 (1.8)	Railway July-Aug 1977	20 (3.6)	7 5	18 20	1.7×10^{-6} 5.4×10^{-4}
Coccinellidae (Ladybirds)	10 (0.7)	Railway July-Aug 1977	7 (1.3)	7	19	2.2×10^{-9}
Calomicrus circumfusus (Coleoptera)	20 (1.4)	Railway July-Aug 1977	18 (3.3)	14	42	3.3×10^{-11}
Cantharidae (Sailor beetles)	8 (0.5)	Soldiers Road July-Aug 1975	8 (3.7)	4 3	13 7	9.6×10^{-4} 1.5×10^{-3}
Symphyta (Sawflies)	8 (0.5)	Railway July-Aug 1977	3 (0.5)	3	23	2.6×10^{-4}
Tipulidae (Craneflies)	7 (0.5)	Studland May 1977	4 (3.7)	4	7	5.7×10^{-5}
Alydus calcaratus (Heteroptera)	9 (0.6)	Soldiers Road July-Aug 1976	7 (12.1)	5	9	1.9×10^{-3}

where n = the total number of items identified in the sample

n_i = the number of items of type i in the sample

p_i = the probability of type i occurring.

The extremely low probabilities in Table 4.9 show that in the examples selected, the occurrence of different items of the same type in one sample is not independent.

To investigate further this aspect of prey selection a slightly more sophisticated version of the same technique was used. It was again assumed that the probability of an individual consuming a particular prey type was given by the proportion of that prey type in the diet during the sample period. It would not then be expected that each sample would contain this proportion of the prey but that the proportion in different samples would follow the binomial distribution. Deviations from the binomial can be tested using the chi^2 statistic. It was not possible to treat prey which was rare in this way because the method is unreliable when the probability of the particular prey type being eaten is low. Chi^2 was therefore calculated for the commoner prey groups during several sampling periods and the results are shown in Table 4.10.

For many of the prey types there was a significant departure from the binomial. Eleven out of twenty-one tests were significant at the 5% level. The departure from the binomial was always such that there were more samples with high numbers and more with low numbers of the prey type than expected. In other words, prey of a particular type was aggregated in a few samples.

Thus for many prey types the occurrence of different

TABLE 4.10 TESTS FOR THE AGGREGATION OF ITEMS FROM PARTICULAR PREY TYPES IN INDIVIDUAL FAECAL SAMPLES. THE TABLE SHOWS CHI^2 TESTS FOR THE DEPARTURE OF THE DISTRIBUTION OF DIFFERENT PREY TYPES IN DIFFERENT FAECAL SAMPLES FROM THE EXPECTED BINOMIAL DISTRIBUTION, DURING INDIVIDUAL SAMPLING PERIODS. FOR FURTHER EXPLANATION SEE TEXT.

Site and sample period	No. of faecal samples (N)	Prey group	Percentage occurrence during sample period	Chi^2	Expected Chi$^2_{0.05}$ with (N-1) degrees of freedom & level of significance
Soldiers Road July 23-August 13, 1975	27	Opiliones	17.6	35.3	38.9 not sig.
		Araneae	13.0	32.2	" " "
		Pentatomidae	9.0	50.5	" sig $p < 0.01$
Soldiers Road July 28-August 3, 1975	12	Formicidae (queens)	33.6	54.9	19.7 sig $p < 0.001$
Railway April & May 1976	11	Isopoda	36.4	6.8	18.3 not sig.
		Araneae	16.7	8.1	" " "
		Lepidoptera larvae	15.2	15.6	" " "
		Carabidae	10.6	19.0	" sig $p < 0.05$
Soldiers Road April & May 1976	8	Curculionidae	42.6	31.6	14.1 sig $p < 0.001$
		Isopoda	14.8	20.6	" sig $p < 0.01$
		Araneae	14.8	6.6	" not sig.
Studland May 18-24, 1977	14	Curculionidae	36.7	20.9	22.4 not sig.
		Isopoda	14.7	25.4	" sig $p < 0.05$
		Araneae	14.7	21.3	" not sig.
Railway July 15-August 15, 1977	39	Curculionidae	12.4	84.4	55.8 sig $p < 0.001$
		Araneae	18.0	68.0	" sig $p < 0.005$
		Diptera	9.5	63.7	" sig $p < 0.01$
		Lepidoptera larvae	9.3	54.8	" not sig.
Railway September 9-15, 1977	8	Araneae	13.3	6.7	14.1 not sig.
		Diptera	27.3	20.7	" sig $p < 0.005$
		Apoidea	15.6	19.3	" sig $p < 0.01$

items of the same type in one sample is not independent; the occurrence of one item increases the probability of another occurring. This can happen both for some prey types that are common in the diet and for some rare types. The effect is sometimes a very strong one, judging by some of the extremely low probabilities in Table 4.9.

(ii) Associations between different prey groups

A further aspect of prey selection is the relationship between different prey groups within individual faecal samples. This aspect was initially investigated by using the chi^2 statistic in a similar way to the previous analysis. Chi^2 values were calculated for the combined occurrence of two prey groups within individual samples during a single sampling period. The results are shown in Table 4.11. A notable rise or fall in chi^2 compared with the chi^2 value for each separate prey group occurred in several cases. A rise would be expected if the prey from the two groups tended to occur together in the same faecal samples, and a fall if the two groups tended to occur in different samples. However, since no way was known of testing the significance of these changes in chi^2 an alternative method was used.

Spearman's rank correlation coefficient was calculated between pairs of prey groups. For each prey group during one sample period individual faecal samples were ranked according to the proportional occurrence of that particular prey. In faecal samples where the prey group did not occur, samples with a larger number of total identified prey items were ranked below those with a smaller number. Two of the correlations were significant at the 5% level (Table 4.11). There were positive

TABLE 4.11 ASSOCIATIONS BETWEEN PREY GROUPS IN THE DIET OF *L.agilis*. FOR FURTHER EXPLANATION SEE TEXT

Sampling period	Prey group pair	Individual chi^2 values	Combined chi^2	Spearman rank correlation coefficient
Late summer 1975	Araneae	35.3	59.5	+0.55*
	Opiliones	32.2		
"	Shield bugs (Pentatomidae & Alydidae)	50.2	39.2	-0.06
	Araneae	35.3		
"	Shield bugs	50.2	32.6	-0.35*
	Opiliones	32.2		
"	Hymenoptera (excluding Formicidae) & Diptera	38.5	30.0	-0.30
	Araneae	35.3		
"	Hymenoptera & Diptera	38.5	38.2	-0.19
	Opiliones	32.2		
"	Hymenoptera & Diptera	38.5	55.4	+0.08
	Shield bugs	50.2		
Early summer 1976	Araneae	9.0	15.5	+0.30
	Opiliones	9.1		

* Denotes value significant at the 5% level.

correlations between Araneae and Opiliones in both the sampling periods investigated but one correlation was not significant.

In general, the rank correlations are in agreement with what might be expected from the changes in chi^2. In the previous section it was found that the occurrence of one item of a particular type in a faecal sample may often increase the probability of another item of the same type occurring. It also seems that it may affect the probability of other items of different types occurring.

4.8 The prey of L.agilis and L.vivipara in relation to microhabitat utilization

The distinct dietary differences found between the two lizard species seem to be determined largely by differences in selection for prey size and hardness. Another possible cause of differences in diet is exposure to different prey owing to differences in microhabitat utilization between the two species.

In practice it is difficult to make direct observations of microhabitat utilization of the two species because individuals forage predominantly beneath and within dense vegetation. For these two species, therefore, examination of their diets is a useful way to investigate possible microhabitat differences.

One possible microhabitat difference is the degree to which each species uses the ground as opposed to the vegetation above ground. Individuals of _L.agilis_ commonly eat both prey which occurs predominantly on the ground

(Carabidae, Staphylinidae, Araneae (Pardosa sp.), Isopoda) and prey which occurs predominantly in the vegetation (Curculionidae, Pentatomidae). Similarly individuals of L.vivipara eat both predominantly ground-living prey (Araneae (Pardosa sp.)) and prey living predominantly in the vegetation (Homoptera). The few casual observations made on foraging individuals of both species also showed that both species foraged on the ground and in the vegetation. This was observed both in Calluna and gorse (Ulex europaeus).

In order to investigate possible microhabitat differences by examining dietary differences, it is necessary to choose a prey group in which prey selection for other reasons, such as size or hardness, differs little between the two lizard species. The spiders are an ideal group for the purpose. They were eaten frequently by both lizard species, both species could eat the largest spiders available and the size distribution of the spiders taken by the two lizard species was very similar (Table 4.6).

The species of spider identified were divided into four classes by Dr P. Merrett.

The four classes were

I Species entirely ground-living
II Species mostly ground-living
III Species living mostly above ground in the vegetation
IV Species living entirely above ground.

All the species of spider eaten (Appendix I) were placed into one of these four categories and the result is shown in Figure 4.14. Whilst both lizard species eat the ground-living prey species, L.vivipara eat fewer

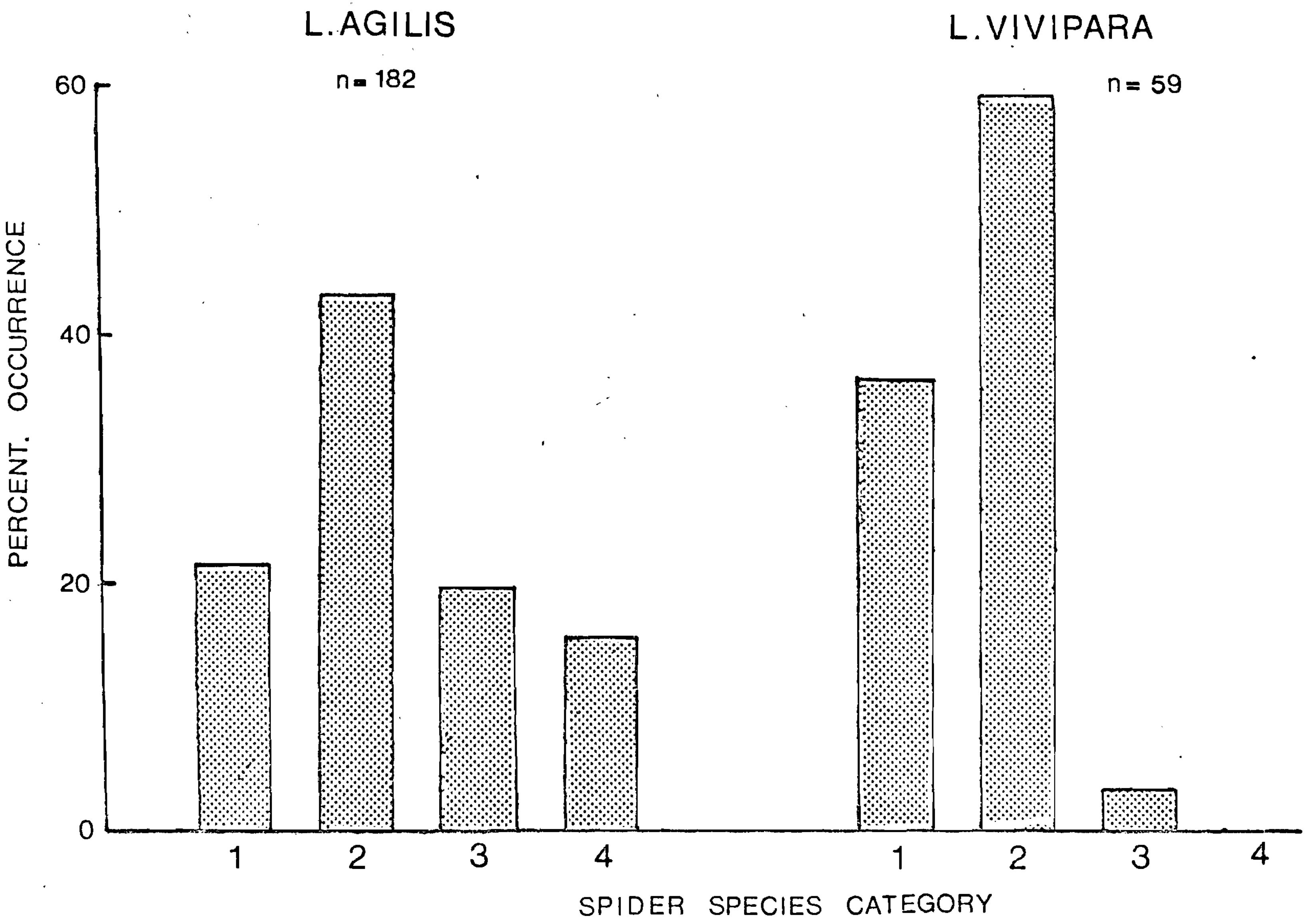

FIGURE 4.14 Comparison of frequency distributions of spider species categories in the diets of L.agilis and L.vivipara. For explanation of the spider species categories see text (section 4.8).

spiders living above ground.

This result is slightly surprising because of the fact that L.vivipara is considered more agile and a better climber than L.agilis (Smith 1951), and the greater weight of L.agilis suggests that L.vivipara is better adapted for foraging in vegetation compared with L.agilis.

4.9 Discussion

(i) Methodology of faecal analysis

The diets of L.agilis and L.vivipara have been investigated and compared by faecal analysis and many of the conclusions reached are obviously dependent on the method not being subject to any large sources of bias.

One possible source of bias is that some prey groups may not leave any detectable remains in the faecal samples. For example, Bibby (1977) thought that Collembola were probably not detectable in the faecal samples of the Dartford Warbler (Sylvia undata) and since Collembola were not found in the lizard faeces the same conclusion may be applicable. However, most Collembola were probably too small to be important prey in the diet of the lizards.

Upon consideration of the wide variety of different types of prey which did leave readily identifiable remains in the faecal samples it seems unlikely that any important prey groups would be completely undetectable in the samples. Perhaps a more important source of bias may have been that caused by differences in conspicuousness between different prey groups in the remains. Bibby (1977) found that the number of beetles in the diet of the Dartford Warbler was overestimated compared with the number of spiders for this reason. However prey was probably less well preserved in the Dartford Warbler faeces than in the lizard faeces; Bibby counted spiders from matching pairs of chelicerae, whereas the more fragile carapaces and genitalia were also frequently found intact in the lizard faeces. With more parts available for identification there is less chance that the number of spiders taken will be underestimated.

Faecal analysis should obviously not be considered an absolutely exact method but it probably gave reasonable estimates of the proportions of the different prey groups in the diet of the lizards.

(ii) The prey of L.agilis in relation to the invertebrate fauna of the habitat

Both seasonal and inter-site variation in the prey of L.agilis has been identified. How far can these variations be related to known changes in the abundance of different invertebrate groups?

The only comprehensive account of the changes in the abundance of invertebrates on Dorset heathland is that of Bibby (1977) although other studies have considered separate invertebrate groups. This study concerned the food of the Dartford Warbler (Sylvia undata) and two sampling methods were used, a D-vac suction net and pitfall traps.

These results are applicable only to the Soldiers Road data. Even here, however, the comparison should be made with caution bearing in mind that there were probably differences between the heathland of the Soldiers Road site and that of Bibby's sites. The results obtained by Bibby should be taken as indicating broad trends in the changes of abundance of invertebrates in a heathland habitat.

The occurrence of several prey groups in the diet (Hymenoptera, Opiliones, Heteroptera, Orthoptera) increased during the year. Of these groups, the large Hymenoptera taken by L.agilis were not adequately sampled by either pitfall traps or the suction net. The heathland Orthoptera overwinter as eggs and become adult in late summer, so it appears that individuals of L.agilis take the larger, more active adults rather than the smaller nymphs. Also for reasons relating to their life histories, the numbers of Opiliones and Heteroptera would be expected to increase during the year and Bibby (1977) found late summer peaks in the numbers of harvestmen in pitfall traps and the biomass of Heteroptera in the D-vac suction net.

Two prey groups, woodlice and weevils, were taken more frequently in the spring than at other times of year. There is no evidence of a corresponding peak in the abundance of these groups in the habitat although possibly woodlice may be more active during the cooler, damper days of spring. Both groups, however, may have been taken in large numbers at this time of year because there was little alternative prey available. Numbers of invertebrates in heather in the spring are low compared with a late summer peak (Bibby 1977).

Two prey groups, spiders and lepidopteran larvae, showed little seasonal variation in their proportion in the diet. Merrett (1967, 1968 and 1969) and Bibby (1977) have both found that, owing to the great variety of species, large numbers of spiders are present on heathland throughout the season. Nevertheless, Bibby (1977) did find some seasonal variation. There was a peak in the biomass in the D-vac in August and September and the high proportion of spiders in the diet of juveniles may reflect this, but this remains uncertain because of the small sample size for juveniles. There was also a peak in May and June of spiders over 4 mm caught in pitfall traps. This may be related to the early summer peak at Soldiers Road.

Although the species of spiders eaten were generally common heathland species, the relative numbers of the different species in the diet often do not show a good correspondence with the numbers caught in pitfall traps by Merrett (1967, 1968 and 1969). There are therefore large differences between the ways that pitfall traps and lizards sample the spider fauna.

The peak period of abundance of lepidopteran larvae on heathland was in late summer (Bibby 1977). The slight increase in the proportion of larvae in the diet during the year at the Soldiers Road site may reflect this.

Thus, with the exception of the high proportion of weevils and woodlice taken in the spring, seasonal trends in the proportion of various prey groups in the diet are paralleled by corresponding trends in the abundance of the prey groups in the habitat.

It is also possible to relate differences in the diet of L.agilis between the two contrasting habitats of Soldiers Road and the Railway to probable differences in the abundance of different prey groups at the two sites. Bibby (1977) also sampled invertebrates by means of pitfall trapping on sites consisting of different mixtures of grasses, gorse, and bracken. The habitat of these sites, therefore, has some strong resemblances to the Railway site and the invertebrate fauna of these sites might be expected to differ from a typical heathland fauna in similar ways.

Invertebrate groups which were caught notably more frequently in pitfall traps in the grassy habitats compared with heathland were Homoptera, Isopoda, Carabidae, Orthoptera and Acarina (Bibby 1977). Of these Homoptera were taken too rarely by *L.agilis* to make comparison possible, Acarina were not taken at all, but Orthoptera, Isopoda and Carabidae were all taken more frequently at the Railway site than at Soldiers Road.

The various trapping methods used to sample invertebrates all give biased information on the relative abundance of different prey groups, so it is better to use them as indicators of seasonal changes in the abundance of individual prey groups. Such seasonal variation can in many cases be related to seasonal changes in the diet of *L.agilis*. Individuals of *L.agilis* can also respond to more rapid changes in the abundance of prey. This was shown by the sudden appearance of ant queens in large numbers in the diet. The lizards may also have exploited the temporary abundance of bees and hover-flies, caused by the flowering of the *Calluna*. Thus *L.agilis* is an opportunistic predator, capable of rapidly responding to and exploiting temporary abundances of food.

L.agilis is a diurnally active predator which searches for prey using mainly visual and some olfactory stimuli. One consequence of these and other aspects of the predatory behaviour of individuals is that part of the total invertebrate fauna, itself inadequately sampled by the various trapping methods, may in practice be unavailable to the lizard.

Several potential prey groups are nocturnal and therefore perhaps unavailable to L.agilis. Harvestmen are one such group although the most abundant species, Phalangium opilio, may often be active in the daytime (P. Merrett pers. comm.). Dartford Warblers (Sylvia undata) do not in general take harvestmen and Bibby (1977) has suggested that this is because of the nocturnal habits of this group. The large numbers of harvestmen taken by L.agilis therefore suggests that individual lizards are able to find this prey in its daytime retreats where perhaps it is inaccessible to Dartford Warblers.

Several of the species of beetle taken, such as some of the Carabidae, were also predominantly nocturnal although most were probably diurnal (T. Heijerman pers. comm.). Again the nocturnal species may be found in their daytime retreats. Most species of woodlice are largely nocturnal yet woodlice were taken frequently at both sites. At the Railway site large numbers of woodlice were active in the daytime, at least in the spring (pers. obs.). Earthworms may have been rendered unavailable by their nocturnal habits but they are also very scarce on heathlands (Bibby 1977). Thus although the period of activity of different prey obviously influences its availability, few prey groups seem to be completely unavailable because of their nocturnal habits. The lizards may be able to find some of these nocturnal groups in their daytime retreats.

Some potential prey may be too quick and alert to be caught by L.agilis. Avery (1966) found that L.vivipara took few spiders of the genus Pardosa and suggested that this was because they were too fast-moving. However, in this study both L.agilis and L.vivipara were found to take large numbers of this genus of spider. Some species of Diptera are perhaps too alert to be caught frequently and this may account for their rarity in the diet during most sampling periods. Other species of Diptera, which were taken frequently in a few sampling periods, must have been easier to catch.

There were few, if any, invertebrates too large to be taken by adult L.agilis. Individuals were found to have taken the large ground beetle, Carabus problematicus, probably the largest beetle available, lepidopteran larvae over 50 mm long and a damsel fly approximately 45 mm long. Thus adults seem to be able to take the largest invertebrates available although some prey was probably too large to be taken by juveniles. The sting of bees also seems to have been no deterrent to adult L.agilis.

(iii) Prey Selection of L.agilis

Individuals of L.agilis do not take every potential prey item they encounter, they are selective. The evidence for such selection and the criteria used for selection by individual lizards are discussed below.

Some potential prey groups were not taken at all, probably because they are distasteful. These included ants and millipedes and probably ladybirds.

The most important criterion for prey selection was prey size. Adult L.agilis did not take items below 2 mm in length but selection went further than just a minimum size limit. Within separate prey categories selection can be demonstrated by comparing the size of prey eaten by L.agilis (Table 4.5) with the size of invertebrates caught by Bibby (1977) in his invertebrate survey of heathland, although it must be remembered that the sampling methods themselves provide a biased sample of the sizes of invertebrates in the habitat, the D-vac in particular probably not sampling many large items. However the comparisons given below clearly illustrate that much prey size selection by L.agilis is taking place, despite the biases of the sampling methods.

Small Hymenoptera (< 4 mm) can be very numerous in D-vac suction net catches in heather (Bibby 1977) but they were not taken by L.agilis. Mean prey length for the two hymenopteran groups in Table 4.5 was much greater than this.

Similarly small Diptera (< 4 mm) are also more common than larger Diptera (> 4 mm) in the same D-vac catches but were seldom taken by adult L.agilis which generally took the larger Diptera.

The most common size class of larvae caught in the D-vac suction net was 6-12 mm (Bibby 1977) although pitfall traps generally caught larger larvae than this.

The mean size of the larvae taken by L.agilis was much larger than that of larvae caught by both trapping methods.

The Heteroptera provide a particularly clear case of prey selection for size. Both pitfall traps and a D-vac suction net catch many more Heteroptera in the size class 2-4 mm than those over 4 mm in length (Bibby 1977). The smallest heteropteran taken by L.agilis was 3.8 mm and the mean prey length between 6 and 10 mm in different sampling periods (Table 4.5). Large shield bugs (Pentatomidae and Alydidae) accounted for approximately a third of all the Heteroptera eaten (Table 4.3) yet they are very rarely caught by either of the trapping methods used by Bibby. The small homopteran Ulopa reticulata (2-3 mm) which is the major constituent of homopteran pitfall and D-vac suction trap catches in heather (Bibby 1977) was only once found in the faecal samples.

All of the staphylinidae eaten by L.agilis measured between 13 and 15 mm and were mostly one species. Smaller staphylinidae occur frequently in pitfall trap catches in heather (Bibby 1977, R. Snazell pers. comm.) but were not taken by the lizards.

The final example is that of spiders. Comparing the sizes of the spiders taken by L.agilis (Table 4.6) with the sizes of the spiders sampled by Bibby (1977), the D-vac suction net catches much smaller spiders than those taken by L.agilis, by far the commonest size class in the suction net being 2-3 mm. Pitfall traps however gave a similar size distribution to those in Table 4.6, 4-6 mm being the most common size class. The only obvious difference was that pitfall traps caught a substantial number of spiders in the size class 2-3 mm whereas L.agilis took few spiders of this size.

It is evident, therefore, that within many prey groups, adult L.agilis preferentially select larger prey items, often despite their scarcity in the environment compared with smaller items. This selection of prey for size seemed to take place in a similar way at both the Railway and Soldiers Road sites, despite the differences in the taxonomy of the prey taken between the sites, since the means of the prey size distributions were similar.

The extent of the selection is striking. Dartford Warblers (Sylvia undata) also select larger items than those generally available (Bibby 1977) but the degree of selection is not as great as it is in L.agilis. For example, amongst the heather-dwelling heteropterans, species measuring 2-3 mm were 32 times more abundant than Nabis ericetorium (6-8 mm) but were eaten only 3.4 times more frequently by Dartford Warblers. In the case of L.agilis, Nabis was taken much more frequently than the smaller bugs.

It is possible that these conclusions regarding prey size selection may have been influenced by methodological error. For example, small items might not be recognized so easily in the faecal samples. Small items, however, although not as immediately obvious in the remains as larger items were revealed by thorough searching; size was probably not the most important factor influencing the detectability of the remains and any error from such an effect is unlikely to be large enough to affect the large degree of prey selection.

Pitfall traps and the D-vac suction net will also give biased estimates of the size of prey in the habitat. Pitfall traps generally catch larger invertebrates than the suction net. However, again the magnitude of the selection demonstrated is such that the general conclusion is unlikely to be affected by such errors.

A further factor which may influence prey selection is the nutrient content of the prey. The mineral nutrient content of various heathland invertebrates has been analysed by Bibby (1977). With one exception, there was little variation between different prey groups in their mineral content and thus little chance for individual lizards to markedly increase their consumption of a particular nutrient by prey selection. The exception was calcium which was over fifteen times more concentrated in millipedes, woodlice and snails than in other prey. It might be expected that females of L.agilis would have a high calcium demand in the spring to supply the calcium required for the eggs. Various species of birds have been found to select food rich in calcium, such as snails and bones, probably to provide calcium for egg-laying (e.g. Royama 1970). Woodlice formed a much larger proportion of the diet of L.agilis in the spring than at other times of year. It is therefore possible that females are selecting woodlice for their calcium content. This hypothesis can be tested by comparing the numbers of woodlice eaten by males and females. During May (combined samples) woodlice constituted 18%

(n = 100) of the diet of females and 23% (n = 136) of that of males.

Thus woodlice are not eaten preferentially by females; they do not appear to be taking a larger proportion of woodlice than would be expected. Nevertheless, the large number of woodlice eaten may still be important in providing calcium for the eggs and may supply the requirement adequately, making selection unnecessary.

Individuals of L.agilis, therefore, although taking prey within a broad range of types and sizes, show a distinct preference for larger prey. They ignore some distasteful prey, but there is no evidence of any selection of prey on the basis of its mineral nutrient content.

So far the simple idea of a lizard moving through the habitat and taking whatever prey is encountered, although being somewhat selective according to the principles outlined below, has seemed adequate to describe predation by L.agilis. But the strong preference for larger prey despite their relative scarcity poses a problem. It suggests that many small items encountered are ignored; yet many small items are taken. If individuals are indeed ignoring a proportion of small items and there are no differences between these and the small items taken it is not easy to see how such a strategy could fit an optimal diet model (e.g. Krebs 1978). Such items should either be taken or ignored.

It is likely, therefore, that the predatory behaviour of L.agilis is more complex. Individuals may be searching specifically for large prey items which might result in fewer smaller items being encountered. Further evidence of the complexity of the predatory behaviour of the lizards came from the statistical comparison of the prey within individual faecal samples.

This showed that in many cases, the occurrence of items of a particular prey type in the same faecal sample was not independent. Thus an individual, having taken an item of this type, was then more likely to take the same type of item again. It was especially interesting that this occurred not only for common prey types but also for rare ones.

Two different types of explanation are possible. The first concerns the predatory behaviour and prey selection of the lizard, the second the distribution of the prey. Concepts such as a 'specific search image' (Tinbergen 1960) cannot explain the present results for rare prey since they deal only with the overrepresentation of common prey in the diet, and repeated exposure to the prey is required for their formation. Even for the commonest prey types (e.g. queens ants, Soldiers Road 1975) the results imply that a few individuals will sometimes take many more alternative prey than expected. A specific search image would be expected to form in response to this very common prey in all individuals.

To explain the present results in terms of the predatory behaviour of the lizards one has to postulate that many individuals are actively seeking out certain types of prey (sometimes very rare) whilst ignoring other types of prey (sometimes much commoner). The advantage to the individual that would be gained by this is not at all obvious. Therefore, it seems more likely that non-random, clumped prey distributions in the habitat are responsible for producing these strange effects.

It does not seem unlikely that such clumped prey distributions could occur. However, to produce some of the extremely low probabilities found, the degree of clumping would have to be remarkable. Possibly, in these cases, a combination of a clumped prey distribution and a behavioural response of the lizard may be involved. For example, having found one 'clump' an individual may then be more likely to search in similar types of places.

(iv) L.agilis and L.vivipara

The taxonomic analysis of the diets of L.agilis and L.vivipara revealed several differences between the species. L.agilis appeared to take a wider variety of prey than L.vivipara; several common prey groups were not taken at all by L.vivipara. Since these were in general the harder-bodied prey groups this difference is better illustrated by considering prey hardness specifically. The striking dissimilarity between the prey hardness distributions between the two species would seem to explain most of the more obvious differences in prey taxonomy.

Comparison of the hardness of prey taken by L.vivipara and by smaller individuals of L.agilis showed that the differences in prey hardness could not be explained by differences in snout-vent length or head width between the two populations. Thus individuals of L.vivipara seem to be ignoring harder prey items which they are capable of consuming. This view was supported by the occasional appearance of a hard-bodied prey item, such as a weevil, in the faecal samples of L.vivipara. Avery (1966) found that L.vivipara did eat woodlice and beetles, but not in proportion to their abundance and he suggested that they were a second choice, only eaten when little else was available. However, this does not explain why they are a second choice for L.vivipara but not for L.agilis.

The high degree of prey selection for size that is practised by individuals of L.agilis has already been demonstrated. Individuals of L.vivipara have also been shown to select prey larger than that generally available in the habitat (Avery 1966). However the degree of selection is clearly not as great since L.agilis on average takes larger prey, although both species take a broad range of sizes.

From the comparison of prey length distributions of different age classes of L.agilis it appeared that there was a clear difference between the size of prey taken by juveniles and young sub-adults, and other age classes but little difference between that taken by adults and sub-adults. The more detailed investigation of the relationship between prey size and snout-vent length was not inconsistent with this view, but did not lend it strong support since the asymptotic regression fitted the data only slightly better than the linear one. In other species of lizard both linear relationships between mean prey size and lizard length (Schoener 1968b) and relationships where mean prey size does not increase once individuals have reached a certain length (Rose 1976) have been found.

The relationship with snout-vent length, however, accounted for only a small percentage of the total variance in prey size, most of which was caused by variation in the size of prey taken by each individual lizard. The concept of the total variance in prey size (the niche width) being divided into the 'within phenotype component' (WPC) and 'between phenotype component' (BPC) (Roughgarden 1972, 1974) is essentially similar and Roughgarden (1974) has made several theoretical predictions as to how the proportion of these two components will change with the varying levels of resources and numbers of species. This concept and the analysis of variance used in the present work are not strictly comparable, however, both because of several methodological differences and because Roughgarden (1974) restricted his analysis to the relationship between jaw size and prey size in adult lizards. The jaw size of adults is likely to be influenced to a greater extent by genetic factors than is the variation in snout-vent length of the whole population, which is largely determined by age (see chapter 7). The inclusion of juvenile and sub-adult lizards in the analysis will increase the 'between phenotype' component although it should be remembered that the distribution of snout-vent lengths used in the analysis was not representative of the distribution in the population.

The high proportion of the total variance in prey size of L.agilis attributable to variation within each snout-vent length, despite the inclusion of sub-adults and juveniles in the analysis, indicates that the population consists of generalists, each individual utilizing most of the range of prey sizes used by the whole population. The slightly lesser amount attributable to within snout-vent length variation for L.vivipara indicates that individuals are more specialized.

The difference between the size of prey taken by the two species appeared to be largely explicable by differences in snout-vent length or head width between the two populations. Individuals of L.vivipara selected smaller items than individuals of L.agilis of the same length, but the difference narrowed as snout-vent length increased.

The amount of overlap between both prey hardness and prey size distributions of L.vivipara and different age classes of L.agilis decreased with increasing size and age of L.agilis. The data indicated that prey size and hardness were largely independent of each other and assuming this to be true, then there is only a 38% overlap in prey utilization between adult L.agilis and the L.vivipara sample, but a 74% overlap between juvenile/young sub-adult L.agilis and L.vivipara. Taken together, therefore, the prey hardness and prey size differences constitute a considerable separation of food resources between L.vivipara and adult L.agilis.

Other studies of the diet of L.vivipara in different countries and habitats are compared with the present work in Table 4.12. All the studies illustrate the importance of spiders in the diet of L.vivipara; Homoptera and Diptera in varying proportions were the other most important groups. For L.agilis, the anallysis of the diet in the USSR (for location see Figure 10.1) by

TABLE 4.12 COMPARISON OF THE PREY OF *L.vivipara* IN DIFFERENT COUNTRIES AND HABITATS

Country	Habitat	Percentage by number of major prey groups in diet						Reference
		ARANEAE	OPILIONES	HOMOPTERA	DIPTERA	HYMENOPTERA	OTHERS	
FINLAND	Peat bog	26	1	10	8	9	46	Koponen & Hietakangas (1972)
"	Grass	21	8	29	10	7	25	Itiames & Koskela (1971)
"	Sea shore	37	2	14	19	2	26	"
"	Meadows	41	4	23	9	7	16	"
"	Damp heath forest	28	2	1	52	1	16	"
"	Dry heath forest	37	0	2	12	19	30	"
ENGLAND	Coarse grass	22	6	23	7	4	38	Avery (1966)
"	Heathland & coarse grass	19	11	30	5	11	24	"
"	Dry heathland & coarse grass/scrub	44	10	5	12	2	27	Present work

Rashkevitch and Semenikhina (1974) shows Coleoptera to be particularly important (Table 4.13).

Analysis of these studies in terms of prey hardness (Figure 4.15) shows that soft-bodied prey predominates in the diet of L.vivipara in all the different locations but the prey hardness distribution of L.agilis in the USSR is similar to that in England.

Both Finland and the west of England are outside the range of L.agilis. Thus there was no obvious expansion of the niche of L.vivipara to include more harder-bodied prey in these allopatric populations, compared with the diet in Dorset where the two species are sympatric.

The absence of any niche expansion in the allopatric populations of L.vivipara suggests either that interactions with L.agilis are not important in causing L.vivipara to take predominantly soft-bodied prey, or alternatively that interactions with L.agilis in sympatric populations may have influenced the diet of L.vivipara in the past, but individuals of L.vivipara now lack the behavioural ability needed to alter their diet so that individuals in allopatric populations may take more hard-bodied prey.

TABLE 4.13 COMPARISON OF THE PREY OF *L.agilis* (a) IN RUSSIA (DATA FROM RASHKEVITCH & SEMENIKHINA (1974), (FOR LOCATION OF STUDY SEE FIGURE 10.1) AND (b) IN ENGLAND, PRESENT WORK (FIGURES IN PARENTHESES ARE PERCENTAGES BY NUMBER)

	(a)	(b)
COLEOPTERA		
TOTAL	346 (47.7)	350 (24.0)
CARABIDAE	107 (14.8)	54 (3.7)
COCCINELLIDAE	80 (11.0)	10 (0.7)
OTHERS	104 (14.3)	266 (18.2)
COLEOPTEROUS LARVAE	55 (7.6)	20 (1.4)*
ARANEAE	55 (7.6)	237 (16.2)
OPILIONES	- -	87 (6.0)
HYMENOPTERA		
TOTAL	44 (6.1)	201 (13.8)
FORMICIDAE	35 (4.8)	73 (5.0)
OTHERS	9 (1.2)	128 (8.8)
LEPIDOPTERA		
TOTAL	166 (22.9)	161 (11.0)
ADULTS	20 (2.8)	34 (2.3)
LARVAE	146 (20.1)	127 (8.7)
DIPTERA	5 (0.7)	116 (7.9)
ORTHOPTERA	40 (5.5)	50 (3.4)
HETEROPTERA	7 (1.0)	88 (6.0)
HOMOPTERA	21 (2.9)	31 (2.1)
ISOPODA	12 (1.7)	93 (6.4)
DERMAPTERA	8 (1.1)	5 (0.3)
MOLLUSCA	12 (1.7)	1 (0.1)
OTHERS	9 (1.2)	41 (2.8)
TOTAL	725	1461

* Unidentified larvae, probably mostly coleopterous.

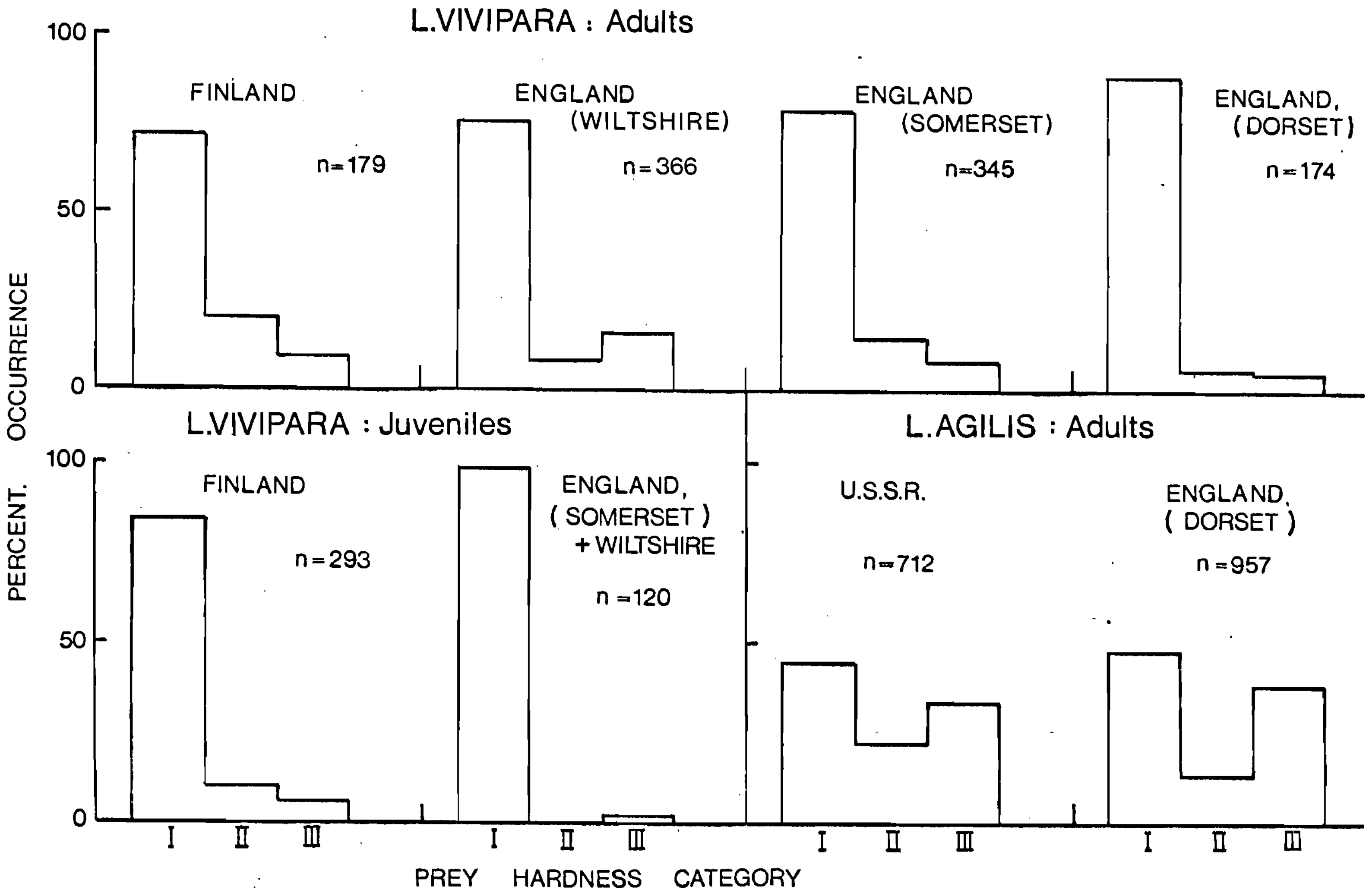

FIGURE 4.15 Frequency distributions of prey hardness for L.agilis and L.vivipara in different countries. The distributions were compiled using taxonomic data on diet from other studies and the same prey hardness classification as used previously in this chapter. The data were taken from Koponen & Hietakangas (1972), Finland; Avery (1966), Somerset and Wiltshire; Rashkevitch & Semenikhina (1974), U.S.S.R.; this study, Dorset.

CHAPTER 5

FOOD CONSUMPTION OF LACERTA AGILIS

5.1 Introduction

The studies of Avery (1971, 1976 and 1978) on the food consumption and activity of small heliothermic lizards (Lacerta vivipara, Podarcis muralis and Podarcis sicula) provide a baseline with which these aspects of the biology of other species of lizard can be compared.

In particular, these studies relate to the important question of whether, within natural variation in levels of food abundance, the rate of food consumption of these lizards is sensitive to changes in the abundance of prey. This is important because, if food consumption is insensitive to such changes, it would suggest that we cannot look towards levels of prey abundance for an explanation of the density and distribution of these lizard populations. On the other hand, if food consumption is sensitive to changes in prey abundance, then it is probably important in determining the density and distribution of these lizard populations and competition for food both between individuals and with other species is also likely to be important.

The available evidence from studies on L.vivipara and P.muralis/sicula tends to support the former point of view. For both L.vivipara in England (Avery 1971) and P.muralis/sicula in Italy (Avery 1978) ad libitum food consumption in the laboratory was the same as food consumption in the field in optimal climatic conditions. Thus in optimal conditions individual lizards appear to be feeding at their maximum rate, which is probably largely determined by stomach volume (Avery 1978). In sub-optimal conditions however food consumption is reduced. There is no evidence that under optimal climatic conditions either L.vivipara or P.muralis/sicula are unable to maintain this maximum rate of food consumption at any time during the year. The food consumption of P.muralis/sicula was the same in optimal conditions in April as it was in August. Individuals of L.vivipara appear to be able to feed at their maximum rate at any time during the year if weather conditions are good (R. Avery pers. comm.). This line of investigation, therefore, indicates that rates of food consumption are relatively independent of the amount of available food at least within the normal range of natural food densities encountered. This may be possible because of the relatively low rates of food consumption of lizards compared with homeothermic vertebrates (McNab 1963) where direct relationships between rates of feeding and available prey are well known (e.g. Gibb 1956).

There is evidence, however, which suggests that there are seasonal differences in food consumption for both L.vivipara (Avery 1966, table 5.1a) and L.agilis (Rashkevitch & Semenikhina 1974, table 5.1c). The mean number of prey items in the stomachs of individuals was lower in the spring than later in the year. Avery (1974) found that female, male and sub-adult L.vivipara all lost fat between March and June. Whilst for females the synthesis of the clutch causes much of this loss

TABLE 5.1 THE NUMBERS OF PREY ITEMS IDENTIFIED IN LIZARD STOMACHS OR FROM EQUIVALENT STANDARD FAECAL SAMPLES AT DIFFERENT TIMES OF YEAR (a) L.vivipara (DATA CALCULATED FROM AVERY (1966)), (b) L.agilis. THE NUMBERS IN BRACKETS ARE THE NUMBER OF SAMPLES. A STANDARD FAECAL SAMPLE WAS OBTAINED BY KEEPING INDIVIDUALS IN CAPTIVITY FOR FOUR DAYS (SEE METHODS), (c) L.agilis IN THE U.S.S.R. DATA CALCULATED FROM RASHKEVITCH & SEMENIKHINA (1974)

(a)

Sample Period	Number of prey items per stomach (adults) at two different sites	
April/May	2.55 (20)	2.93 (18)
July	5.98 (31)	10.5 (20)
September	7.60 (19)	6.95 (14)

(b)

Sample Period	Number of prey items per standard faecal sample	
	RAILWAY	STUDLAND
April/May	6.6 (9)	7.7 (14)
July/August	14.1 (39)	-
September	16.0 (8)	-

(c)

Sample Period	Number of prey items per stomach
March	1.0
May	3.7
June	6.0
July	6.7
August	7.0

(Avery 1975b), the reasons for the loss in males and sub-adults are not clear. If there is indeed a seasonal difference between food consumption in the spring and the summer then the previous argument would indicate that it is not caused by differences in prey densities but probably by seasonal differences in meteorological conditions.

In this part of the work the problem of the factors affecting the food consumption of L.agilis is approached in a similar way and comparisons are drawn with L.vivipara and P.muralis/sicula.

5.2 Materials and Methods

(i) Seasonal variation in weight

Seasonal variations in weight were examined because they may be indicative of changes in the rate of food consumption and of the levels of fat reserves. It was not possible to sacrifice individuals in order to look at fat reserves directly.

Changes in weight of individual lizards were followed, where possible, by mark and recapture. The weights of all adult L.agilis caught curing four different time periods during the year were also compared. Data for 1976 and 1977 and for different sites was combined. As the main cause of variation in weight between individuals is variation in snout-vent length the data was examined by calculating deviations for each lizard from a log:log regression of weight against snout-vent length, obtained using all the data. Males and females were treated separately; the overall regression equations are given in chapter 7 (equations

7.5 and 7.6). The means of the deviations from the regression were calculated for four time periods during the year.

(ii) Food consumption

Food consumption was measured by using methods (a) and (b) of Avery (1971) which involve the measurement of the production of faecal and nitrogenous excreta respectively, of lizards caught in the field.

Individuals of L.agilis were captured by hand at the Railway site and at Studland at three separate times, April and May, mid July to mid August and September. The lizards were brought back to the laboratory and kept for four days in small plastic containers without food. They were allowed to select their preferred body temperatures for five hours each day under the heat from a 60 watt bulb. All excretory material was collected. Each individual was fed before being returned to the exact place of capture.

The excretory material was separated into faecal and nitrogenous components and these were dried at 65° C and weighed. Avery (1971 and 1978) has obtained relationships between the output of these two quantities and food consumption for L.vivipara, Podarcis muralis and Podarcis sicula in the laboratory. Such a calibration of the technique was not made for L.agilis and so the output of faecal and nitrogenous excreta is used mainly as a measure of relative food consumption. Using this measure, food consumption at different times of year was compared and the factors affecting variation in food consumption of individual lizards were investigated. This was thought justified since it has been well established by Avery (1971 and 1978) that the output of nitrogenous and faecal excreta of lizards kept in the laboratory is strongly correlated with food consumption.

The factors affecting variation in the output of nitrogenous and faecal excreta of individual L.agilis were investigated using multiple regression analyses. The variables used are listed in Table 5.4a. The number of prey items in each faecal sample was estimated by faecal analysis. The length of these items was estimated by methods described in chapter 4. These two variables were included to examine the relative importance of the number and size of prey items eaten in their effect on food consumption. An index of prey hardness was also included in order to examine the effect of the thickness of the integument of the prey on the weight of the faecal component. The index was calculated by giving each prey item a score of one, two or three according to its prey hardness category (chapter 4), summing these scores for each sample and dividing by the number of prey items. Four environmental variables were included. The means for temperature and solar radiation for the previous three days included the value for the day of capture and only the previous two days if the capture was made after 12.00 B.S.T. If the capture was made before this time the value for that day was excluded. These values for the days before the capture date were included because production of nitrogenous and faecal excreta may be related to the weather conditions of the previous few days rather than to the conditions when the individual was captured. Finally, the time of capture, coded as the number of hours after 8.30 am B.S.T., was included in order to see if there was any consistent increase or decrease in the measures of food consumption used during the day.

Multiple regression analyses were carried out using computer programs.

(iii) Seasonal variation in prey

Prey items identified by faecal analysis were assigned to one of thirty-four categories (table 4.3). Seasonal variation in the diversity of prey eaten by L.agilis was then quantified by using the diversity index of Simpson (1949), $1/\sum_{i}^{n} P_{i}^{2}$, where p_i is the proportion of the ith taxonomic category eaten.

Seasonal variation in prey size and hardness was also examined. The method of prey size determination is described in the previous chapter (Section 4.2 (ii)). For prey hardness, each prey item was assigned to one of three categories (see section 4.2 (iii)).

(iv) Stomach volume

It was not possible to determine the stomach volume of L.agilis directly as has been done for L.vivipara and P.muralis/sicula (Avery 1973 and 1978) because the technique involves the dissection of individual lizards. Stomach volume was therefore determined indirectly from stomach capacity by allowing individual lizards with empty stomachs to feed until satiated.

Lizards were kept in plastic bowls (30 x 50 cm) provided with water and some cover and allowed to thermo-regulate for five hours each day under heat from a 60 watt bulb. Each individual was not fed for at least four days and then allowed to feed ad libitum on mealworms for approximately 2 hours.

The stomach capacity in terms of dry weight was obtained by assuming the dry weight:wet weight ratio of mealworms to be 0.39 (Avery 1971). Low values of stomach capacity for lizards of a given weight were excluded on the grounds that these individuals had not eaten until satiated. This was thought justified because Avery (1973 and 1978) has shown that there is a good relationship between stomach volume and body weight both for L.vivipara and P.muralis/sicula. Stomach capacities were converted to stomach volumes by using a value for the density of mealworms of 950 mg/ml (Avery 1973). Avery (1978) has shown that the stomach volume of P.muralis/sicula obtained directly corresponds closely to that obtained from the maximum voluntary intake of food in the laboratory.

5.3 Results

(i) Seasonal variation in weight

The changes in weight of individual L.agilis caught during the spring of 1976 at the Railway study area are shown in Figures 5.1 and 5.2. The weights of most males decreased whilst females showed a slight weight gain. This pattern is, in general, confirmed by Figure 5.3 which shows the mean deviation from the weight predicted by overall log:log regression of weight against snout-vent length, for four time periods. Males were, on average, lighter in May/June than in April/May

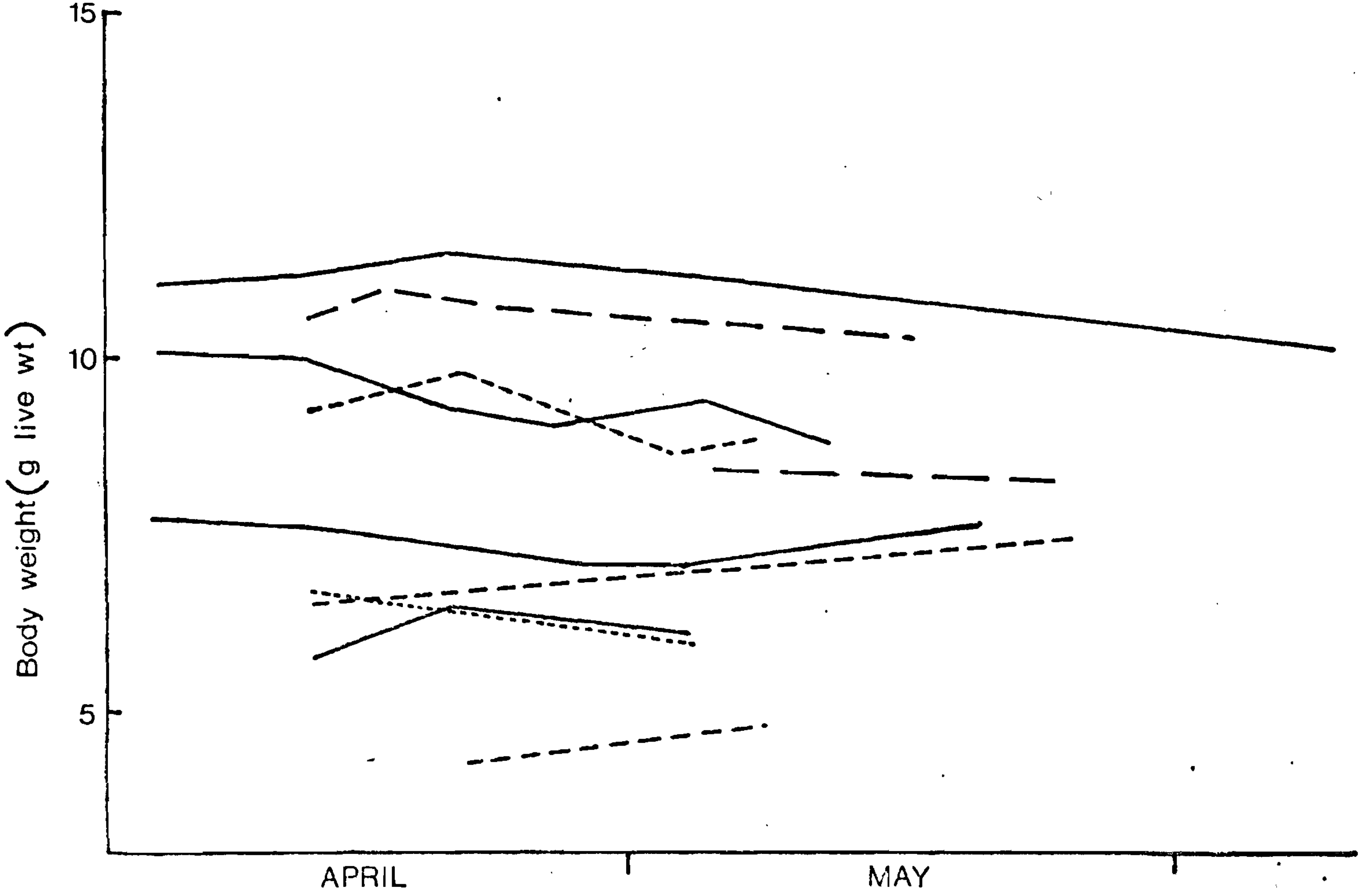

FIGURE 5.1 Changes in body weight of male L.agilis at the Railway site, spring 1976. Each line represents an individual male.

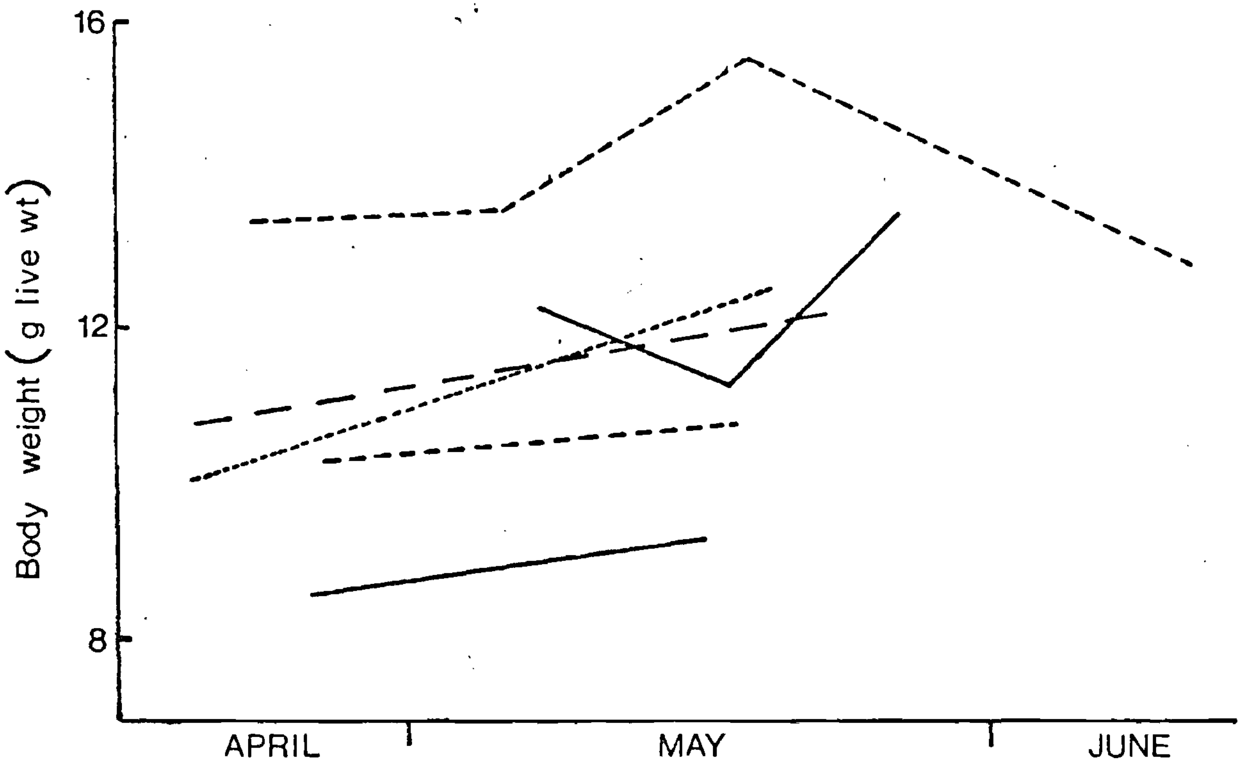

FIGURE 5.2 As for Figure 5.1 but for females.

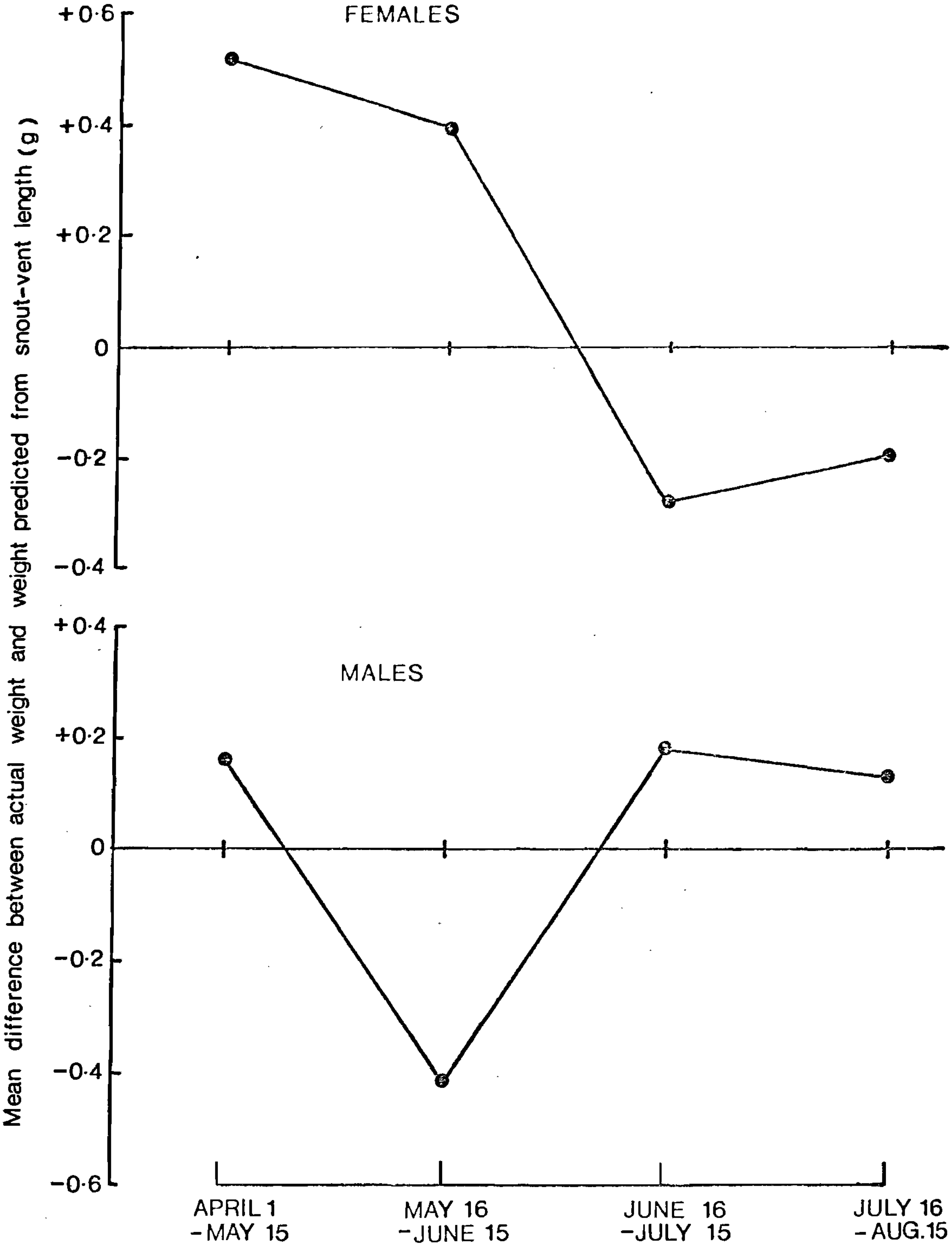

FIGURE 5.3 Seasonal variation in the body weight of L.agilis. Each point represents the mean difference between the observed weight and the weight predicted from snout-vent length for all individuals caught during each period. Combined data from different sites and for 1976 and 1977.

whereas the weight of females remained relatively constant. The decrease in weight of females between May/June and June/July is presumably caused by the laying of the clutch. At this time males, on average, gain weight. An insufficient number of lizards was caught in September to provide an adequate sample for the period immediately before the onset of hibernation.

Finally the data for seasonal variation in weight were examined by an analysis of variance (Table 5.2). This showed that variation between groups accounted for 9.9% of the overall variation for males and 9.2% for females. Both values of F are significant ($p < 0.05$). Thus although much of the variation in weight between individuals (apart from that explained by variation in snout-vent length) is explained by other factors, there is a significant seasonal pattern of weight change.

(ii) Food consumption

A comparison of the number of prey identified from standard faecal samples (faecal samples collected from lizards kept for four days in the laboratory, during which time the gut is emptied) at different times of year may provide evidence of seasonal differences in food consumption. Table 5.1b shows the mean number of prey items identified per sample for three sampling periods. There is no significant difference between the mean number of items for the two spring samples. The July/August and September samples are also not significantly different. The mean number of items for the combined July/August and September samples is significantly greater ($p < 0.001$) than for the combined

TABLE 5.2 ANALYSIS OF VARIANCE TABLE FOR THE MEAN DEVIATION FROM THE WEIGHT PREDICTED BY SNOUT-VENT LENGTH FOR *L.agilis* IN FOUR DIFFERENT TIME PERIODS (SEE FIGURE 5.3)

(a) FEMALES (b) MALES

	Source of variation	Degrees of freedom	Sums of squares	% of TOTAL	F
(a)					
	Between groups	3	10.2	9.2	2.82
	Within groups	83	100.3	90.8	
	TOTAL	86	110.6		
(b)	Between groups	3	5.9	9.9	3.64
	Within groups	99	53.1	90.1	
	TOTAL	102	58.9		

spring samples.

This result indicates that food consumption is lower in April and May than in July, August and September and this is generally supported by the data for production of nitrogenous excreta. Figure 5.4 shows three regressions of dry weight of nitrogenous excreta (X_2) against body weight plotted on log:log coordinates. The three regressions are

(a) $\log X_2 = 1.90 + 0.44 \log W$ ($n = 35$, $r = 0.40$) (5.1)

(b) $\log X_2 = 0.44 + 1.36 \log W$ ($n = 38$, $r = 0.67$) (5.2)

(c) $\log X_2 = 1.59 + 0.76 \log W$ ($n = 12$, $r = 0.88$) (5.3)

These regressions are all significant ($p < 0.05$). The slope of equation 5.2 is significantly greater than that of equation 5.1 and that of equation 5.3. The slopes of equations 5.1 and 5.3 are not significantly different. The three regression lines are directly compared in Figure 5.6(i). The food consumption in the spring is lower than in July/August but only for adult lizards. The discrepancy increases with body weight. There is also more variation in the production of nitrogenous excreta in the spring sample than in the other two samples.

In contrast, there is little difference in the output of faecal excreta (X_1) between the three sampling periods (Figures 5.5 and 5.6(ii)). The three regressions are given by

(a) $\log X_1 = 1.91 + 1.04 \log W$ ($n = 32$, $r = 0.78$) (5.4)

(b) $\log X_1 = 1.31 + 1.39 \log W$ ($n = 39$, $r = 0.71$) (5.5)

(c) $\log X_1 = 1.95 + 1.19 \log W$ ($n = 12$, $r = 0.94$) (5.6).

All of the three regressions are significant ($p < 0.01$).

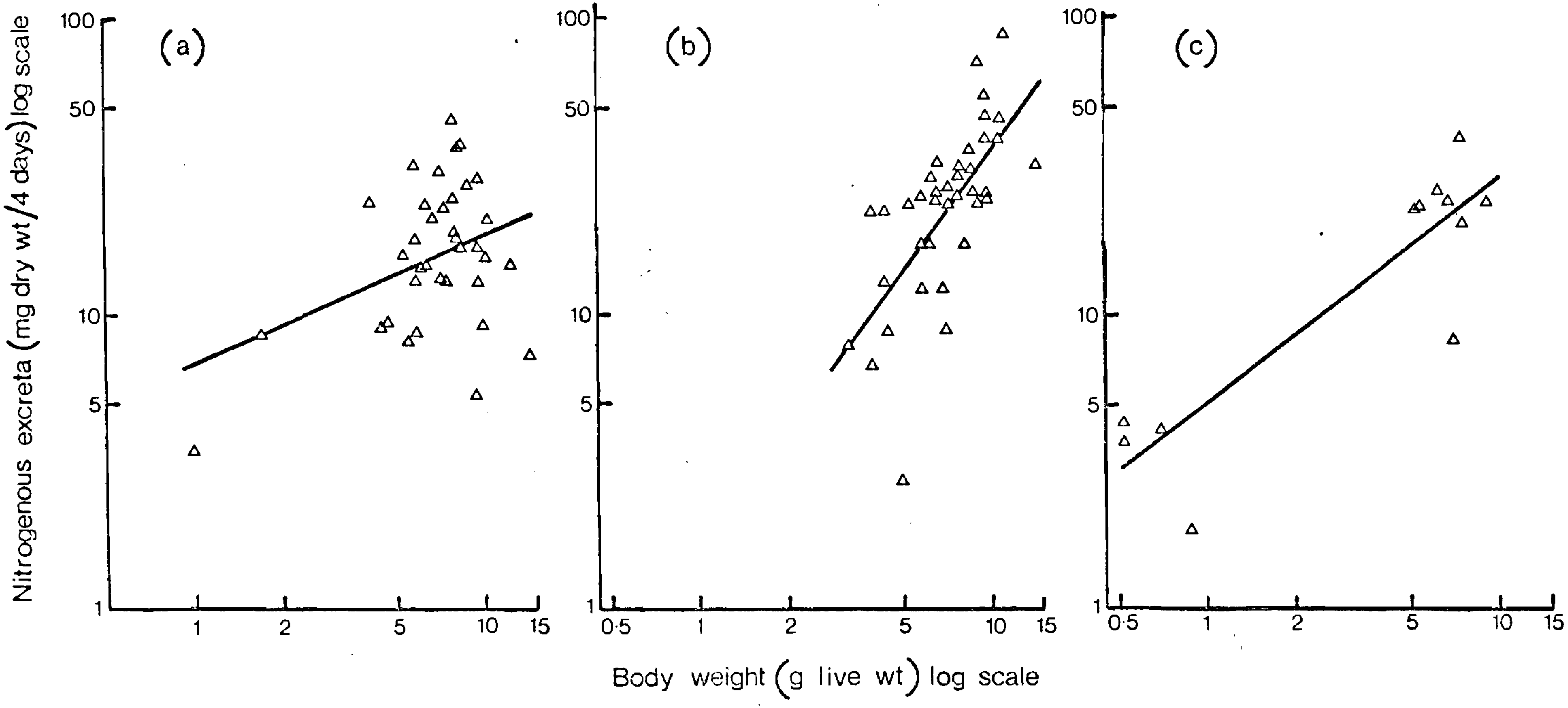

FIGURE 5.4 Regressions of dry weight of nitrogenous excreta produced in four days against body weight for L.agilis in three sampling periods in 1977. (a) April and May, (b) 15th July - 15th August, (c) September. For the regression equations see text.

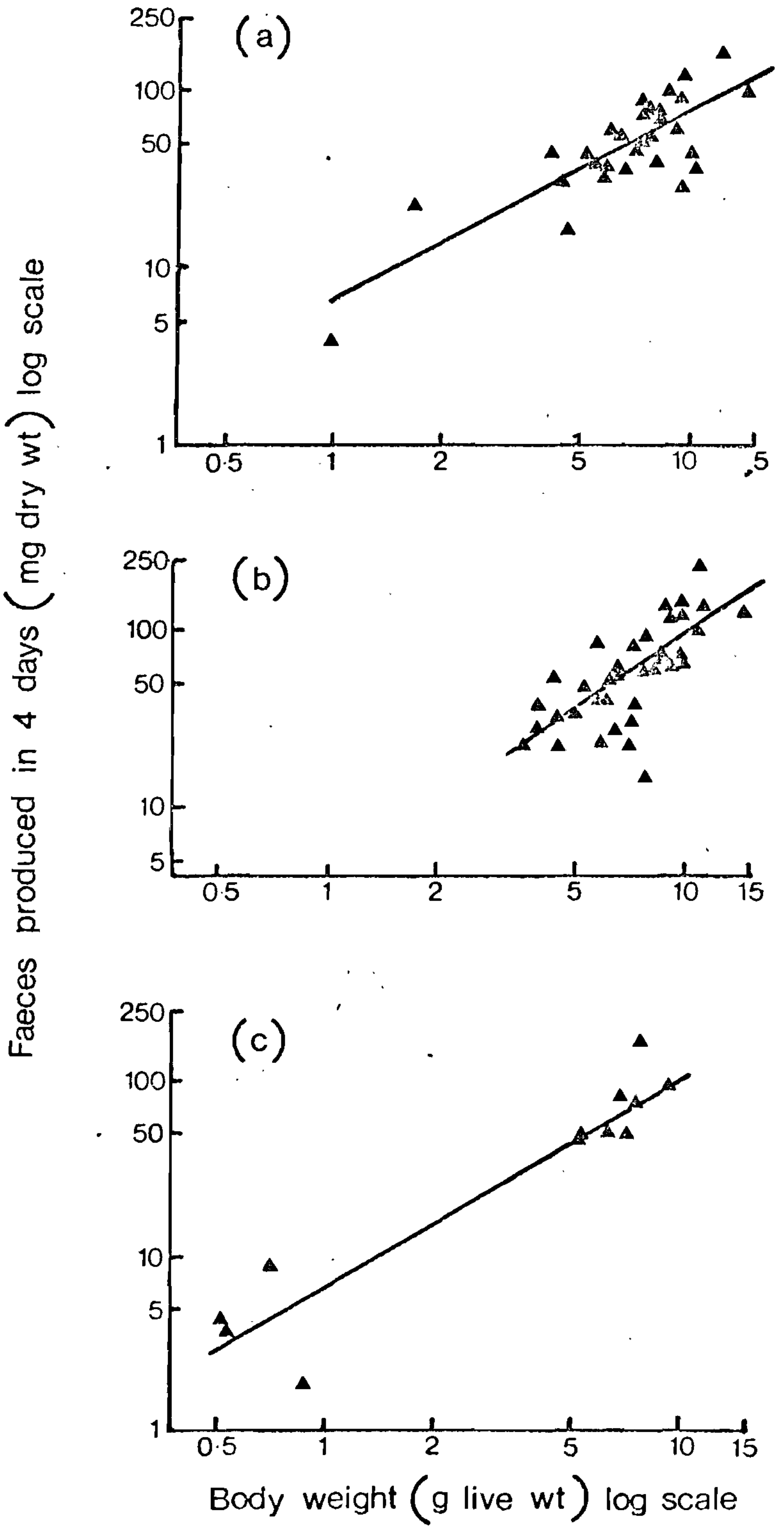

FIGURE 5.5 The same as for Figure 5.4 but for production of faecal excreta.

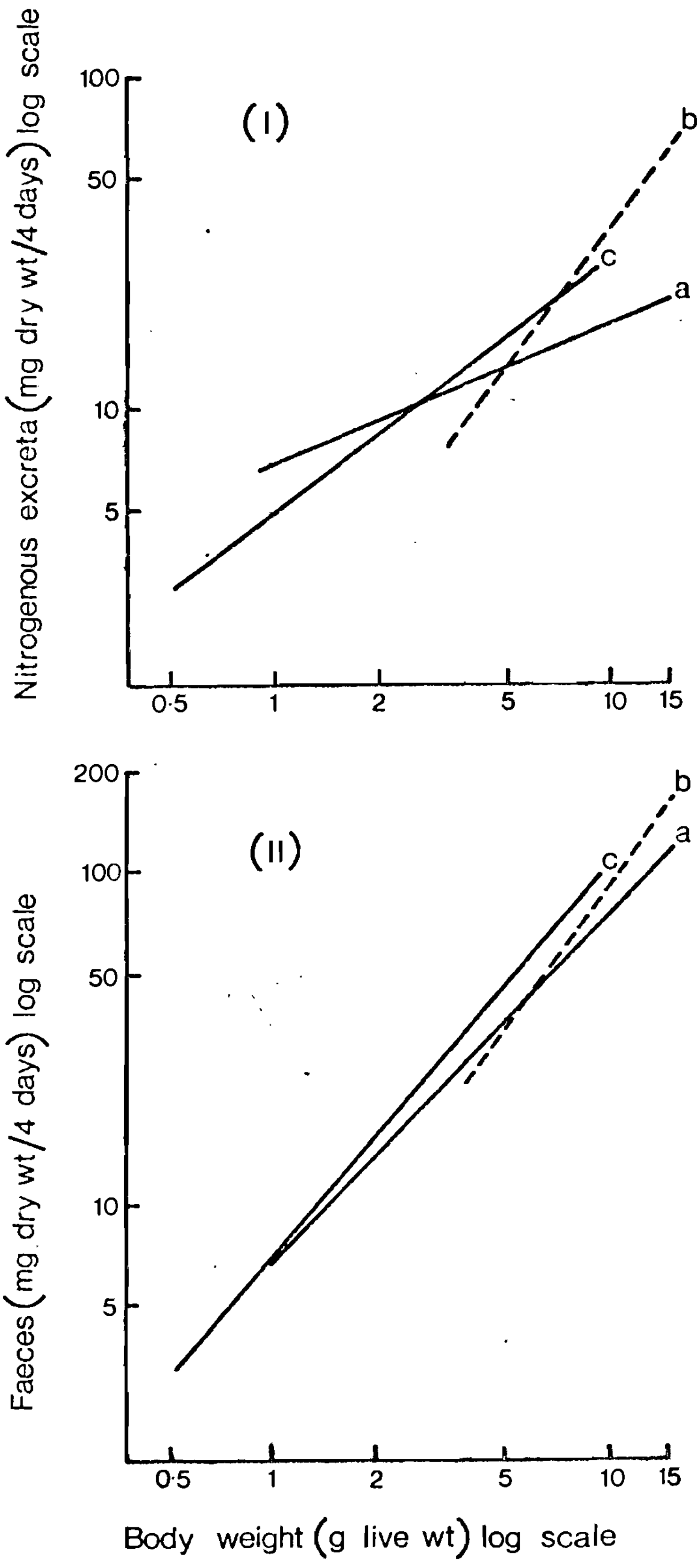

FIGURE 5.6 Comparison of the regression lines in (i) Figure 5.4 and (ii) Figure 5.5.

None of the three, however, is significantly different from any other.

The data for the number of prey items per sample and for the production of nitrogenous excreta both indicate that food consumption is greater during July/August than during April/May. The production of nitrogenous excreta for a 10 g lizard is 93% greater in July/August compared with April/May. Since to obtain an absolute value of food consumption endogenous nitrogenous excreta must first be subtracted (Avery 1971) the real difference in food consumption will be slightly greater than 93%. Production of faecal excreta, however, suggests that there is little difference in food consumption between the sampling periods.

Data for mean net daily solar radiation (langleys) and mean temperature (mean of mean daily temperatures (24 hours)) are shown in Table 5.3. The difference between the mean daily net solar radiation for the April/May and July/August sampling periods was not significant. Mean daily solar radiation for both these periods was significantly greater than mean solar for September ($p < 0.05$). Temperatures were highest in July/August and lowest in April/May. All the differences between the mean temperatures for the different sampling periods were significant ($p < 0.001$).

The factors affecting the output of faecal and nitrogenous excreta were investigated using multiple regression analyses. The initial analysis was carried out using all eleven variables (Table 5.4a) for the combined July/August and September sampling periods.

TABLE 5.3 METEOROLOGICAL DATA FOR SAMPLING PERIODS (1977) DURING WHICH THE PRODUCTION OF NITROGENOUS AND FAECAL EXCRETA OF L.agilis WAS MEASURED

Sampling period	Total daily net solar radiation (Langleys)		Daily Temperature °C	
	Mean	Range	Mean	Range
April 13th - May 24th	438.4	180.0-707.2	10.6	6.4-16.6
July 12th - August 15th	420.6	163.3-605.1	16.1	13.5-19.8
September 6th - September 15th	321.7	123.6-471.2	13.6	11.4-15.9

TABLE 5.4 (a) THE VARIABLES USED IN THE MULTIPLE REGRESSION ANALYSES TO INVESTIGATE THE FACTORS AFFECTING PRODUCTION OF FAECAL AND NITROGENOUS EXCRETA (X_1 AND X_2)

(b) MATRIX OF CORRELATION COEFFICIENTS BETWEEN THESE VARIABLES FOR THE COMBINED JULY/AUGUST AND SEPTEMBER SAMPLES (n=46) (ADULTS AND SUB-ADULTS ONLY). CORRELATIONS SIGNIFICANT AT THE 5% LEVEL ARE DENOTED BY AN ASTERISK

(a) X_1 = Dry weight of faecal excreta (mg dry wt/4 days)
X_2 = Dry weight of nitrogenous excreta (mg dry wt/4 days)
X_3 = Number of prey items in faecal excreta
X_4 = Mean length of these items (mm)
X_5 = Lizard weight (g live wt)
X_6 = Mean temperature on the date of capture (°C)
X_7 = Mean temperature of the three days before the date of capture (°C)
X_8 = Total net daily solar radiation on the date of capture (langleys)
X_9 = Mean net daily solar radiation for the three days before the date of capture (langleys)
X_{10} = Time of capture (hours after 8.30 B.S.T.)
X_{11} = Prey hardness index

(b)

	X_1	X_2	X_3	X_4	X_5	X_6	X_7	X_8	X_9	X_{10}
X_1										
X_2	0.65*									
X_3	0.35*	0.28								
X_4	0.20	0.33*	-0.17							
X_5	0.71*	0.61*	0.21	0.15						
X_6	-0.20	0.09	0.11	0.06	0.10					
X_7	-0.15	-0.06	-0.04	0.07	0.01	0.78*				
X_8	0.02	0.15	-0.11	0.19	0.09	0.25	0.36*			
X_9	0.03	0.32*	-0.04	0.26	0.05	0.42*	0.44*	0.41*		
X_{10}	0.21	0.17	0.13	-0.05	0.14	-0.16	0.05	-0.18	-0.07	
X_{11}	0.57*	0.38*	0.30*	0.26	0.35*	0.04	-0.03	0.003	-0.01	0.05

Data for juvenile lizards (caught only in September) were excluded.

A matrix of correlation coefficients between the eleven variables is shown in Table 5.4b. Faecal weight (X_1) is significantly correlated with weight of nitrogenous excreta (X_2), number of prey items (X_3), lizard weight (X_5) and prey hardness (X_{11}). The weight of nitrogenous excreta (X_2) is significantly correlated with faecal weight (X_1), mean prey size (X_4), lizard weight (X_5), mean solar radiation (previous three days) (X_{11}), and prey hardness (X_{11}).

Since both the production of faecal and nitrogenous excreta (X_1 and X_2) are positively correlated with lizard weight (X_5), partial correlation coefficients between X_1 and X_2 and the other variables were calculated. (Table 5.5). These assess the effect of the variable on X_1 and X_2 for a given lizard weight. The significant partial correlation between X_1 and X_2 shows that they vary together independently of the effect of lizard weight on each variable. This is consistent with their both being related to food consumption. Faecal weight is also significantly correlated with the number of items (X_3) and prey hardness (X_{11}), which is not surprising, but not with mean prey size (X_4). Prey hardness is the most important variable explaining 24% of the variation in X_1 not accounted for by variation in lizard weight (X_5). The meaning of the negative correlation between X_1 and mean temperature (X_6) is not known.

The index of prey hardness is one of the most important variables affecting faecal weight, despite the crude nature of its calculation. Faecal weight is

TABLE 5.5 PARTIAL CORRELATION COEFFICIENTS BETWEEN THE VARIABLES X_1 AND X_2 (DRY WEIGHT OF FAECAL AND NITROGENOUS EXCRETA) AND EIGHT OTHER VARIABLES (LISTED IN TABLE 5.4a) WITH THE EFFECT OF LIZARD BODY WEIGHT (X_5) ELIMINATED. CORRELATIONS SIGNIFICANT AT THE 5% LEVEL ARE DENOTED BY AN ASTERISK

	X_1	X_2
X_1	-	0.39*
X_2	0.39*	-
X_3	0.29*	0.15
X_4	0.13	0.31*
X_5	-	-
X_6	-0.39*	0.029
X_7	-0.24	0.083
X_8	0.063	0.19
X_9	0.007	0.37*
X_{10}	0.16	0.11
X_{11}	0.49*	0.23

therefore not a good measure of food consumption because the weight of the integument of the prey rather than its calorific value largely determines the faecal weight. There is also a significant correlation between lizard body weight (X_5) and prey hardness (X_{11}) (Table 5.4b). Thus food consumption measured by faecal weight will be biased, with the consumption of larger lizards over-estimated relative to that of smaller lizards.

Besides having a significant partial correlation with faecal weight (X_1), the weight of nitrogenous excreta is also significantly correlated (partial correlation eliminating lizard weight) with mean prey size (X_4) and solar radiation (previous three days) (X_9) (Table 5.5). Although the normal correlation coefficient between X_2 and prey hardness (X_{11}) is significant (Table 5.4b) the partial correlation coefficient is not (Table 5.5). This shows that the significant correlation is mostly caused by the correlation of both X_2 and X_{11} with lizard weight.

The variation in variables X_1 and X_2 for lizards of a given weight has so far been examined. The high positive correlations between lizard body weight (X_5) and both X_1 and X_2 show that the food consumption of larger lizards is greater than that of smaller lizards. But how is this increase in food consumption with weight achieved? In theory, larger lizards must either eat larger prey or eat prey at a faster rate. The data give little indication as to which of these two possibilities is more important. Neither the correlation of lizard body weight (X_5) with the number of items per sample (X_3) nor that of lizard weight with mean prey size (X_4) is significant (Table 5.4b). The absence of a significant correlation between X_5 and X_4 is consistent with the relationship between snout-vent length and mean log prey size (Figure 4.8). There is only a small increase in mean prey size once individual lizards have reached a snout-vent length of approximately 55 mm. Since juvenile lizards were not included in the analysis, the minimum size of individuals in the combined July/August and September sample is approximately 55 mm and so the lack of a significant correlation between X_4 and X_5 is perhaps less surprising. The large variance in the sizes of prey eaten by each individual (see section 4.5(i)) will also tend to obscure the correlation between X_4 and X_5. However, the absence of significant correlations between both X_3 and X_4, and X_5 is surprising considering the highly significant correlation between both X_1 and X_2, and X_5.

The effect of a log transformation on six of the variables was investigated. A matrix of correlation coefficients between the logs of these variables is shown in Table 5.6. In general, there is little difference between these and the linear correlation coefficient (Table 5.4b), although there was a notable increase in the value for X_1 against X_4.

None of the environmental variables selected have a great influence on X_1 or X_2 or the number of prey items (X_3). The only significant relationship was that between X_2 and mean net solar radiation (previous three days) (X_9).

TABLE 5.6 CORRELATION MATRIX OF LOG TRANSFORMED VARIABLES LISTED IN TABLE 5.4a (COMBINED JULY/AUGUST AND SEPTEMBER SAMPLES). CORRELATIONS SIGNIFICANT AT THE 5% LEVEL ARE DENOTED BY AN ASTERISK

	log X_1	log X_2	log X_3	log X_4	log X_{11}
log X_1					
log X_2	0.67*				
log X_3	0.38*	0.27			
log X_4	0.38*	0.28	-0.13		
log X_{11}	0.57*	0.41*	0.30*	0.32*	
log X_5	0.70*	0.62*	0.21	0.20	0.36*

The time of capture (X_{10}) also seems not to be related to X_1, X_2 or X_3 (Table 5.4b). Thus there was no apparent increase in the amount of faecal material in the gut during the day. Individuals caught shortly after emergence in the morning still had substantial amounts of faecal material in their guts.

Since the correlations between faecal weight and prey hardness and lizard weight and prey hardness place limitations on the use of faecal weight as a measure of food consumption the effect of the environmental variables on the production of nitrogenous excreta alone was further investigated by also including data from the April/May sampling period.

A multiple regression analysis was first carried out on the data for the production of nitrogenous excreta (X_2) in April and May only. Variables X_2 and X_5 (lizard weight) were log transformed. The matrix of correlation coefficients between the variables is shown in Table 5.7a and the partial correlation coefficients between the environmental variables and log X_2 with the effect of X_5 eliminated, in Table 5.7b. None of the correlations between X_2 and environmental variables is significant. The correlations between the solar radiation variables and X_2 are generally higher than those between the temperature variables and X_2.

The matrix of correlation coefficients for the combined April/May, July/August and September samples is shown in Table 5.7c, and the partial correlations between log X_2 and the four environmental variables, eliminating X_5, in Table 5.7d. The partial correlation

TABLE 5.7 (a) CORRELATION MATRIX OF NITROGENOUS EXCRETA, LIZARD WEIGHT AND THE FOUR ENVIRONMENTAL VARIABLES (VARIABLES LISTED IN TABLE 5.4a) FOR APRIL/MAY SAMPLE ONLY.
(b) PARTIAL CORRELATIONS OF FOUR ENVIRONMENTAL VARIABLES AGAINST LOG X_2 (NITROGENOUS EXCRETA) WITH THE EFFECT OF LOG X_5 (LIZARD WEIGHT) ELIMINATED. APRIL AND MAY SAMPLE.
(c) AND (d) SAME AS FOR (a) AND (b) BUT FOR COMBINED APRIL/MAY, JULY/AUGUST AND SEPTEMBER SAMPLES. VALUES SIGNIFICANT AT THE 5% LEVEL ARE DENOTED BY AN ASTERISK.

(a)

	log X_2	log X_5	X_6	X_7	X_8
log X_2					
log X_5	0.42*				
X_6	0.18	0.09			
X_7	0.06	0.04	0.93*		
X_8	0.21	-0.07	0.59*	0.54*	
X_9	0.15	0.13	0.89*	0.93*	0.53*

(b)

	X_6	X_7	X_8	X_9
log X_2	0.16	0.05	0.27	0.10

(c)

	log X_2	log X_5	X_6	X_7	X_8
log X_2					
log X_5	0.49*				
X_6	0.28*	0.08			
X_7	0.18	0.02	0.93*		
X_8	0.10	-0.02	0.30*	0.31*	
X_9	-0.14	0.03	0.33*	0.33*	0.51*

(d)

	X_6	X_7	X_8	X_9
log X_2	0.27*	0.18	0.12	-0.17

between mean temperature (X_6) and X_2 is significant although not that between mean temperature for the previous three days (X_7) and X_2. In contrast to the case where the April/May and July/August/September samples are treated separately, the temperature variables are more important than the solar radiation variables.

(iii) Seasonal variation in prey

Table 5.8 shows the number of prey categories found (out of a total of thirty-four categories) and an index of prey diversity for different sites and sampling periods during the year. Indices of prey diversity for the April and May samples are consistently lower than for samples later in the year.

This difference in diversity is illustrated by Figure 5.7. In the spring the diet is dominated by a few common prey categories. In the late summer samples there is a much greater number of prey categories which account for between 5 and 10% of the diet than in the spring. The early summer sample appears intermediate.

Individuals also eat larger prey items in late summer than in spring (Table 5.9). The mean prey size for the total late summer/autumn samples is significantly greater than for the spring samples ($p < 0.001$).

Seasonal differences in prey hardness were also evident. In the April and May samples (Figure 5.8) prey from category III (hard) consistently constitute the largest proportion of the diet whereas in the summer samples category I prey (soft) was most common.

TABLE 5.8 SEASONAL VARIATION IN THE TAXONOMIC DIVERSITY OF PREY ITEMS TAKEN BY L.agilis. FOR EACH SAMPLE, THE NUMBER OF PREY CATEGORIES (LISTED IN TABLE 4.3) PRESENT, AND THEIR DIVERSITY, CALCULATED USING SIMPSON'S INDEX, ARE SHOWN.

STUDY AREA	SAMPLE PERIOD	NUMBER OF PREY ITEMS IDENTIFIED	NUMBER OF PREY CATEGORIES	SIMPSON'S INDEX OF DIVERSITY $\frac{1}{\sum p_i^2}$
Soldiers Road	April & May 1976	54	12	4.19
Railway	April & May 1976	66	13	4.98
Railway	April & May 1977	59	16	5.53
Studland	May 1977	109	14	5.18
TOTAL APRIL AND MAY SAMPLES		288	21	6.22
Soldiers Road	1st June-15th July 1975 & 1976	97	21	6.90
Railway	1st June-15th July 1975 & 1976	54	17	10.49
TOTAL JUNE AND EARLY JULY SAMPLES		151	24	9.29
Soldiers Road	15th July-15th August 1975	216	23	9.13
Soldiers Road	15th July-15th August 1976	58	12	7.51
Railway	15th July-15th September 1975 & 1976	70	22	15.12
Railway	15th July-15th August 1977	550	30	12.14
Railway	September 1977	128	21	7.41
TOTAL LATE JULY, AUGUST AND SEPTEMBER SAMPLES		1022	34	14.73

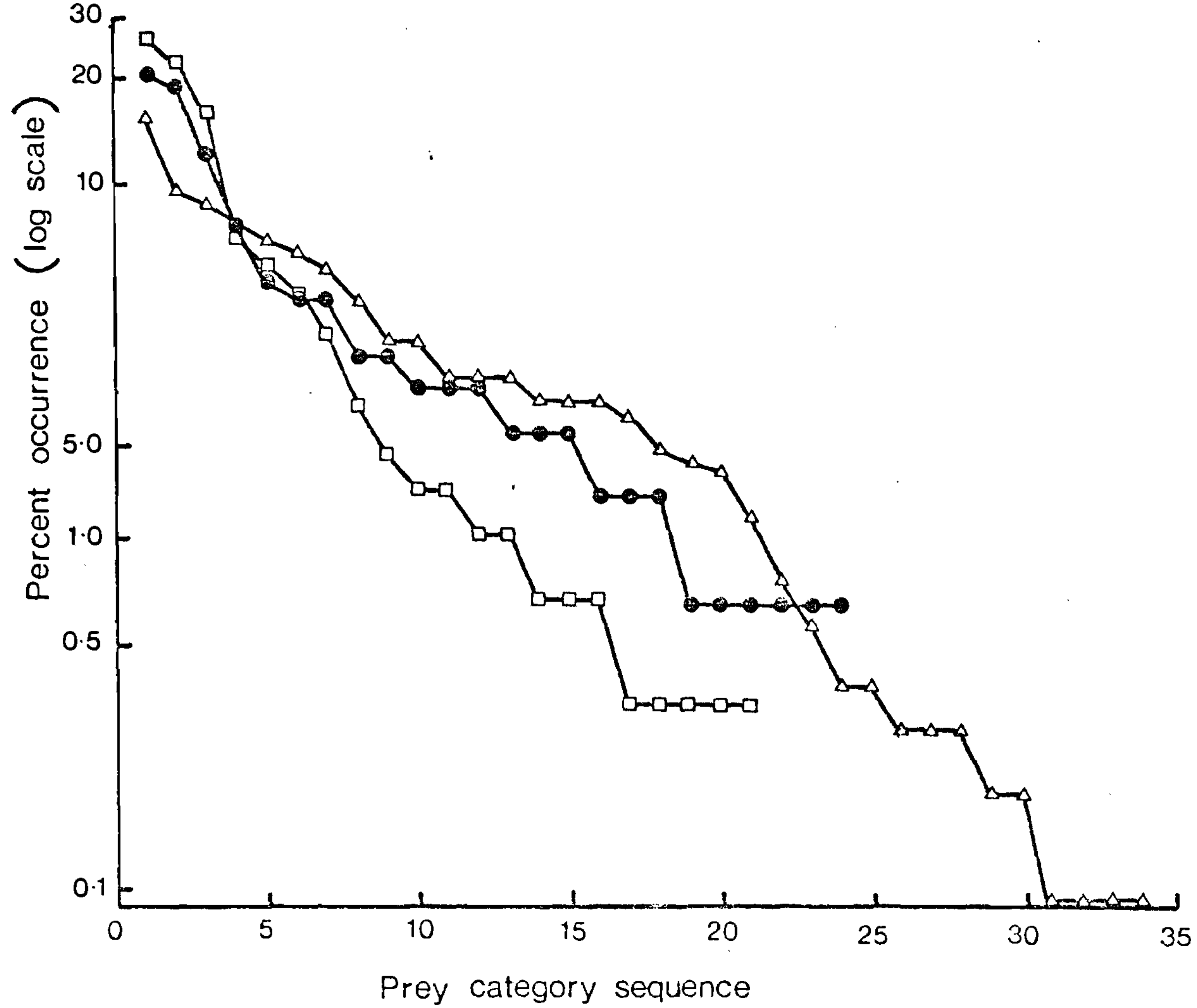

FIGURE 5.7 The diversity of prey taken by L.agilis in three sampling periods. Prey categories have been ordered according to their percent occurrence in the diet during each sampling period and plotted against the log of their percent occurrence. Data from different sites have been combined. Squares, spring samples (April and May); circles, early summer samples (1st June - 14th July); triangles, late summer samples (15th July - 15th September).

TABLE 5.9 SEASONAL VARIATION IN PREY SIZE

SITE	SAMPLE PERIOD		NUMBER OF PREY ITEMS MEASURED	MEAN PREY LENGTH (mm)	VARIANCE
(a) SOLDIERS ROAD	APRIL/MAY	1976	41	7.59	14.76
(b) RAILWAY	"	1976	54	10.04	44.94
(c) RAILWAY	"	1977	53	8.75	19.13
(d) STUDLAND	MAY	1977	104	8.06	17.42
TOTAL SPRING SAMPLES			252	8.55	23.69
(e) SOLDIERS ROAD	JULY/AUGUST	1975	187	8.91	50.95
(f) "	"	1976	53	18.21	262.88
(g) RAILWAY	JULY/AUG/SEPT	1975 & 1976	62	13.74	183.53
(h) "	JULY/AUGUST	1977	521	10.10	92.90
(i) "	SEPTEMBER	1977	126	9.40	34.31
TOTAL SUMMER/AUTUMN SAMPLES			949	10.44	96.25

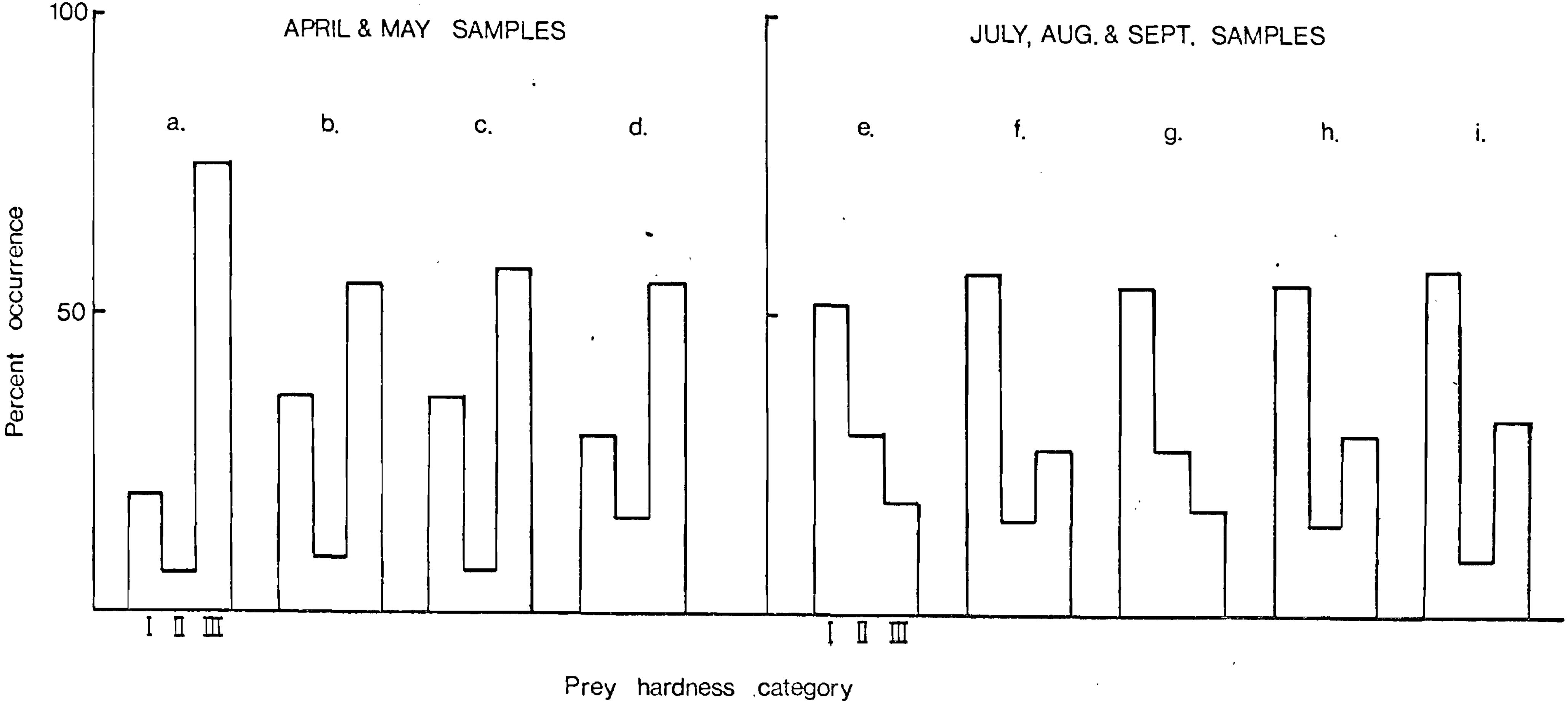

FIGURE 5.8 Comparison of the hardness of the prey taken by L.agilis in the spring and summer. For definitions of prey hardness categories see section 4.2(iii). Letters refer to sites and sampling periods listed in table 5.9.

(iv) Stomach Volume

Stomach capacity and volume was estimated from the maximum voluntary intake of mealworms eaten by individual <u>L. agilis</u> in the laboratory. The relationship between stomach capacity (c) and body weight (log:log data) is given by

$$\log C = 3.87 + 1.06 \log W \ (r = 0.79,\ n = 14) \ (5.7).$$

Converting this capacity to stomach volume by assuming perfect packing and a density of mealworms of 950 mg ml^{-1} (Avery 1973) the regression of stomach volume against body weight is

$$\log V = 1.07W - 2.05 \ (r = 0.79,\ n = 14) \ (5.8)$$

and for stomach volume against snout-vent length (L),

$$\log V = 2.98L - 12.6 \ (r = 0.79,\ n = 14) \ (5.9).$$

This relationship is shown in Figure 5.9. The relationship between volume and body weight is isometric and it therefore follows that volume is approximately related to the cube of the snout-vent length.

The main assumptions made in estimating volume in this way are that each lizard fed until satiated and that the cause of the low values of capacity (which were excluded) was that these individuals had not fed until satiated.

5.4 Discussion

(i) Seasonal variation in weight

Most of the variation in the weight of individuals can be explained by variation in snout-vent length (equations 7.5 and 7.6) (p 189). Part of the variation in weight of individuals not explicable by variation in snout-vent

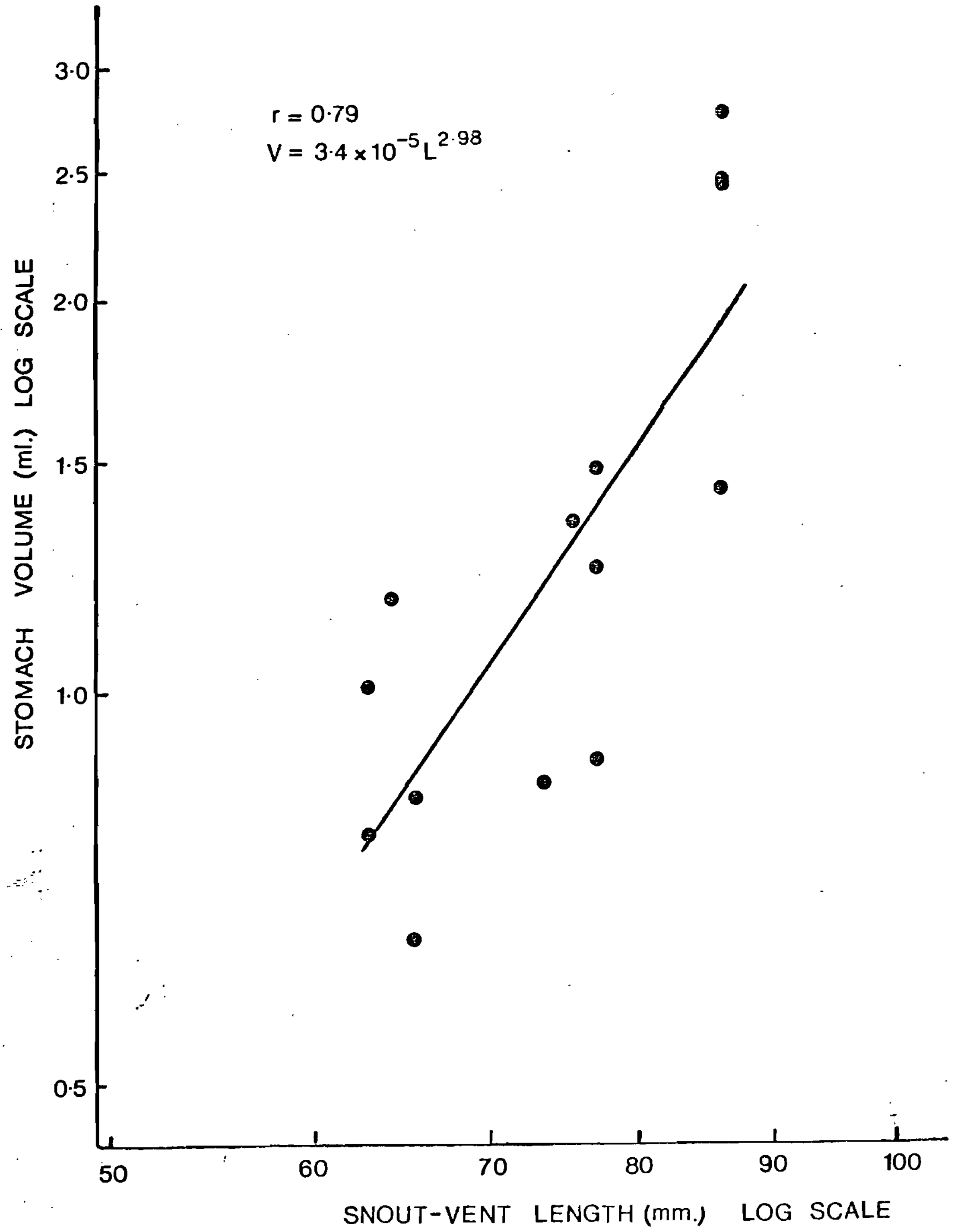

FIGURE 5.9 Regression of stomach volume against body weight for <u>L.agilis</u>.

length could be attributed to seasonal variation.

Seasonal variation in weight is likely to be related to consistent changes in the fat reserves of individuals. Avery (1974) has investigated seasonal changes in reserves of fat of L. vivipara. Fat reserves of male L. vivipara were at their lowest in June, males depleting their fat bodies between March and June. Likewise male L. agilis lost weight between April and June, and weights were lowest in May/June. The weights of females remain almost constant during the spring although a weight increase was observed for some individuals in 1976. Between March and June, in the case of L. vivipara females, a transfer of energy from the fat bodies to the clutch takes place (Avery 1975b), but since the final weight of the clutch is about twice that of the fat lost there is a net gain in weight. The absence of any large gain in weight of female L. agilis in the spring suggests that fat present on emergence from hibernation is used for synthesis of the clutch.

For both sexes, there appears to be little increase in weight between June/July and July/August. For females this may partly be because of variation in the time of egg laying. The latest date a female was observed laying eggs was 3rd July 1977 and in 1977 late June was probably the time when most females laid. The June/July sample will therefore consist of both females which have already laid their eggs and those which are about to lay. In the July/August sample all females will have laid and so although individual females may in fact increase in weight at this time this may not be reflected in a difference between the June/July and July/August samples. A further complication is the possibility that females may not breed every year.

Both males and females have relatively high weights after spring emergence (April/May sample). This suggests either that the energy demands of the winter result in only a small decrease in weight or that there is a considerable increase in weight between July/August and winter submergence, followed by a larger weight loss over winter.

(ii) Food consumption: seasonal variation

Both the data for the number of prey items per standard faecal sample and that for the production of nitrogenous excreta indicate that there was a large seasonal difference in the food consumption of <u>L.agilis</u> in 1977. The production of nitrogenous excreta suggested that the food consumption of a 10 g lizard was approximately 100% greater in July/August than in April/May. The number of prey items per faecal sample was also approximately 100% greater in July/August. Part of the difference in food consumption may be explained by differences in prey size, individuals eating larger prey in July/August than in April/May.

The results from the number of prey items per faecal sample suggest that food consumption in September is similar to that in July/August. Although the slope of equation 5.2 (p.109) (production of nitrogenous excreta in July/August) is significantly greater than the slope of equation 5.3 (production in September) this is mainly caused by the inclusion of juvenile lizards in the

September sample. There is little difference in the production of adults between the two samples.

The data for the production of faecal excreta, however, indicate that food consumption is similar in all three sampling periods. This anomaly can be explained by the greater hardness of the prey eaten in April/May. Since faecal weight has a high positive correlation with prey hardness, faecal weight is increased in April/May compared with the other two samples.

This positive correlation of prey hardness with faecal weight and the positive correlation between lizard body weight and prey hardness make faecal weight unsuitable as a measure of the food consumption of L.agilis. Avery (pers. comm.) has also encountered this problem with P.muralis/sicula. In retrospect, it can be seen that Avery (1971) was able to use faecal weight as a measure of the food consumption of L.vivipara without encountering these difficulties because this species eats very few prey which do not belong to prey hardness category I (soft, see section 4.6).

What factors, therefore, might account for the seasonal difference in food consumption? One possibility is that the seasonal difference in food consumption is caused by changes in prey availability. The low diversity of the prey eaten by L.agilis in April and May suggests that the range of items available is restricted. The diet in the spring is dominated by a few prey categories. Unless these prey categories occur at very high densities in the spring it is probable that the greater range of prey items available in the summer will result in a greater quantity of food being available. The predominant prey categories in the diet in the spring are weevils, spiders and woodlice (Table 4.3). There is no evidence that these are more common in the spring than in the summer. Bibby (1977) in a study of food available to the Dartford Warbler (Sylvia undata) on heathlands in Dorset did not find that weevils were present in greater numbers in heather in spring than in summer. The peak biomass for spiders occurred in September and June. Woodlice however may be caught in greater numbers in pitfall traps in the spring than later in the year (R. Snazell unpublished data). These prey categories apparently predominate in the diet in the spring because there is little else available. In the summer, when more prey categories become available at high density, the diet becomes more diverse. Bibby (1977) found that the abundance of invertebrates in heather increased during the summer. The biomass of invertebrates caught in a D-vac suction net reached a peak in August and September. The biomass of invertebrates caught in August was approximately four times that caught in May. The available evidence, therefore, indicates that, as the season progresses, a greater range and quantity of invertebrates becomes available to L.agilis.

A second possibility is that the seasonal difference in food consumption of L.agilis is caused by seasonal differences in weather conditions. In theory both solar radiation and temperature affect food consumption by influencing the proportion of time an individual lizard must spend basking and thus the amount of time available for feeding.

From examination of the environmental data for the different sampling periods it is evident that the seasonal difference in food consumption probably cannot be explained by changes in solar radiation as mean daily solar radiation was no greater in July/August than in April/May. Temperatures, however, were higher in July/August and so could be responsible. This conclusion is generally confirmed by the results of the multiple regression analysis. Although the amount of solar radiation in the previous three days had a significant effect on the production of nitrogenous excreta when the July/August/September sample was treated separately, the effect disappeared on combination with the spring sample. Solar radiation, therefore, does not explain the difference in food consumption between the two samples. In contrast, the temperature variables were unimportant when the two samples were treated separately but on combination the partial correlation between mean temperature and production of nitrogenous excreta was significant (although the correlation with mean temperature over the previous three days was not). This suggests that temperature is important in explaining the seasonal difference in food consumption. However, there are two arguments which suggest another factor is involved. The first is that although the partial correlation between mean temperature and production of nitrogenous excreta was significant it explained only 8% of the variation in production. The second is that, within both the April/May and July/August/September samples, temperature did not explain any of the variation in production of nitrogenous excreta. Thus production of nitrogenous excreta is apparently low even on warm days in the spring, and high on cool days in the summer. The most likely reason for this is the seasonal difference in prey availability. However, other factors such as the behaviour of individual lizards cannot be ruled out. In practice it is very difficult to separate the effect of prey availability and the effect of environmental variables on food consumption.

(iii) Food consumption: general considerations

The production of nitrogenous excreta has so far been used as a comparative measure of food consumption because the laboratory calibration procedure (Avery 1971) was not carried out.

However, it is of interest to convert the data for the production of nitrogenous excreta into units of food consumption by using the calibration for L.vivipara (Avery 1971). The calibration involves calculating the endogenous production of nitrogenous excreta (E end) for lizards of a given weight in the laboratory. Although Avery (1978) found that there was a difference between L.vivipara and P.muralis/sicula in the production of endogenous nitrogenous excreta this difference appeared to be related to the difference in metabolism between the two species, caused by the higher preferred body temperature of P.muralis/sicula. Since the mean preferred body temperature of L.vivipara is similar to that of L.agilis (Spellerberg 1976) there is some justification for using the calibration for L.vivipara although the results should be treated with caution.

Using the equation for E end for L. vivipara (E end = $1.42\ W^{0.74}$) the food consumption of L. agilis for the combined July/August and September samples was

$$F = 19.9\ W^{0.92} \qquad (n = 49,\ r = 0.69)\ (5.10)$$

This compares with the food consumption of L. vivipara

$$F = 23.7\ W^{0.64} \qquad \text{(Avery 1971)}$$

and P. muralis/sicula

$$F = 34.7\ W^{0.65} \qquad \text{(Avery 1978)}$$

where the units of F are mg dry wt day^{-1}.

The increase in food consumption with body weight is greater for L. agilis than for the other species. The difference in food consumption therefore varies isometrically with body weight. Over a wide range of weights the food consumption of L. agilis lies between that of L. vivipara and P. muralis/sicula. For a 2 g lizard the food consumption of L. agilis is approximately equal to that of L. vivipara and for an 8 g lizard it is approximately equal to P. muralis/sicula.

For both L. vivipara (Avery 1973) and P. muralis/sicula (Avery 1978) the stomach capacity is very similar both to the daily food consumption in the field under optimum conditions and to the daily ad libitum food consumption in the laboratory. This similarity suggests that food intake and stomach volume are directly related (Avery 1978).

The equation relating stomach capacity to body weight for L. agilis (equation 5.7) can be rewritten for comparison with equation 5.10.

$$C = 47.8\ W^{1.06}.$$

In contrast to the species studied by Avery, there is a large difference between the food consumption in the field and the stomach capacity. For a 5 g lizard the stomach capacity is 166% greater than the food consumption from equation 5.10. Thus food consumption during July/August and September was not limited by stomach volume. Although some of this discrepancy between stomach capacity and food consumption may be explained by the fact that all of the lizards were not caught during optimum meteorological conditions, this seems unlikely to account for such a large discrepancy. The conclusion is not dependent on the use of the calibration for *L.vivipara*. Even in the hypothetical case of the endogenous production of nitrogenous excreta being zero the food consumption of *L.agilis* would only be increased by 40%.

The stomach volume of *L.agilis* is much larger than that of both *L.vivipara* (Avery 1973) and *P.muralis/sicula* (Avery 1978). As with *L.vivipara*, the relationship between volume and body weight is isometric. The stomach volume of *L.agilis* is between 150 and 210% greater than that of *L.vivipara* and between 40 and 150% greater than *P.muralis/sicula* depending on body weight. The main error in the determination of the stomach volume of *L.agilis* was probably that all the individuals did not feed until satiated. This would lead to underestimation of the volume so the difference between *L.agilis* and other species are, if anything, conservative. The large volume of the stomach of *L.agilis* is also illustrated by the large number of prey items identified from some faecal samples (Appendix IV). Rashkevitch and

Semenikhina (1974) also found that the stomachs of some individuals of L.agilis contained large amounts of food. One individual had 16 g of remains in its stomach and another 12 g.

The differences in stomach volume between L.agilis and both L.vivipara and P.muralis/sicula are of a different order from the comparatively small differences found by Avery (1978) between L.vivipara and P.muralis/sicula. They suggest that, at least in the short term, individuals of L.agilis are capable of maintaining a much higher food consumption than either L.vivipara or P.muralis/sicula. The data for production of nitrogenous excreta provide confirmation of this suggestion. Whilst the greatest value for the food consumption of an individual of P.muralis/sicula was approximately 200 mg dry wt day^{-1} (Avery 1978), for L.agilis (July/August and September sample) there were nine values of food consumption over 200 mg dry wt day^{-1} and three exceptionally high values (578, 471 and 343 mg dry wt day^{-1} for lizards with body weights of 11.1, 9.0 and 9.7 g).

For individuals to take advantage of feeding at a high rate they must be able to store the energy rapidly as fat. Therefore one would expect to observe rapid increases in weight of individual L.agilis. Some rapid increases in weight were recorded for several lizards in the laboratory (Table 5.10).

The great variability in the slopes of equations 5.1, 5.2 and 5.3 (relating production of nitrogenous excreta to body weight) shows that there are distinct seasonal differences in the relative food consumption of

TABLE 5.10 SOME GAINS IN BODY WEIGHT OF INDIVIDUAL *L.agilis* KEPT IN THE LABORATORY

Initial weight (g)	Final weight (g)	Days over which weight gain recorded	Wt. gain (g day^{-1})
10.4	12.0	10	0.16
12.0	13.6	9	0.17
10.8	12.8	11	0.18
4.6	7.0	30	0.08
5.0	6.6	8	0.20
7.0	10.2	24	0.13

different sized lizards. In contrast, there is little variation in the slopes of the equations relating food consumption to body weight for P.muralis/sicula (Avery 1978). The probable cause of this is the limitation placed on food consumption by stomach volume. The large difference between the stomach capacity and the average daily food consumption of L.agilis makes it possible for the slopes of these equations to vary greatly.

Thus in the spring, the food consumption of larger lizards is depressed to a much greater extent than that of smaller lizards, whereas in July/August the food consumption of larger lizards is relatively high; the larger the individual lizard the greater the seasonal variation in food consumption. The reasons for this effect are not known. The food consumption of sub-adult lizards showed little seasonal variation. This is consistent with the finding that the rate of increase in weight of sub-adults was constant throughout the season (Figure 7.1a).

At least half of the clutch of an individual female L.vivipara is synthesised from energy from spring food assimilation, the remaining energy required coming from lipid deposits (Avery 1975b). The low food consumption of L.agilis in the spring, especially of large individuals, and the absence of a large weight gain in females, suggest that energy from spring assimilation is less important compared with energy from lipid deposits, in the synthesis of the clutch of L.agilis. Moreover if the marked degree of positive allometry for the relationship between stored lipid deposits and body weight of

L.vivipara found by Avery (1974) is paralleled in L.agilis, then large individuals of L.agilis, because of their relatively high food consumption in the summer, will be able to store large amounts of lipids. Since large lizards need less energy during winter than small lizards (Avery 1974), large individuals of L.agilis are likely to have relatively high reserves of fat on emergence from hibernation. These must be important in providing energy for the synthesis of the clutch, especially in larger lizards where food consumption is relatively lower. Lipid deposits of L.agilis probably provide an amount of energy for clutch synthesis somewhere between the value of 50% for L.vivipara and that of 100% for the adder (Vipera berus), where individuals do not feed at all during the spring (Prestt 1971).

(iv) Annual food consumption

Equation 5.10 was used to estimate the summer food consumption and equation 5.1 (converted to units of food consumption by using the calibration for L.vivipara (Avery 1971) was used for the spring consumption. The timing of spring emergence is examined in section 6.3 and, based on this data, it was assumed that individuals emerged and began feeding at the spring rate in mid April. Food consumption in June was not measured but casual observations on the amount of food available suggested it was higher than in the spring. It was therefore assumed that for most of this period individuals fed at the summer rate. It was unusual to see many adults active after mid September so it was assumed that feeding ceased at this time. Annual food consumption was therefore calculated on the basis that individuals fed at the spring rate for 50 days and at the summer rate for 100 days, and also that sub-adults weighed 1.5 g for the first 50 days and 3.7 g for the next 100 days (see section 7.3(ii)), and that the weight of adults remained constant throughout the year.

Estimates of the annual food consumption of different aged L.agilis are given in Table 5.11. The consumption of the different age classes was similar and was approximately 30% greater than the value for L.vivipara (Avery 1976), but it was still much smaller than the annual consumption of P.muralis in Italy (Avery 1978).

(v) L.agilis and L.vivipara: diet and food consumption

Finally, the diet and prey selection of L.agilis and L.vivipara is examined in terms of the food consumption of both species and its relationship with prey density. It is relevant, however, to consider first the contribution made by the different prey length categories to the total dry weight of prey taken. An estimate was obtained by a regression of prey length against dry weight for several different prey categories. Most of the data was taken from Bibby (1977), each point being the mean of several weighings. Caterpillars were excluded because of the very different length: dry weight relationship for this prey class. The overall regression using log:log data was

$$\log W = 2.10 \log l - 2.66 \qquad (n = 10, r = 0.92)$$

where W = prey weight (mg dry wt) and l = prey length (mm). The contribution of different prey length categories in terms of dry weight was then calculated for L.agilis (July/August 1977 sample) and L.vivipara (total sample). For each 1 mm length class the product of the number of prey

TABLE 5.11 ANNUAL FOOD CONSUMPTION OF *L.agilis* (1977)

Age class or live weight	Annual food consumption	
	$g g^{-0.7} yr^{-1}$	$KJ g^{-0.7} yr^{-1}$
sub-adult	12.7	94.5
7.5 g	11.8	87.5
12.0 g	12.2	91.0

items (n_i) and the dry weight obtained from the above regression (w_i) gave the total dry weight of that length class. The dry weight of each prey item over 20 mm was estimated separately. Most of these items were caterpillars; the dry weight of caterpillars was given by the equation

$$W = 1.23 \times 10^{-3}\ l^3 + 0.2405 \text{ (Bibby 1977).}$$

Figure 5.10 shows the percentage contribution to the total dry weight ($\Sigma\, n_i W_i$) of different 5 mm length classes. The dry weight of items below 5 mm in length taken by L.agilis is small considering the large number of items of these lengths taken. The importance of Lepidoptera larvae to L.agilis is shown by the large contribution to the total dry weight of prey over 20 mm.

If the total dry weight ($\Sigma\, n_i w_i$) of the July/August 1977 sample is divided by the total number of prey items, the mean weight of the prey items is obtained (11.6 mg dry wt). The daily food consumption of a lizard weighing 7.5 g (the mean live weight of the lizards in the sample) at this time was 126.9 mg dry wt day^{-1}. The number of items taken daily is, therefore, 10.9, which, assuming an 8 hour day, is equivalent to one item every 44 minutes.

If the same calculation is carried out for L.vivipara, the mean dry weight of the prey items is 3.8 mg dry wt, the daily food consumption 53.8 mg dry wt day^{-1}, so, for a 3.6 g lizard, the number of items taken daily is 14.0 or one item every 34 minutes. The greater food consumption of L.agilis is therefore achieved by taking larger prey rather than by taking prey at a faster rate.

Since larger items are much rarer than smaller ones (see section 4.9(iii)) it would appear that individuals

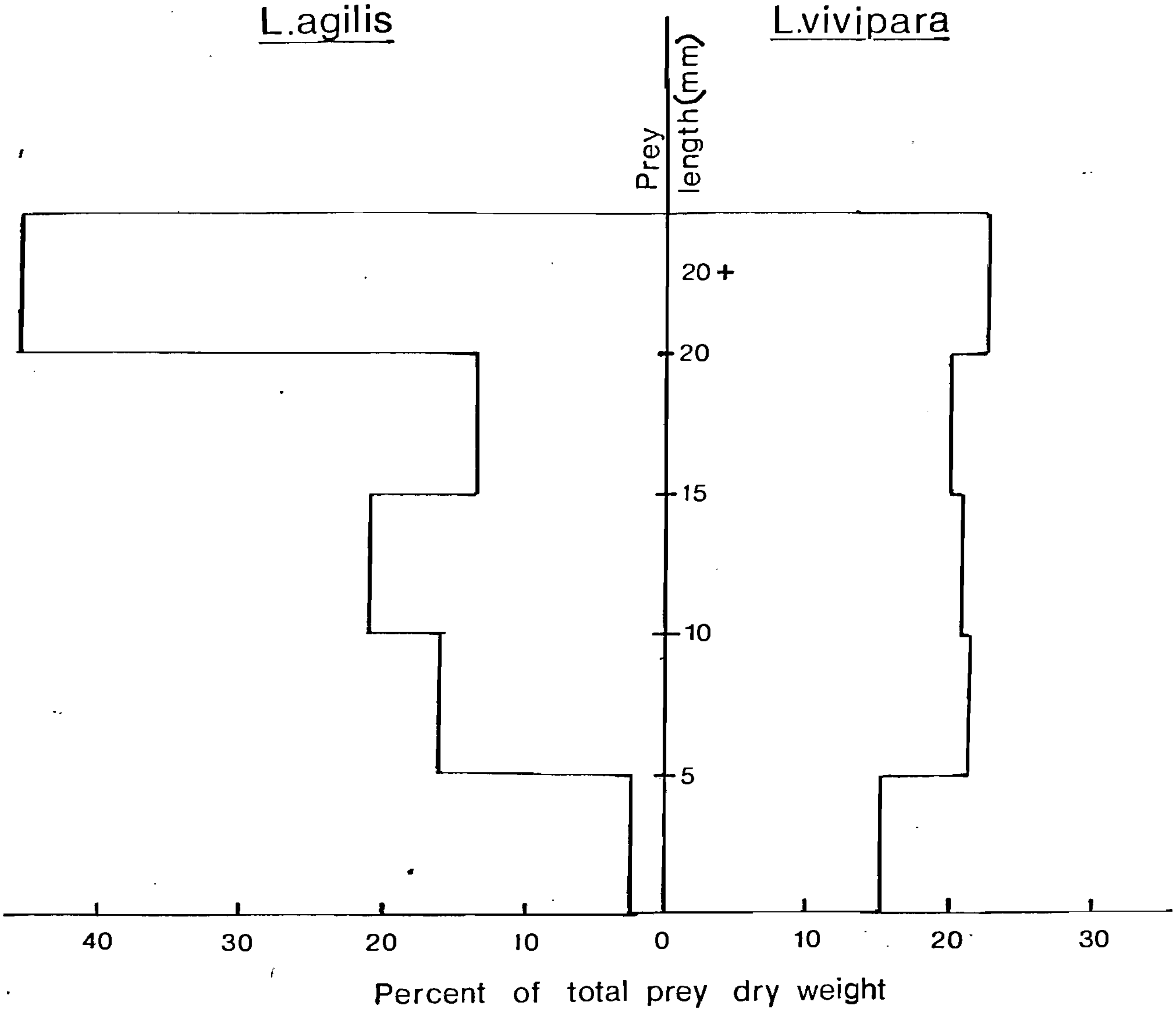

FIGURE 5.10 Comparison between L.agilis and L.vivipara of the contribution to the total prey dry weight of different 5 mm prey length classes. L.agilis, July/August 1977 sample; L.vivipara, total sample.

of L.agilis have a harder task catching the requisite number of items each day than individuals of L.vivipara. To maintain the required level of food consumption in the long term individuals of L.agilis probably have to exploit local and seasonal abundances of prey, which they are better able to do than individuals of L.vivipara because of their larger stomach volume. The exploitation of seasonally abundant prey by L.agilis was well illustrated by the large number of ant queens taken at Soldiers Road in 1975 (Figure 4.2). It is also possible that the clumping of certain prey groups in individual faecal samples (section 4.7(i)) reflects the exploitation of locally abundant prey.

L.vivipara, on the other hand, has not the same need of locally and seasonally abundant prey which, in any case, it could not exploit as effectively; so one might expect individuals to adopt a more conservative foraging strategy, compared with the more opportunistic L.agilis. Some dietary differences between the species seem to support these speculations. First, L.agilis took a wider range of prey than L.vivipara (both taxonomically and in terms of prey hardness) and second, the percentage of the total variance in prey size caused by 'between' snout-vent length variation was greater in L.vivipara than L.agilis, indicating that individuals are more specialized.

In conclusion, the comparative strategies of L.agilis and L.vivipara (in their extreme forms) could be explained as follows: L.agilis is opportunistic, exploiting, where possible, seasonal or local concentrations of prey by feeding at high rates. L.vivipara has a conservative foraging strategy and, consequently, a more specialised and more predictable diet. The large stomach capacity of individual L.agilis, their ability to exploit temporary abundances of food, and the notable seasonal variation in food consumption all suggest that the amount of available food does limit the food consumption of L.agilis, at least during part of the year.

CHAPTER 6

GENERAL AND REPRODUCTIVE ECOLOGY OF LACERTA AGILIS

6.1 Introduction

The data presented in this chapter concern several different but related aspects of the ecology of Lacerta agilis. They were collected mainly during the course of examining the feeding ecology of L.agilis and provide a framework within which feeding and other aspects of the ecology of L.agilis can be considered. Some of the data, particularly that concerning reproduction, may be of relevance to the conservation of L.agilis in England.

The main theory in this chapter concerns the calculation of the reproductive effort of L.agilis. The concept of reproductive effort in lizards was first considered by Tinkle (1969b). Tinkle and Hadley (1975) have since examined reproductive effort in several species of iguanid lizards in the U.S.A. in more detail. There follows first, however, a brief account of some previously published data concerning the life history of L.agilis.

Details of the life history of L.agilis in England are given by Smith (1951) and by Simms (1970) (for Lancashire lizards). Krasavtsev (1936) quotes similar details for L.agilis exigua Eichwald in Russia (near Moscow, 58.5 ° N) as does Rudeberg (1956) for L.agilis in Sweden, largely from observations in an outdoor enclosure.

Hibernation begins in the latter half of September or early October (Smith 1951). Krasavtsev (1936) found hibernacula were usually of single occupancy, and usually old burrows of Sorex or Microtus; hibernation began in early September and was broken in late April. Simms (1970) found early April was the average time of first emergence for male L. agilis with females emerging a few weeks later.

Mating takes place in May and June but is most frequent in May (Smith 1951) and in early May in Russia (Krasavtsev 1936). The time between mating and egg-laying was between 39 and 45 days for four different females and the eggs were laid between the 17th and 24th of June (Rudeberg 1956). Simms (1970) has obtained fourteen egg-laying dates between mid-June and early July. The number of eggs in a clutch are reported to be 6-13 (Smith 1951), 5-11 mean 7 (Simms 1970), 4-9 mean 6.5 (from 11 clutches) (Liberman & Pokrovskaja 1943) and 8-9 maximum 14 (Krasavtsev 1936).

Incubation time is 7-12 weeks (Smith 1951) and was between 63 and 72 days for the females observed by Rudeberg (1956). Hatching takes place in late August or early September (Simms 1970), early August (Krasavtsev 1936) and juveniles have also been observed in Dorset in early August (Smith 1951), which is probably about the earliest date that hatching is ever likely to take place in England. Liberman and Pokrovskaja (1943) have found that the maximum speed of development of the egg takes place at 32°C.

6.2 Materials and Methods

The majority of methods relevant to this chapter are to be found in chapter 3.

The following procedure was used to measure the temperature conditions for the incubation of the clutch. A clutch was uncovered by excavating the same hole as that made by the female lizard, taking care not to disturb the more compact sand immediately above the clutch. A thermistor lead was then inserted amongst the eggs and the sand replaced, the other end of the lead being hidden. Temperatures were read using a Yellow Springs telethermometer in conjunction with series 400 thermistor probes.

6.3 Spring emergence and behaviour

Observations on the spring emergence and behaviour of L.agilis were made at the Railway site in 1976; some additional observations were made in 1977.

The first individual was seen on 1 March 1976 but generally it was very unusual to see any lizards in March and lizards were not seen regularly until April. The timing of the emergence of the thirteen males and seven females that were known to have overwintered along the Railway bank is illustrated in Figure 6.1. Males emerged approximately two weeks before females.

The most common overwintering sites were holes along the small bank beside the line and in the wall behind it, which formed a step up to higher ground to the north. Each overwintering site was normally occupied by only one lizard although one site seemed to be used by two males during one winter. Of the four males that overwintered along the Railway bank both in 1975-76 and 1976-77 three used the same site in each year and one changed to a site only a few metres from that used the previous year. This new site had been occupied by a larger lizard in the

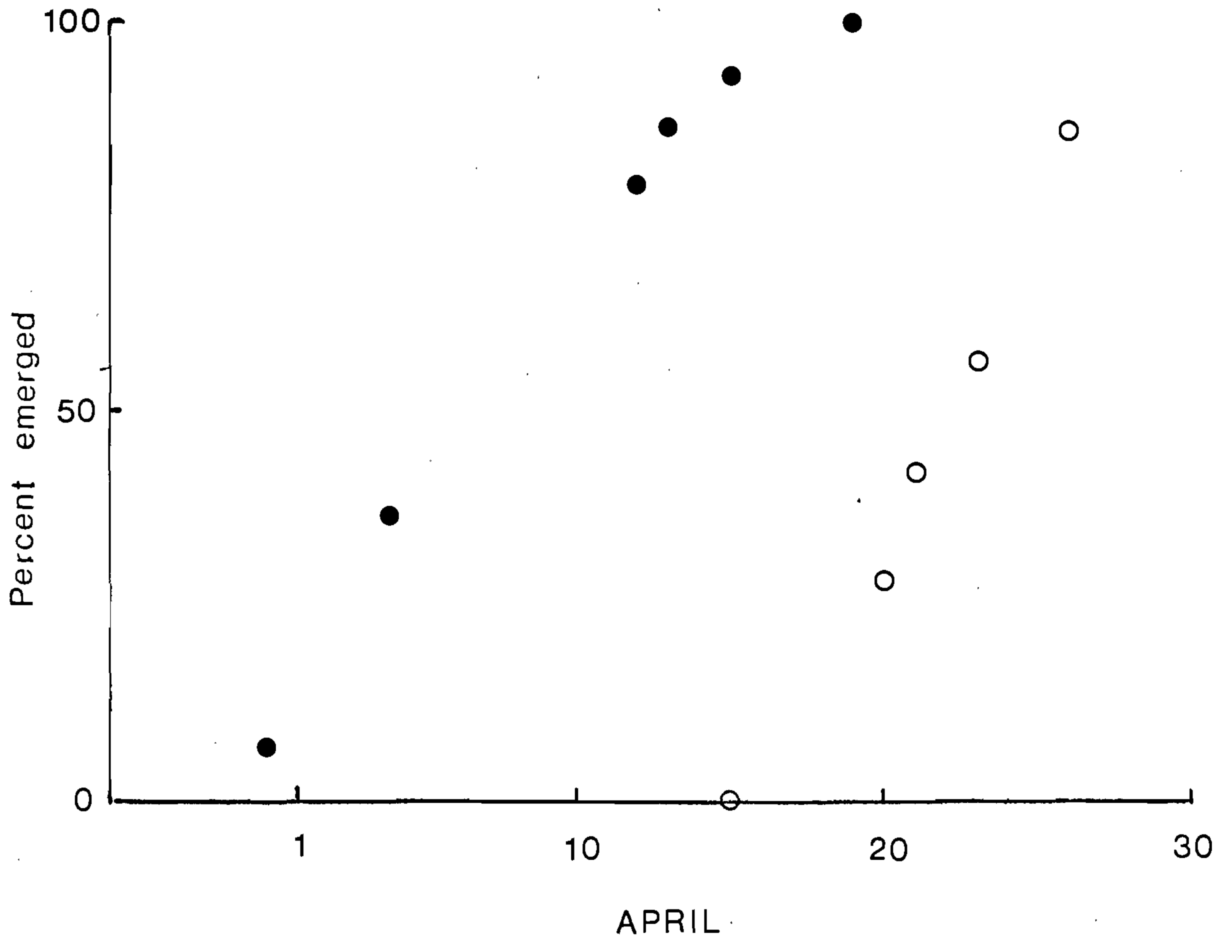

FIGURE 6.1 The spring emergence of L.agilis. The percentage of the total known overwintering population (14 males, 7 females) that had emerged during April 1976 is shown for males (closed circles), and females (open circles).

previous year.

After emerging from their overwintering holes, males spent long periods basking, rarely moving more than a metre from the holes. Males basked even in overcast conditions when they would have no chance of raising their body temperature to the preferred level. Individual males were occasionally observed feeding at this time, usually when prey was sighted while an individual was basking.

On 17 April 1976 several males were observed to have left the immediate vicinity of their overwintering sites. After this date it became increasingly rare to see a male in the immediate vicinity of his overwintering site. Overwintering holes were still used as overnight sites but not necessarily by the same lizard that overwintered there.

Shortly after this local dispersal of males occurred the first females were seen. In contrast to the males, females did not bask for long periods outside their overwintering holes.

Courtship behaviour between pairs was first observed in 1976 on 23 April and was seen regularly during the following two weeks but not after 6 May. In 1975 however, a much cooler spring, copulation between a pair on another site was observed on 25 May, and in 1977 mating was also later than in 1976.

6.4 Egg-laying

Observations on the egg-laying behaviour of L.agilis were made mainly at the Railway site during 1977. All of the egg-laying sites found were in bare sand, usually on a sandy slope with a predominantly southerly aspect. The female digs a characteristically shaped hole in the bare sand, inclined at about 30° to the horizontal. The clutch is deposited at the base of the hole; the depth of six clutches found in 1977 varied between 60 and 90 mm and the mean depth was 70 mm. The hole is usually filled in with sand after the clutch is laid, but the entrance to the hole can often still be seen, enabling the clutch to be located. Many of these characteristic egg-laying holes, however, do not contain eggs. Some females therefore probably indulge in preliminary excavations before digging the burrow in which they lay. Some of these excavations were also seen on some bare slopes of clay slag, as opposed to the normal sand, but no eggs were ever found in these holes.

The majority of egg-laying activity in 1977 took place between 23 June and 3 July. After a warmer spring it would probably take place earlier, in early or mid June. It was normal for the eggs of several females to be laid on the same area of bare sand. On one occasion two females laid in the same burrow.

Only one marked female was caught while egg-laying. However, this capture was of interest because the bare sand where the female was found was 130 m away from her normal home range area. This female was seen at one of her normal basking sites on 20 June, was found at the egg-laying site 130 m away on 27 June and was again back at the original basking site on 15 July. (Figure 6.4). This movement is greater than those associated with normal movements within the home range (see chapter 8). Furthermore, she did not go to the closest area of bare sand for a sand patch on which other females laid was located only 20 m from one of her normal basking sites (Figure 6.4).

The temperature of one clutch during several sunny days during the incubation period is illustrated in Figure 6.2. This particular clutch was laid in bare sand on a south-east facing slope at a depth of 80 mm. The site became shaded at approximately 14.30 B.S.T. which explains why the temperature of the clutch declined after this time. Also shown in Figure 6.2 is the shade temperature at ground level at the same general location. The clutch temperature reached a maximum of 32°C and at this time was approximately 9°C warmer than the ground temperature.

6.5 Clutch size and reproductive effort

Of five clutches found one consisted of five eggs, two of six and two of seven. The mean weight of the eggs measured was 0.64 g (n = 15, range 0.49 - 0.96 g). Of particular importance, however, is the relationship between clutch size and the size of the female. This relationship is usually obtained by dissecting pregnant females, which in this case was not possible. One female was weighed immediately before and after egg-laying and from the weight loss it was estimated that this female (snout-vent length 74 mm) laid five eggs, which was later confirmed by excavation of the clutch. However, this was the only case where it was possible to obtain

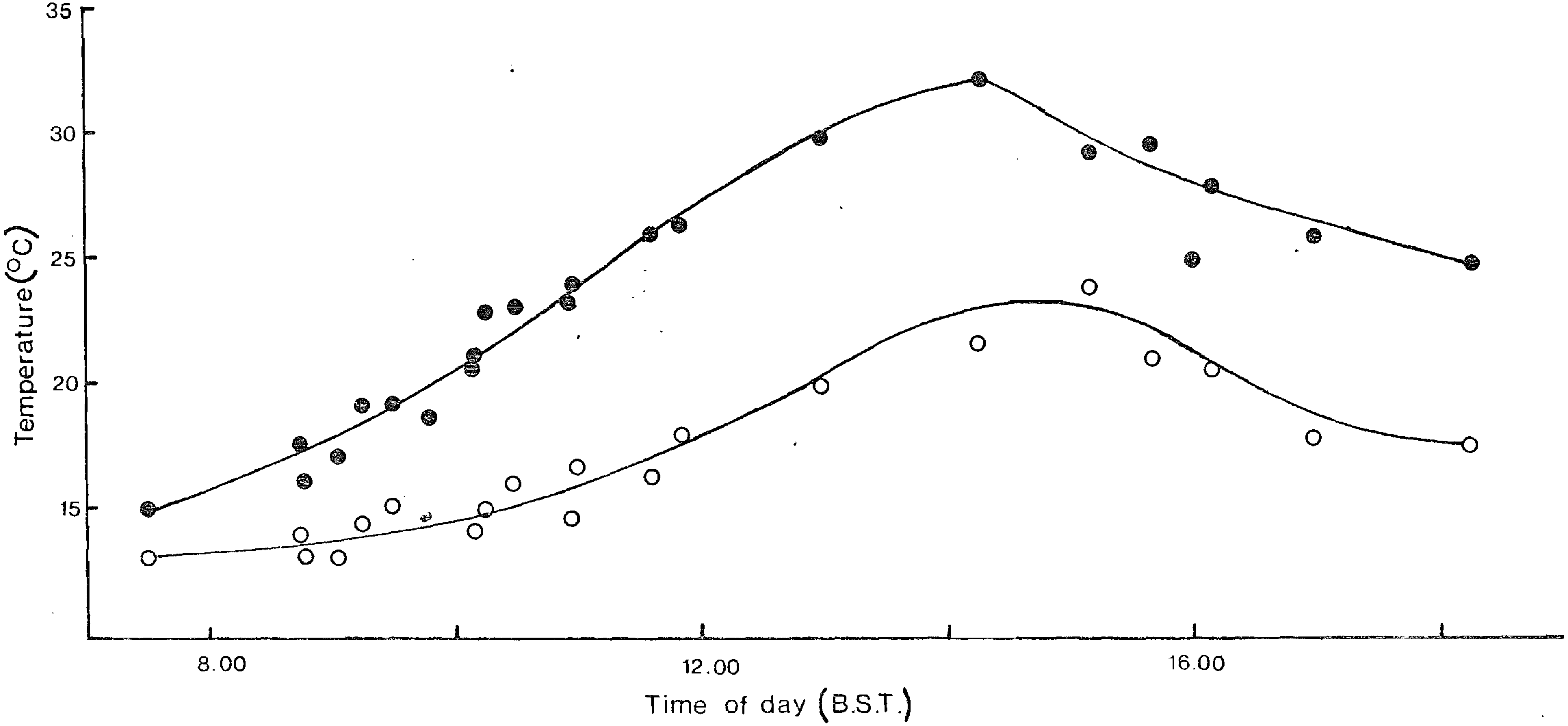

FIGURE 6.2 Comparison of the temperature of one clutch of eggs of L.agilis, at a depth of 80 mm in bare sand (solid circles), with ground temperature (shade) at a nearby location (open circles). Data for five predominantly cloudless days in late July and early August 1977 have been combined. Curves fitted by eye.

a direct relationship between snout-vent length and clutch size for a single lizard. However it was possible to make an indirect estimate of this relationship from the weights of some females weighed before and after egg-laying. The relationship between snout-vent length and these weights is shown in Figure 6.3. The weights of females before egg-laying are all of gravid females in late June and early July 1977. Of the females weighed after egg-laying one was of a female kept in a small vivarium, one of a gravid female taken into captivity in 1975, who subsequently laid her eggs in captivity, the rest being females caught immediately after egg-laying in late June and early July 1977. All of these females were in an emaciated condition.

From Figure 6.3 a female of snout-vent length 74 mm would lay five eggs and a female of snout-vent 88 mm eight eggs. This is approximately the range of clutch size variation normally quoted in the literature.

It is now possible to estimate the reproductive effort of females of L.agilis, which is the proportion of the total energy budget of an organism devoted to reproduction (Tinkle & Hadley 1975). The annual food consumption of different aged L.agilis was estimated in the previous chapter. The annual food consumption (c) was converted to annual assimilation (A) by the equation

$$A = c - (c - 0.89c) + (c - 0.93c) \quad \text{(Avery 1975b).}$$

It was then assumed that the calorific value of lizard food was 5240 cal g dry wt^{-1} (Avery 1971). The resulting annual assimilation of L.agilis in calories is shown in Table 6.1.

The energy content of the clutch was determined by

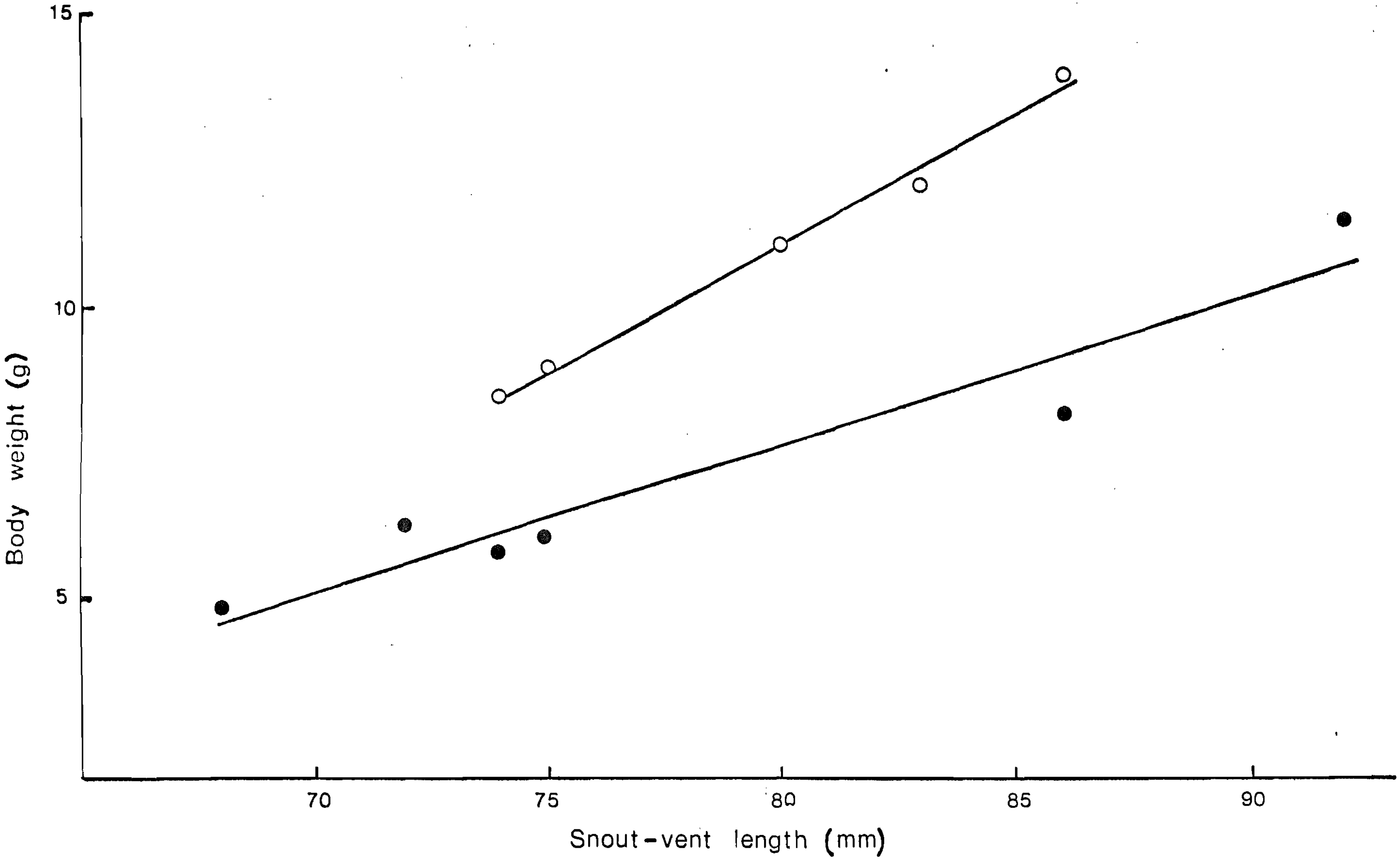

FIGURE 6.3 Regressions of body weight against snout-vent length for females caught before (open circles) and after (closed circles) egg-laying.

TABLE 6.1 REPRODUCTIVE EFFORT OF L.agilis AND L.vivipara. THE ESTIMATES FOR L.vivipara ARE CALCULATED FROM DATA IN AVERY (1975b). THE VALUES FOR THE ANNUAL ASSIMILATION OF L.vivipara ARE THE MEANS OF THREE DIFFERENT YEARS.

(a) L.agilis

Snout-vent length (mm)	Live weight (g)	Annual assimilation (cals)	Energy in clutch (cals)	Reproductive effort
72	7.5	70328	7606	0.11
78	9.7	86039	11028	0.13
84	12.0	101604	14831	0.15

(b) L.vivipara

Snout-vent length (mm)	Live weight (g)	Annual assimilation (cals)	Energy in clutch (cals)	Reproductive effort
55	2.4	25819	2070	0.080
60	3.5	33831	2994	0.088
65	4.3	39387	3695	0.094

assuming that the water content of L.agilis eggs was 40.3% (Liberman & Pokrovskaja 1943) and that their energy content was 6.37 cal/mg ash-free dry wt (the mean of the value for several different lizard species, Tinkle & Hadley, 1975).

The reproductive effort of different aged females of L.agilis is shown in Table 6.1.

6.6 Dispersal of juveniles and sub-adults

On hatching juveniles burrow vertically upwards; the small exit hole above the clutch can sometimes be observed. It was not possible to obtain detailed data on the movements of juveniles but observations suggested that, during the time before their first winter, most juveniles tended to stay near to the area of bare sand where they were born. It was often possible to observe several juveniles together basking at the interface between the sand and the vegetation.

The position of the sightings made of sub-adults in the spring of the following year is also shown in Figure 6.4b. The sub-adults tended to remain in the immediate vicinity of the areas of bare sand. By July a more general distribution of sub-adults over the area was apparent (Figure 6.4c).

6.7 Age at maturity

Little information was obtained on the age of individuals at sexual maturity. Both males and females do not mature until they are at least 20 months old. Most males probably mature at this date. The smallest breeding female observed measured 68 mm in snout-vent

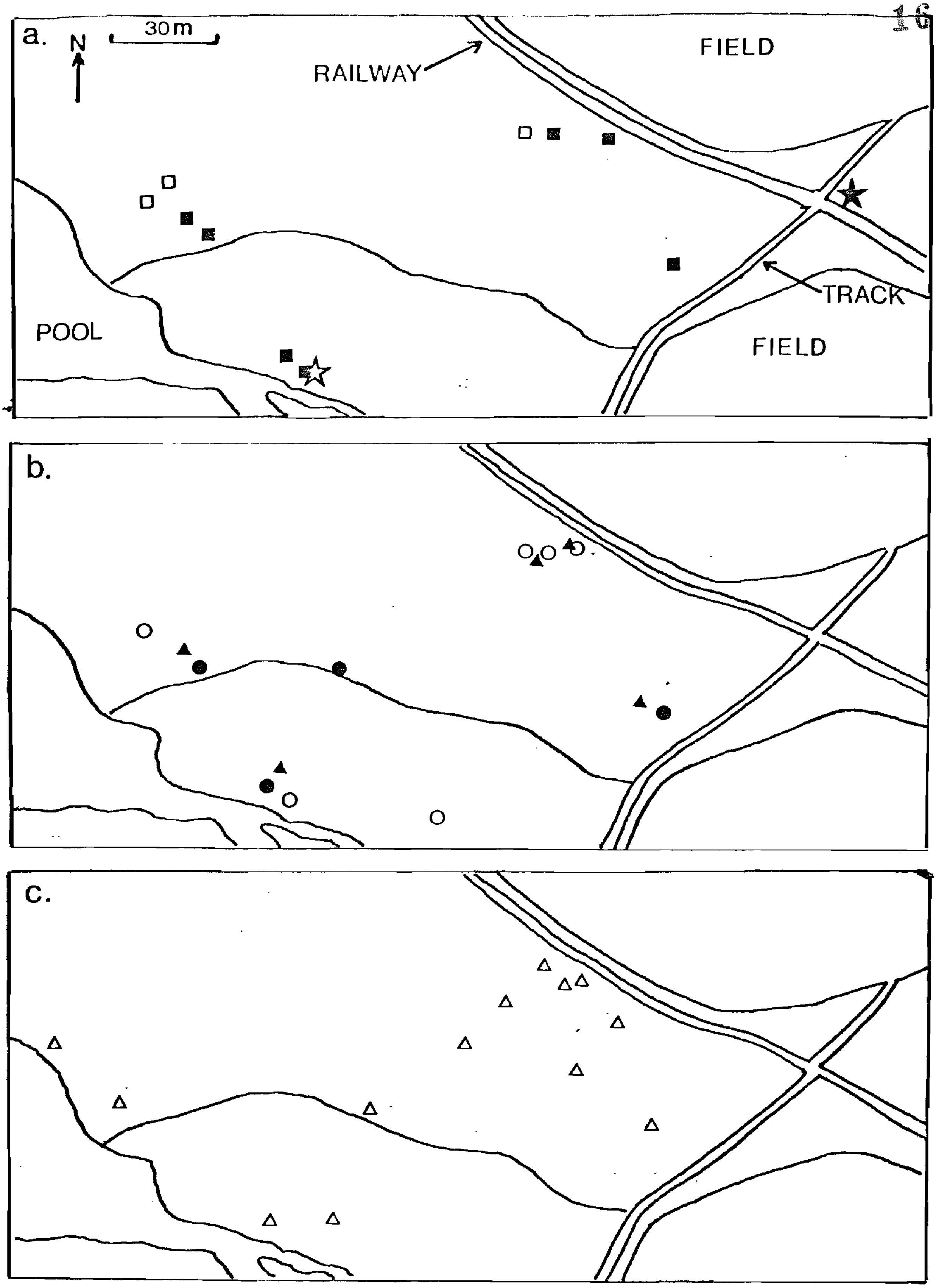

FIGURE 6.4 The dispersal of juvenile and sub-adult L.agilis. a. shows the area to the west of Figure 2.2 Closed squares, major areas of bare sand; open squares, areas of clay slag. The position of the egg-laying site of one female is shown by the open star; the closed star shows the nearest point of her normal known home range area. b. Circles show areas where some egg-laying activity was observed (i.e. digging) in June/July 1977. Closed circles show those areas where eggs were definitely known to have been laid. Triangles show sub-adult sightings in spring 1977. c. Triangles denote sub-adult captures in July, August and September, 1977.

length. One female definitely did not breed in the year following her sub-adult year.

6.8 Longevity

It was not possible to estimate mortality directly by the capture and recapture of marked individuals because too few lizards were marked.

However, the annual adult mortality can be estimated from the ratio of sub-adult to adult lizards in the population (Avery 1975a). If the annual age specific mortality (P_a) after year one is assumed constant it is given by the equation

$$P_a = \frac{100\ N_i}{N_a + N_i} \quad \text{(Avery 1975a)}$$

where N_a = number of adults
and N_i = number of sub-adults

further assumptions being that the sex ratio is unity, age specific natality is constant from year to year and age specific immigration is the same as emigration.

Table 6.2 shows the number of sub-adults and adults caught in three different populations. P_a was calculated on the assumption that these numbers gave an unbiased estimate of the ratio in each population.

Four different estimates of P_a lie between 25 and 36%. An annual adult mortality of 28% means that an individual that has survived until the latter part of its sub-adult year has a mean life expectancy of between three and four years.

These estimates seem consistent with the snout-vent length distribution of individuals in different populations

TABLE 6.2 NUMBER OF ADULTS (N_a) AND SUB-ADULTS (N_i) IN DIFFERENT POPULATIONS OF <u>L.agilis</u>, AND ANNUAL AGE SPECIFIC MORTALITY AFTER AGE ONE $\left(P_a = \frac{100\ N_i}{N_a + N_i}\right)$

Study Area and dates		Method of Capture	N_i	N_a	P_a
Soldiers Road	July/Aug 1975	Pitfall traps	6	15	29%
Soldiers Road	July/Aug 1976	Pitfall traps	10	18	36%
Railway	15 July - 15 Aug 1977	Hand	9	28	25%
Hartland Moor N.N.R. (After fire)	15 Aug - 7 Sept 1976	Hand	7	21	25%
Total			32	82	28%

(Figure 6.5) when the rate of growth of individuals is considered.

Pianka (1970) and Tinkle & Ballinger (1972) have both used the frequency of tail breakages within lizard populations of an index of the degree of predation. Table 6.3 shows the frequency of tail breakage amongst all individuals of L.agilis and L.vivipara that were captured during the whole study.

6.9 Density

(i) Soldiers Road Study Area 1976

The frequency distribution of the number of times that each individual was caught in the pitfall traps at Soldiers Road during 1976 is shown in Figure 6.6. If each individual had an equal chance of being caught in the traps then it would be expected that this distribution would approximate to a Poisson distribution. In fact, the observed distribution differs markedly from the Poisson; there are both too many animals caught five or more times and too many caught only once.

Lizards that were caught only once were more likely to be caught near the edge of the site than in the centre (Figure 6.7). Of eleven lizards caught only once, four were caught inside the line in Figure 6.7 and there were only two captures of previously marked lizards outside the line.

This suggests that the animals caught only once were lizards whose home ranges were largely outside the study area. Some may also have been transient individuals, not settled in permanent home ranges. Individuals caught

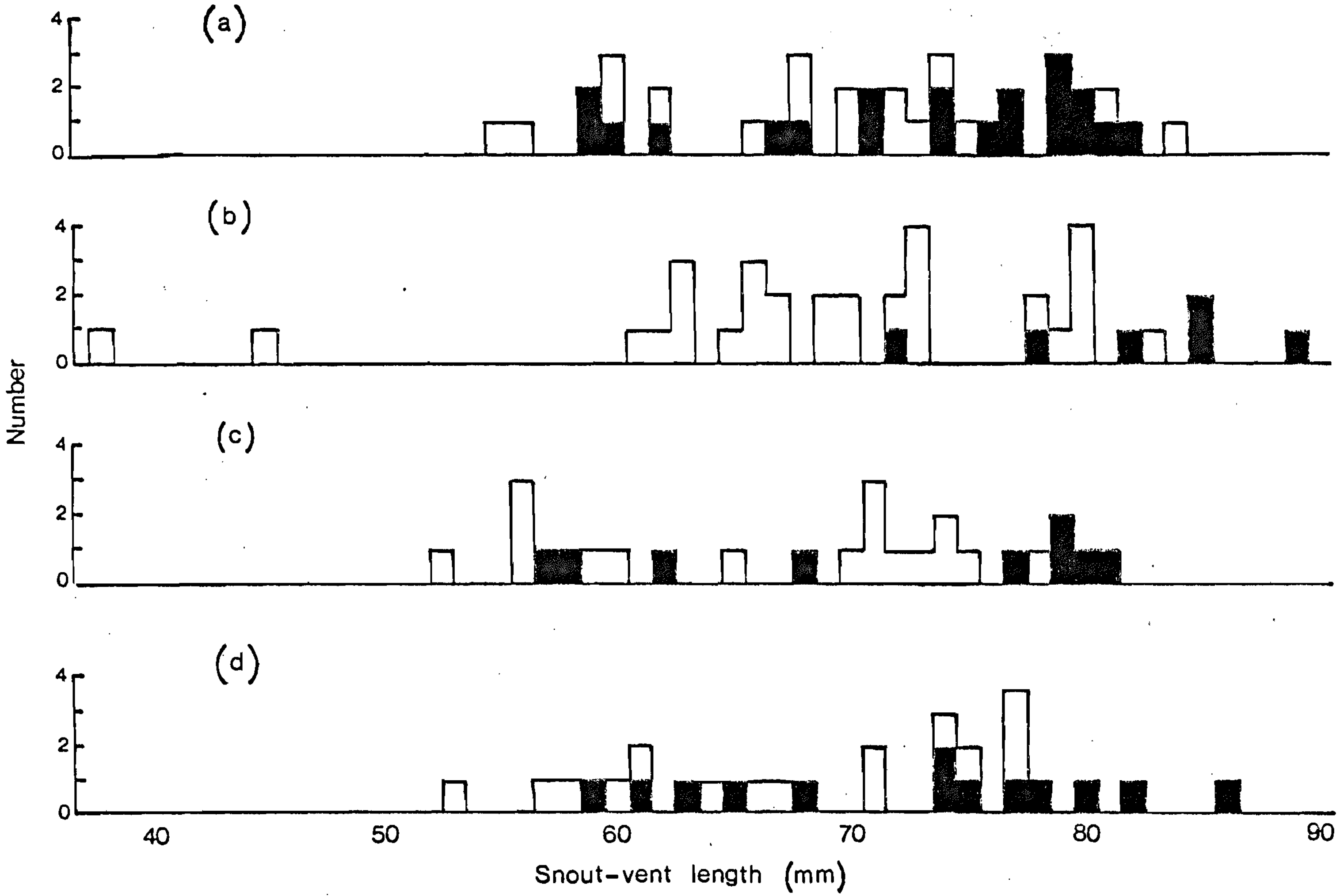

FIGURE 6.5 Frequency distributions of snout-vent length for L.agilis. (a) Railway study area 15th July - 15th August 1977, (b) Railway April and May 1977, (c) Soldiers Road study area July and August 1976, (d) Hartland Moor N.N.R., 15th August - 7th September 1976 (lizards caught after fire). Shaded blocks females; open blocks, males.

TABLE 6.3 PERCENTAGE FREQUENCY OF BROKEN TAILS FOR *L.agilis* AND *L.vivipara*. FIGURES IN PARENTHESES ARE SAMPLE SIZES

	L.agilis	*L.vivipara*
juveniles	-	4 (27)
sub-adults	28 (43)	33 (15)
adult ♂	41 (95)	33 (27)
adult ♀	33 (79)	45 (22)
old ♂ (sv > 75 mm)	56 (24)	-
old ♀ (sv > 80 mm)	46 (28)	-

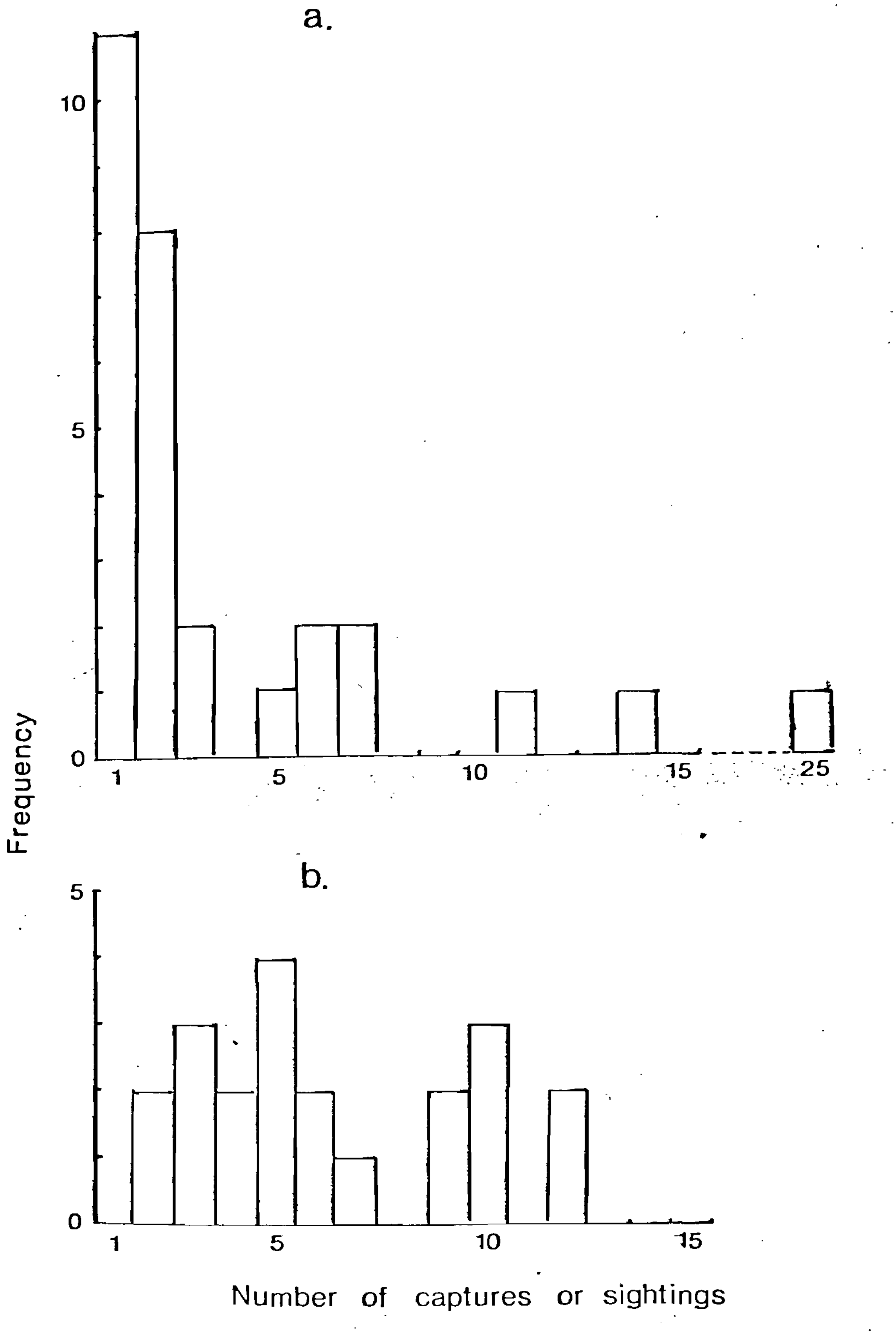

FIGURE 6.6 Frequency distributions of the number of captures or sightings of different individuals of L.agilis.
a. Soldiers Road 1976; b. Railway, April and May 1976.

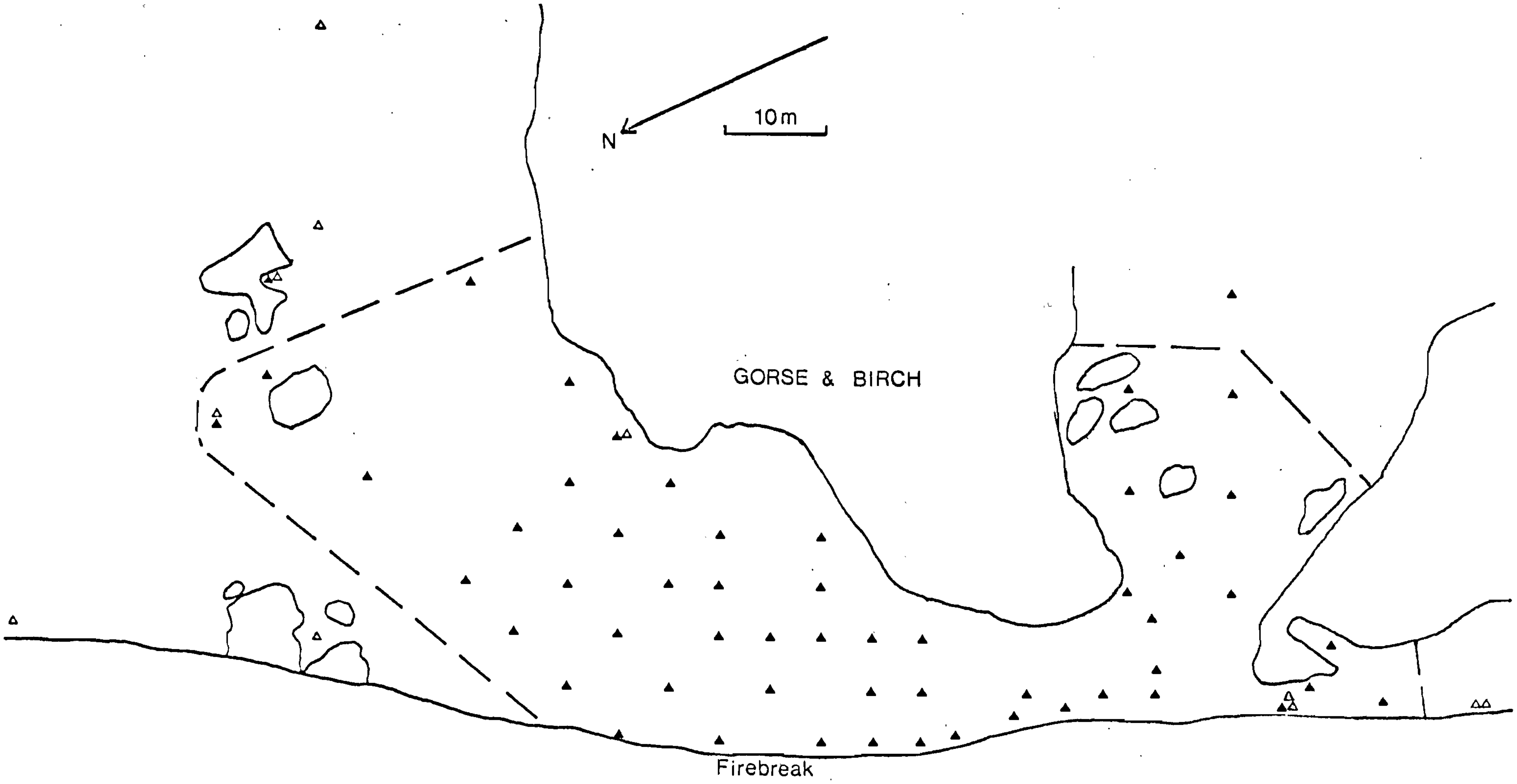

FIGURE 6.7 Captures of *L.agilis* in pitfall traps at Soldiers Road in 1976. Open triangles, capture point of lizard caught only once in 1976; closed triangles, capture point of lizard or lizards caught more than once in 1976. The broken line delineates the area used for the density estimation.

only once were therefore classified as non-residents and excluded from the density calculation.

The large number of captures on many of the other individuals indicated that these were permanent residents and that it was likely that all of these individuals had been caught. This was therefore assumed.

The area of the site inside the boundary line shown in Figure 6.7 was 4000 m^2. The boundary was drawn so as to minimise the number of home ranges that crossed it. The density of L.agilis was therefore 48 individuals $hectare^{-1}$ and the biomass was 301 g $hectare^{-1}$ (using the mean weight of lizards caught more than once).

(ii) Railway Study Area, 1976

Over 90% of captures and sightings of known individuals of L.agilis were made during April and May so the density estimates are for this period. Figure 6.6 shows a frequency histogram of the number of times each animal was caught at this time. This distribution indicates that the majority of individuals had been captured since very few individuals were caught one or two times.

A total of twenty-nine different individuals were seen in the area to the east of the farm trackway (5500 m^2, excluding the area of woodland, see Figure 2.2) giving a population density and biomass of 52 individuals $hectare^{-1}$ and 488 g $hectare^{-1}$.

6.10 Discussion

(i) Spring emergence

The most notable and characteristic feature of the spring emergence of L. agilis is that males emerge several weeks before females. Volsøe (1944) has demonstrated that male adders (Vipera berus) in Finland undergo a period of basking of about four weeks after spring emergence. The function of this basking period is to allow spermatogenesis to occur and this is presumably also the function of the spring basking of male L. agilis.

The priority for males of L. agilis at this time appears to be to complete spermatogenesis as soon as possible, for they seem to take any opportunity to raise their body temperature. They may be observed basking even on dull days when, later in the year, they probably would not emerge at all. This may be one reason why males lose weight in the spring (see previous chapter), for on such days individuals have little chance of feeding efficiently yet their energy expenditure is clearly greater than if they did not emerge. Thus males at this time may have to balance the gain in fitness of rapid spermatogenesis against the associated energetic cost.

(ii) Clutch size and reproductive effort

It would have been desirable to measure many of the quantities needed to estimate the reproductive effort of L. agilis with more precision but in many cases this presented considerable practical difficulties. Nevertheless, it seemed useful to estimate the reproductive effort of L. agilis at this stage.

The method used to obtain the relationship between clutch size and snout-vent length for L. agilis was clearly less precise than the normal method of dissecting gravid females. Another possible method which also avoids the sacrificing of individuals is to collect gravid females and allow them to lay in moist sand in the laboratory. The eggs could then be replaced in suitable sand in the field.

The main problem with weighing females immediately before and after egg-laying was to obtain measurements on enough individuals. It is clearly important that the weighings are made as soon as possible before and after egg-laying since an individual's weight can alter significantly in only a short time through feeding.

Both Williams (1966) and Gadgil & Bossert (1970) considered that reproductive effort should increase with age provided that there is a cost to future reproduction from reproduction at the current age. The increase in reproductive effort with age shown by L.agilis therefore suggests that there would be some cost associated with greater effort at an early age which would result in a lower lifetime effort and decreased fitness. This might come about from an increased probability of mortality or a decrease in the number of eggs laid in future years, both of which could be caused by a higher early effort.

Tinkle & Hadley (1975) have estimated the reproductive effort of three species of lizard (Iguanidae) in a similar way except that they estimated annual assimilation from activity and respiration rather than from food consumption. Effort varied from 0.11 to 0.23. Avery (1975b) estimated the reproductive effort of L.vivipara in terms of the dry weight of the clutch as a fraction of the annual assimilation (dry wt.). The reproductive effort of L.vivipara has been recalculated from the data of Avery as the proportion of annual energy expenditure (annual assimilation) devoted to the clutch, again assuming that the energy content of the clutch is 6.37 cal g dry wt^{-1} (Table 6.1). Reproductive effort is slightly lower than that of L.agilis and does not increase with age to the same extent.

Calculation of the reproductive effort in this manner has so far been carried out for only a few lizard species. However, various indices of effort have been estimated for a far greater range of species. The best of these is probably the ratio clutch calories : body calories (Tinkle & Hadley 1975; Derickson 1976) and this ratio for eleven species of lizard in the U.S.A. varied from 0.42 to 2.42 (Tinkle & Hadley 1975). This ratio for L.vivipara (0.40) indicates that this species has a very low effort. This is consistent with the theory of Avery (1976, 1978) that L.vivipara has little 'spare' energy available and reproduction may be one area where economies in energy expenditure are made. Because of these energetic constraints, the cost of a higher reproductive effort may be relatively greater for L.vivipara than for other species. This, together with the extremely high annual adult survivorship for the species (Avery 1975a) may explain why the reproductive effort shows only a small increase with age.

It is interesting that Sceloporus jarrovi, also a viviparous species, had a low reproductive effort (in Arizona, Tinkle & Hadley 1975). These estimates of reproductive effort do not take into account such reproductive energy expenditures as courtship behaviour and mating, the cost of synthesising the materials of the clutch and any cost involved in carrying the clutch. Viviparous species have to carry the clutch for longer than oviparous species and this may lead to extra energy expenditure for two reasons. Firstly, gravid females may be less efficient feeders. Secondly the incubation of the clutch may involve additional energetic expenditure. This may depend on the prevailing weather conditions. On dull, overcast days, females may bask in order to speed the development of the embryos. The energetic demands of such in situ basking would not be compensated for by equivalent returns from feeding; individuals would probably lose less energy by not emerging at all. Thus females may have to use additional energy in order to speed the development of the embryos, in much the same ways as males do in the spring, to hasten spermatogenesis. This component of reproductive effort would clearly be greater for viviparous than oviparous species. Unfortunately there is no data on the thermoregulatory behaviour of gravid female _L.vivipara_. The viviparous lizard _Sceloporus jarrovi_ undergoes long periods of in situ basking during the winter (Tinkle & Hadley 1973) which may also have the function of quickening the development of the embryo. The extra energy used in this behaviour may be an important additional component of reproductive effort. Congdon, Ballinger & Nagy (1979) have recently measured the energy expenditure of _S.jarrovi_ in winter. Individuals spent more than three times as much energy as they would have in remaining inactive and not basking.

Both *L.agilis* and *L.vivipara* do not become sexually mature until at least their second complete season. Although males of both species are probably mature in their second spring when they are approximately 20 months old, some females of *L.vivipara* may not breed for the first time until the following year (Avery 1975a) and this is also probably true of some females of *L.agilis*. Thus the lifetime reproductive effort of females of either species is much lower relative to the annual effort, when compared with an annual species such as *Uta stansburiana*, which breeds only once, in its first year (Tinkle 1967).

A notable difference between *L.agilis* and *L.vivipara* is in the size of individual eggs. The ratio of egg dry weight : dry body weight of a female *L.agilis* with a snout-vent length of 78 mm is 0.11 compared with a female *L.vivipara* of approximately the same age (snout-vent length 60 mm), where the ratio is 0.05. It should be remembered, however, that the eggs of *L.agilis* were weighed wet. Reptile eggs can absorb considerable amounts of water between laying and hatching (Dmi'el 1967). However there also seems to be a considerable difference between the weights of newly hatched juveniles of each species (chapter 7). The same ratio of egg dry weight : dry body weight for fourteen species of lizards in the U.S.A. varied from 0.03 to 0.20. Pianka (1972) has suggested that species that are K selected may lay relatively larger eggs than r selected species because in a more competitive environment with the population near K, larger juveniles hatching from larger eggs should have a competitive advantage. Derickson (1976) found that *Sceloporus graciosus*, a K selected species, had a larger relative egg size than *S.undulatus*, an r selected species, and juveniles of *S.graciosus* hatching from eggs with higher energy contents had a higher survivorship. However, Tinkle & Hadley (1975) found little evidence that supported the idea of Pianka. Both *L.vivipara* and *L.agilis* have the characteristics of K selected lizard species of a high annual adult survivorship and delayed maturity (Tinkle, Wilbur & Tilley 1970) so this does not seem a likely explanation for the egg size difference.

Why, then, does not *L.vivipara* devote the small amount of energy available to reproduction into producing fewer, larger eggs? Why does not *L.agilis* produce a greater number of smaller eggs? Presumably the advantage of a larger egg/juvenile of *L.vivipara* in terms of an increased probability of survival is not sufficient to outweigh the disadvantage of a decrease in clutch size. For *L.vivipara*, if the clutch size was halved and the egg size doubled the juvenile mortality would have to be reduced from 90% to approximately 80% for the replacement rate (R_0) to remain the same (calculated from data in Avery 1975a). Whether this reduction in mortality occurred would depend on the causes of juvenile mortality and there is no quantitative data on this subject.

Juveniles of *L.agilis* hatch about a month after those of *L.vivipara*, leaving comparatively little time before winter submergence. In these circumstances a larger egg size may be important in enabling the juveniles to survive the energy demands of their first winter.

(iii) Longevity and the life history strategies of L.agilis and L.vivipara

The method used to estimate the annual adult mortality was clearly not ideal and there was not data to support some of the assumptions that were made. The method depends on the samples providing an unbiased estimate of the numbers of the two different age classes in the population. Thus it was not possible to use samples taken in the spring because of the clumped distribution of sub-adults at this time. Later in the year, however, sub-adults appear particularly active and this could also bias the samples. Pitfall trap catches would probably be more prone to be affected than hand catches; searching for and catching individuals in the field depends mainly on finding basking individuals. The two estimates of mortality from the pitfall trap catches were indeed higher than the two other estimates. As **far** as hand capture is concerned, a difference in the conspicuousness of sub-adults and adults was not evident and neither was a difference in the probability of capture once an individual had been seen. Despite the problems associated with the method the four estimates of mortality varied only between 25 and 36%.

These values are slightly higher than those obtained for L.vivipara by Avery (1975a) using the same method (19-21%) but are still low compared with the values for most other lizard species that have so far been examined (see Tinkle 1967; Tinkle, Wilbur & Tilley 1970; Fitch 1973; Tinkle & Hadley 1975).

The life history strategies of both L.agilis and L.vivipara are characterised by delayed maturity, low adult mortality, the spreading of reproduction over several years, and probably low reproductive effort. It is interesting to speculate about how this strategy is adaptive in the environmental conditions existing in southern England.

Tinkle & Ballinger (1972) in their study of the intraspecific comparative demography of Sceloporus undulatus (Iguanidae) in the U.S.A. argued that in a northern population (Ohio), selection would favour genotypes associated with delayed maturity, mainly because of the gains in fecundity with age possible given the low adult mortality. There was no evidence that environmental conditions prevented earlier maturity. In a southern population (Texas) selection favoured early maturity. The primary cause of these differences was considered to be a difference in the degree of predation which led to a high adult mortality in Texas and low mortality in Ohio. A difference in the number of predatory species was probably the main reason for the difference in the level of predation. Pianka (1970) also found that northern populations of Cnemidophorus tigris in the U.S.A. were exposed to less predation pressure than southern populations.

The populations of L.agilis and L.vivipara in England are considerably further north than the northernmost population of S.undulatus studied by Tinkle &

Ballinger in Ohio (39°N). It is possible that this far north, climatic constraints which prevent earlier maturation do exist. Indeed, if a hypothetical female of either *L.agilis* or *L.vivipara* was able to mature in her first year extrapolation of clutch size : body weight relationships indicate that she would not lay any eggs.

The degree of predation is undoubtedly an important factor which influences the life history strategies of *L.agilis* and *L.vivipara*. There are comparatively few potential predatory species. Of the three native British snakes *Vipera berus* takes *L.vivipara* but not *L.agilis* (Prestt 1971), *Natrix natrix* feeds predominantly in wet areas and takes large numbers of amphibians, and the feeding habits of *Coronella austriaca* are largely unknown, although individuals have been known to take both *L.agilis* and *L.vivipara* as well as small mammals (Spellerberg & Phelps 1977). This constitutes an extremely low number of predatory reptile species and can be compared with fifteen species of snake and four of lizard known to be potential predators of *Cnemidophorus tigris* (Pianka 1970).

The frequency of broken and regenerated tails has been used by both Pianka (1970) and Tinkle & Ballinger (1972) to compare the level of predation in different populations of the same lizard species. To use this frequency to estimate the level of predation in a lizard species with reference to other species is more dangerous. The frequency of broken tails in a population depends largely on the longevity of individuals. Thus Tinkle (1972) has adjusted his tail break frequencies for adult *S.undulatus* by dividing by the mean life expectancy after maturity in the population. Following this procedure for L.agilis gives an adjusted frequency of approximately 10% which indicates a low level of predation when compared with the adjusted frequency for different populations of S.undulatus (Tinkle 1972). Furthermore, the data indicate that the majority of breakages in both L.agilis and L.vivipara occur by the time individuals are adult since there was only a small difference in the frequency of breakage between adults and sub-adults.

Thus the available evidence suggests that there is comparatively little predation pressure on adults of L.agilis and L.vivipara and this allows a high adult survivorship and the partitioning of reproduction over several years.

A further important factor which may influence the life-history strategy of L.agilis and L.vivipara is the degree of annual variation in reproductive success. It might be expected that there may be large annual differences in the reproductive success of both species, but particularly L.agilis, owing to the comparatively large annual differences in climate in England. It is even possible that in some years, reproduction could fail completely. Such environmental unpredictability would lead to selection for individuals which spread their reproduction over several years.

(iv) Dispersal

Only one female was identified while egg-laying but this case was particularly interesting, both because of the distance travelled from her normal home range area and because she did not lay on the nearest area of sand. Although females from grass and scrub area of the Railway site, where this female had her home range, mated and became gravid in this area, no egg-laying activity or newly hatched juveniles were ever observed in this part of the site, probably because of the lack of suitable bare sand. These observations suggest that gravid females from the grass and scrub area move to the north-west area of the site to lay their eggs. The observation that the one female did not lay on the nearest suitable sand suggests that reasons other than proximity are important in the choice of an egg-laying site. Perhaps females often choose the area of sand where they hatched.

Juveniles of <u>L.agilis</u> tended to stay in the vicinity of the areas of bare sand during the autumn after hatching and during the subsequent spring. This seems to be followed by dispersal of sub-adults, probably starting in late June or early July. Thus the grass/scrub area of the Railway would be colonized by sub-adults at this time, although new adults were occasionally observed to establish home ranges.

There was also evidence from the pitfall trapping that the process of females leaving an area to lay and the subsequent recolonization by sub-adults also occurred at the Soldiers Road site (see chapter 9). Gravid females were not caught in the traps during the egg-laying period and both juveniles and young sub-adults were rarely caught. However, the number of sub-adults caught in the traps increased sharply later in the year.

(v) Density

Estimates of the density of <u>L.agilis</u> such as those obtained at two sites in 1976 have only limited value unless made for several successive years. Unfortunately it is very time consuming to measure the density of L.agilis (because of the difficulties in catching lizards) and it is therefore not surprising that no data on the density of L.agilis (or any other European lizard) over a long time period has ever been obtained.

If such a long-term study were attempted, the best time to census a population would be in the spring, when the behaviour of individuals makes them conspicuous. It would also be preferable to catch lizards over a wider area than that used in the present study in order to minimise emigration and immigration.

The distinction made between resident and transient lizards was obviously not clear-cut but the data seemed to warrant some such division. Boag (1973) in his study of the wall lizard (Podarcis muralis) in Naples found a very clear distinction between resident and transient lizards.

Table 6.4 shows the density of L.agilis and L.vivipara as measured by different authors in other countries. The values of 50 individual hectare^{-1} was of the same order as the densities measured by Tertyshnikov (1970) in the U.S.S.R.

TABLE 6.4 POPULATION DENSITIES OF L.agilis AND L.vivipara IN DIFFERENT HABITATS

	Country	Habitat	Density Individuals/ha	Author
Lacerta agilis	USSR	Grassy steppe	100	Tertyshnikov (1970)
	"	Wooded belts	70	"
	"	Fescue-wormwood steppes	30	"
	"	Crops	11-30	"
	"	Forest	0.8	"
	England	Dry heathland	48	This study
	"	Grass/scrub/bog	52	"
Lacerta vivipara	USSR	Clearings	28.4	Darevskij & Terentev (1967)
	"	Deciduous forest	25	"
	"	Taiga	1.5	"

CHAPTER 7

GROWTH

7.1 Introduction

The examination of the growth of a species of lizard is important for two main reasons. Firstly, the energy used for growth is an important part of the total energy budget of an individual lizard and so must be determined in order to prepare such a budget. Variations in the amount of energy devoted to growth between different age classes of a lizard and between different species of lizard are an important part of the energetics of the species. Secondly, knowledge of the rate of growth of individuals may assist in estimations of the age of animals in the population.

Little information has been published on the growth of either L.agilis or L.vivipara. Smith (1951) reports that newly hatched individuals of Lacerta agilis have a snout-vent length of 25-31 mm and a year later they average 50 mm. Simms (1970) gives some data on increases in snout-vent length and weight of some marked L.agilis in Lancashire. Avery (1971) has measured the rate of growth of juvenile Lacerta vivipara both in the field and in the laboratory.

In this chapter the growth rates of different age classes of L.agilis and L.vivipara are compared.

7.2 Materials and Methods

The procedure for the capture, measurement and marking of lizards has been described in chapter 3.

Growth is here defined as an increase in snout-vent length. Increases in live body weight are also examined.

Two different methods were used in the treatment of the data on the snout-vent length and weight of the lizards measured. Firstly for individuals within distinct age classes the weight or length of each individual was plotted against the time of capture. This was done for *L.agilis* sub-adults and for both juveniles and sub-adults of *L.vivipara*.

The second method was used for adults of *L.agilis* where separate age classes could not be distinguished and the year of birth of individuals could not be determined with certainty. The rate of growth of adults of *L.agilis* was therefore estimated from the measurements made on marked individual lizards (Appendix V) and the relationship between the rate of increase in snout-vent length and the snout-vent length was examined. For each individual the rate of increase in snout-vent length, for convenience calculated as the increase during 100 days, $(\frac{L_2 - L_i}{t_2 - t_i} \times 100)$, where L_i and L_2 are the snout-vent lengths at times t_2 and t_i, was plotted against the snout-vent length $(\frac{L_2 + L_i}{2})$. The minimum and maximum time periods over which this increase was calculated were 92 and 241 days and it was assumed that no growth took place during the winter (mid September - mid April).

It was not possible to use this method for adults of *L.vivipara* because no recaptures of marked individuals were obtained, and so the growth of adult *L.vivipara* could not be examined.

Definitions of the age class terms used in this chapter are as follows:

Juveniles	- Individuals caught before their first winter
Sub-adults	- Individuals caught at any time during the year following their first winter
Adults	- Individuals that have experienced two winters.

7.3 The growth of *L.agilis*

(i) Juveniles

No information was obtained on the rate of growth of juvenile *L.agilis*. The mean snout-vent length of those juveniles measured was 31 mm and their mean weight 0.6 g.

(ii) Sub-adults

Plots of snout-vent length and weight against date of capture are shown in Figure 7.1. The data from different sites, years and from the two sexes have been combined.

A linear regression was fitted through the data for increase in weight by the method of least squares (Figure 7.1a). The regression equation was

$$W = 0.0324\ T - 1.03 \qquad (n = 55,\ r = 0.76) \qquad (7.1)$$

where T equals the number of days after one day before the first capture and W the weight in grams. From the slope of the line it can be seen that the daily increase in weight was 32.4 mg day^{-1}.

For the snout-vent length data an asymptotic regression of the form

$$L = A - B\ (p^{T}) \qquad (7.2)$$

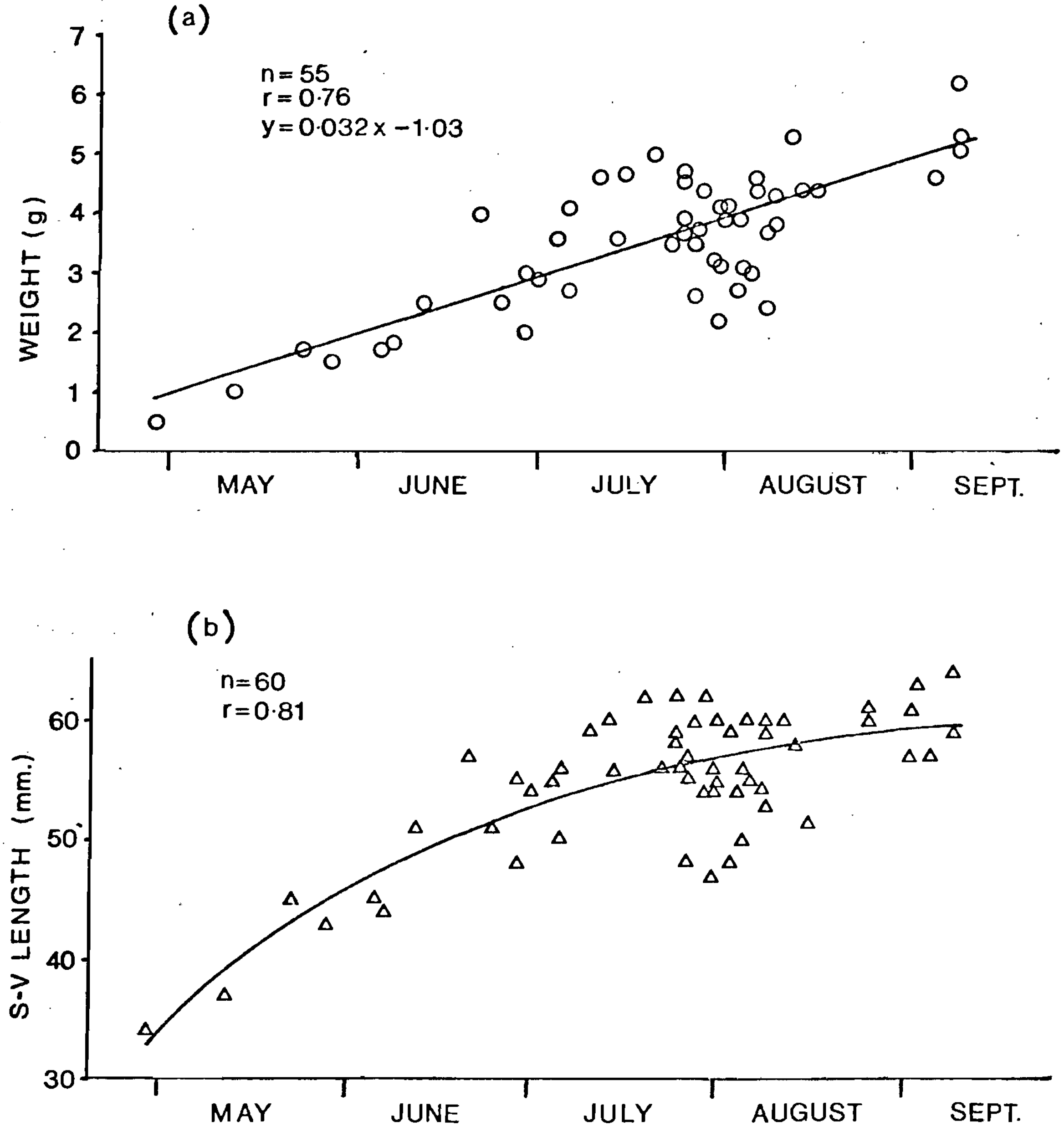

FIGURE 7.1 Growth of <u>L.agilis</u> sub-adults. (a) increase in weight during year and (b) increase in snout-vent length.

where L = S-V length, T = date of capture and A, B and p are constants (A being the asymptote of the curve) gave a better fit than a linear regression. The curve shown in Figure 7.1b was fitted by the method described by Snedecor & Cochran (1967) using an iterative computer programme. The asymptotic value A, of the curve was 62.5 mm. The greater value of r for the snout-vent length data than for the weight data is probably because of day to day variability in weight.

It was not possible to distinguish confidently between male and female sub-adults early in the year but from about early July onwards, males begin to show slight green colouration of the flanks, a characteristic of adult males. Separate linear and asymptotic regressions for weight and snout-vent length of male and female sub-adults were fitted, individuals of undetermined sex caught early in the year being included in both regressions.

The slope of the line for increase in weight of females was greater than that of males (38 mg day^{-1} females, 30 mg day^{-1} males) but this difference was not significant ($F_{1, 56}$ = 162, p = 0.2). Separate asymptotic regressions showed that females were also on average longer at the end of their sub-adult year than males, having a snout-vent length of 63.0 mm compared with 58.5 mm for males. Values of the asymptote for females and males were 71.2 and 59.2 mm respectively.

It can be shown that if weight increases linearly then a curve similar to that in Figure 7.1b would be expected for increase in snout-vent length. Since weight is approximately related to the cube of the snout-vent length (L) (see equations 7.3 and 7.4 below) the relationship between L^3 and date of capture (T) will be approximately linear. Hence L is linearly related to the cube root of T and from this it follows that the relationship between L and T is a curve similar to the asymptotic curve fitted.

Having examined the relationships between age and both weight and snout-vent length, it is of interest to look at that between snout-vent length and weight. These two variables are related as power series with weight being approximately proportional to the cube of the snout-vent length. The data were therefore transformed to natural logarithms for regression analysis. Regression equations for males ($n = 37$) and females ($n = 23$) were

sub-adult males : $\log W = 3.46 \log L - 12.6$ ($r = 0.95$) (7.3)
sub-adult females: $\log W = 3.43 \log L - 12.5$ ($r = 0.96$) (7.4)

The slopes of these two equations were both significantly greater than three (males, $t = 6.96$, $p < 0.001$: females, $t = 5.33$, $p < 0.001$). They were also significantly greater than the slopes for adult males and females given in equation 7.5 and 7.6 below (males, $t = 7.62$, $p < 0.001$: females, $t = 3.50$, $p < 0.001$). Thus both male and female sub-adults are relatively heavier at the end of their sub-adult year than at the beginning.

It was hoped that extrapolation of the curve in Figure 7.1b might provide a reasonable prediction of the growth of adults. This was not the case for the asymptote of the curve was 62.5 mm whereas the largest adult measured was 92 mm in snout-vent length. When compared with an overall growth curve, therefore, the rate of increase of snout-vent length of sub-adults proceeds relatively quickly in the early months of the season but then declines and is relatively slow in August and September. This sharp decline in the rate of increase in the last two months of the season causes the low asymptote of the fitted curve, and is consistent with the high values for the slopes of the regressions of snout-vent length against weight for sub-adults.

Since the increase in weight of sub-adults is apparently linear throughout the year, it is evident that, in the last part of the year, the weight of individuals increases without a corresponding increase in snout-vent length.

(iii) Adults

Measurements of the snout-vent length and weight of marked individuals in the field are shown in Appendix V Using these data the rate of increase of snout-vent length was plotted against snout-vent length for each individual lizard on which sufficient measurements had been obtained (Figure 7.2). Separate linear regressions for males and females were fitted through the data in Figure 7.2. The regression equations were

males : $\Delta L = 41.1 - 0.50\ L$ (n = 12)

females: $\Delta L = 34.9 - 0.38\ L$ (n = 13)

where L is the snout-vent length and ΔL the increase in snout-vent length. Both regressions were highly significant (males, $F_{1,\ 10} = 38.1$, $p < 0.005$: females, $F_{1,\ 11} = 26.4$, $p < 0.005$). The difference between regressions for males and females was also significant (test of difference between the elevations of the lines, $F_{1,\ 22} = 9.48$, $0.025 > p > 0.005$) although there was no significant difference between the slopes of the two lines.

An inverse linear relationship between rate of growth and snout-vent length means that the snout-vent length of an individual will increase asymptotically, reaching the asymptote where the regression line meets the abscissa. The extrapolation of the regression lines in Figure 7.2 therefore give a prediction of the maximum size of individuals. The maximum predicted snout-vent lengths were 82 mm for males and 91 mm for females, in close agreement with the maximum sizes found in the study areas of 84 and 92 mm.

From Figure 7.2 it is also possible to estimate the average annual increase in snout-vent length assuming firstly that a lizard 'growth year' is approximately 150 days (mid April - mid September; data for spring emergence have been given in section 6.3. The date of winter submergence is difficult to determine but it is rare to see more than an occasional adult active after mid-September) and secondly that a male lizard averages 58.5 and a female lizard 63 mm in snout-vent length at the beginning of their first adult year. The snout-vent length at the end of each succeeding year is shown in Table 7.1 which summarises the growth of L. agilis. Weights shown in Table 7.1 were estimated from snout-vent lengths using log:log plots of weight against snout-vent length for adult males ($n = 103$) and females ($n = 87$). The regression equations were

males : $\log W = 2.86 \log L - 10.2$ ($r = 0.94$) (7.5)

females: $\log W = 3.07 \log L - 11.1$ ($r = 0.90$) (7.6)

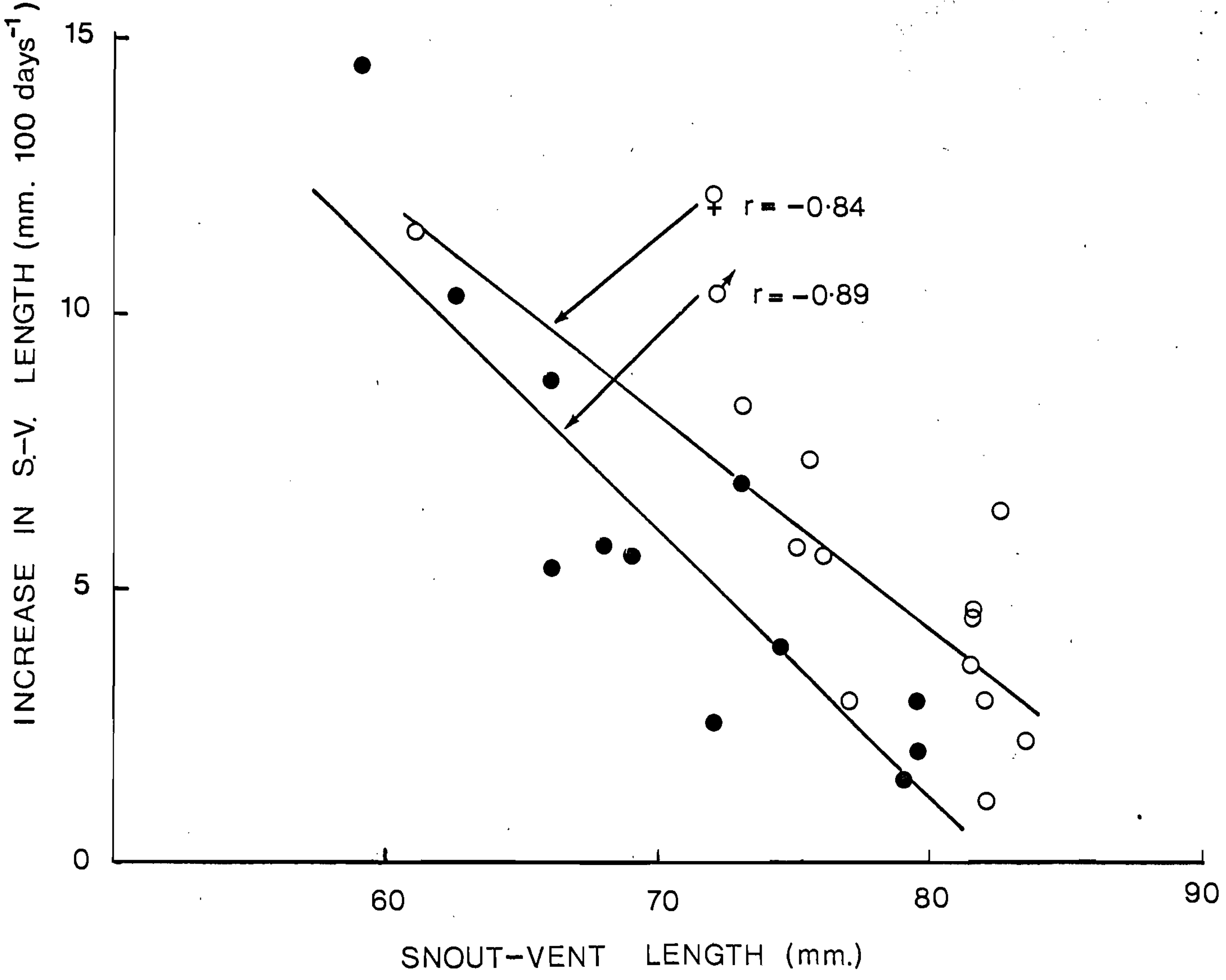

FIGURE 7.2 Growth rate of L.agilis adults. Linear regression of increase in snout-vent length against snout-vent length. Open circles, females; closed circles, males.

TABLE 7.1 COMPARATIVE GROWTH OF DIFFERENT AGE CLASSES OF L.agilis

Age Class	Sex	Snout-vent length at end of year (mm)	Weight at end of year (g)	Growth rate (mg/day)	Growth rate (cals/year)	Instantaneous growth rate (cals/g/day)
Sub-adults	M	58.5	5.0	30	9,630	26.3
	F	62	5.7	38	12,200	34.4
1st year adults	M	71	7.3	15	4,920	5.4
	F	75	8.6	19	6,210	6.1
2nd year adults	M	77	9.2	13	4,070	3.3
	F	82	11.3	18	5,780	3.9
3rd year adults	M	80	10.3	7	2,350	1.6
	F	86	13.1	12	3,850	2.1

Data from lizards caught throughout the period April - September were used. Females caught during June, when many individuals are gravid, were not excluded as they were not significantly heavier than females caught in April and May (see section 5.3(i)).

The rate of growth of the different age classes of adults, in Table 7.1 was calculated assuming that a lizard 'growth year' is 150 days, that there was no loss of weight over winter, that the calorific value of lizard tissue is 6295 cal g dry wt^{-1} (Avery 1971, for L. vivipara) and that the dry weight:wet weight ratio for lizard tissue is 0.34 (Avery 1971, for L. vivipara). It was necessary to assume that there was no weight loss over winter because there is no data on the winter energy expenditure of L. agilis. The estimates of the energy invested by adults on growth therefore include winter energy expenditure. Instantaneous relative weight gain was calculated from the formula

$$k = (\ln W_2 - \ln W_i)/(t_2 - t_i)$$

where W_2 and W_i are the weight at times t_2 and t_i (Brody 1945). This quantity is expressed in calories in Table 7.1.

Both weight specific and actual growth rates decrease as lizards get older and both are greater for females than for males (Table 7.1). Third year adults invest in growth only 28% of the calories invested by sub-adults and the instantaneous growth rate is only 6% of the value for sub-adults. It is notable that the amount of energy invested in growth by sub-adults is much greater than the amount invested by any of the age classes of adults.

7.4 The growth of L.vivipara

(i) Juveniles

The rate of growth of juveniles of L.vivipara was estimated in the same way as for sub-adults of L.agilis, because few recaptures of individuals were obtained. Figure 7.3 shows (a) weight and (b) snout-vent length plotted against time of capture for juveniles caught during 1975 on the Railway study area. Asymptotic regressions (equation 7.2) were fitted through both sets of data. Values of the asymptote for weight and snout-vent length were 1.16 g and 38.2 mm.

To calculate instantaneous relative weight gain (k) the curve in Figure 7.3a was arbitrarily divided into two sections, July/August and September/October, and k was calculated for each period. Values of k for July/August were 29.8 mg g^{-1} day^{-1} or 5.9 cals g^{-1} day^{-1}.

Log:log regression of weight against snout-vent length for juvenile L.vivipara gave the fit

$$\log W = 2.57 \log L - 9.16 \qquad (n = 22,\ r = 0.96).$$

(ii) Sub-adults

The rate of growth of sub-adults of L.vivipara was estimated by the same method used for sub-adults of L.agilis. Data from different sites and years and from both sexes were combined and linear regressions were fitted through both the weight and snout-vent length data (Figure 7.3c and d). The daily increase in weight was 9.9 mg day^{-1}, much less than the value for L.agilis sub-adults (32 mg day^{-1}). The instantaneous relative weight gain of L.vivipara sub-adults was 7.1 mg g^{-1} day^{-1} (15.1 cal g^{-1} day^{-1}) again less than the value for

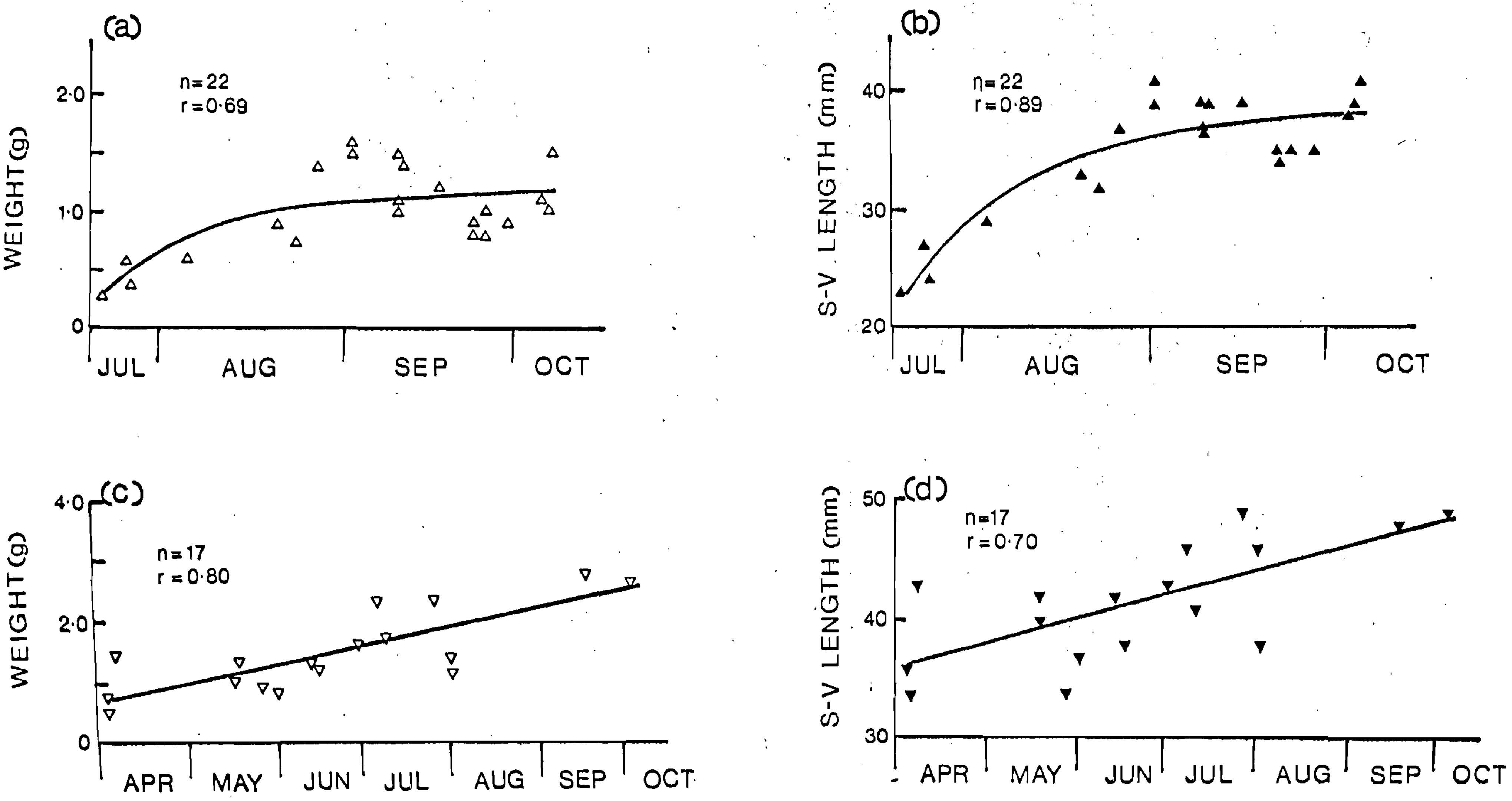

FIGURE 7.3 Growth of *L.vivipara* juveniles and sub-adults. (a) and (b) asymptotic regressions for increase in weight and length for *L.vivipara* juveniles. (c) and (d), linear regressions for increase in weight and length for *L.vivipara* sub-adults.

L. agilis sub-adults (30 cals g^{-1} day^{-1}) and also smaller than the value for L. vivipara juveniles in July/August (64 cals g^{-1} day^{-1}).

These differences in growth between sub-adults of L. vivipara and L. agilis mean that an individual of L. vivipara, on average, weighs 2.7 g and measures 48 mm at the end of its sub-adult year whereas an individual of L. agilis weighs 5.3 g and measures 61 mm.

Log:log regression of weight against snout-vent length for sub-adult L. vivipara gave the fit:

$$\log W = 3.28 \log L - 11.9 \quad (n = 16,\ r = 0.91).$$

It is notable that the slope of the regression line is greater than three (as was also the case for sub-adult L. agilis) although the difference was not significant ($t = 1.25$, $p = 0.3$). However, the slope was significantly different from the slope for L. vivipara juveniles ($t = 2.97$, $0.01 > p > 0.005$). This indicates that sub-adults of L. vivipara are relatively heavier at the end of their period of activity (April - September).

7.5 Discussion

In order to estimate the rate of growth of L. agilis and L. vivipara, data from different sites and from three different years were combined except in the case of juvenile L. vivipara. During two of these years, 1975 and particularly 1976, daily temperatures and amounts of sunshine were higher than during normal summers in Dorset. The prevailing weather conditions can determine the activity of individual lizards (see chapter 9) and also affect the rate of food consumption (Avery 1971). It might therefore be expected that the rate of growth of individuals would be faster during these two exceptional years than during a more normal year, and that the overall pattern of growth obtained from the three years combined data would not be representative of three more normal years.

However, despite these differences between years, high correlations were obtained between the date of capture and both the weight and snout-vent length of sub-adult L.agilis, and between the rate of increase in snout-vent and the snout-vent length of adult L.agilis. It appeared that for sub-adults of L.agilis, the variation between the snout-vent lengths of individuals in any one year was much greater than the variation between years.

The amount of energy devoted to growth rather than other demands diminished, in both relative and absolute terms, as individuals of L.agilis aged. The large amount of energy devoted to growth by sub-adults was particularly notable. Sub-adults do not experience the energy demands of reproduction experienced by adults and it seems that this energy is devoted to growth. Once individuals become adult, the energy demands of reproduction leave little energy available for growth. It is probably important for sub-adults to devote as much as possible of the available energy towards growth so that they are large enough to breed in the following year. In most species of lizard there is a minimum size below which maturity is not attained (see Tinkle, Wilbur & Tilley 1970).

There was a small difference between the rate of growth of male and female L.agilis. The positive correlation between snout-vent length and clutch size for L.agilis (chapter 6) suggests it is advantageous for females to devote more energy to growth so that they can produce the maximum possible number of eggs in future years.

It was established that, towards the end of the summer, sub-adults of L.agilis gained weight without the corresponding expected increase in snout-vent length. This is presumably because individuals are depositing lipids in preparation both for the winter and for the high energy demands of spring (chapter 5). It seems that the lipids are deposited at the expense of energy that previously was going into growth. It would appear that energy is only devoted to growth when there is still 'spare' energy available after other more essential needs have been met, and is diverted away from growth if other more important demands arise. For another example of this, Tinkle & Ballinger (1972) found that the use of energy for production of a clutch in the lizard Sceloporus undulatus (Iguanidae) resulted in a slowing down of growth.

There was also evidence from the relationship between snout-vent length and body weight of lipid deposition at the expense of growth in sub-adult L.vivipara, although this was not apparent from the relationships between weight/snout-vent length and date of capture. Juveniles of L.vivipara, however, did not seem to devote so much energy to the deposition of lipids since the exponent of the power series relationship between weight and snout-vent length was much less than three. This is consistent with the finding of Avery (1974) that there is a marked degree of positive allometry in the relationship between snout-vent length and the quantity of lipid deposits in L.vivipara. In other words, juveniles have relatively small deposits of lipids. Avery (1974) found difficulty in finding a reasonable explanation for this positive allometry and suggested that perhaps larger lizards required less energy for growth. The evidence presented in this chapter suggests that energy for growth is often not a priority and individuals of L.agilis and L.vivipara may divert energy away from growth to lay down lipids when these are required.

Speculating a stage further, it appears probable that in the spring and early summer, sub-adult L.agilis and L.vivipara are devoting all available energy towards growth (the growth rate of sub-adult L.agilis was very rapid at this time) which is the reason why deposits of lipids of sub-adult L.vivipara have fallen to zero in June (Avery 1974) although they were not very great in March. In contrast, the primary energy demand on adults of both species in the spring is reproduction, which is largely financed by stored lipids, approximately 50% of the energy in the clutch of L.vivipara coming from lipid deposits (Avery 1975b) and probably a greater proportion of the energy in the clutch of L.agilis coming from lipids (chapter 5). These lipids are deposited in the last months of the previous year and partly used during the winter. In the case of young lizards where the spring energy demand is growth rather than reproduction, it would seem inefficient for juveniles to store large quantities of lipids and then use the energy for growth as sub-adults the following spring. A more efficient strategy would be for each individual to use the energy immediately for growth as a juvenile and only store sufficient lipids to enable it to survive the most energetically demanding winter. This would perhaps explain the relatively small reserves of lipid found in juvenile L.vivipara in September and March (Avery 1974) and the consequent positive allometry in the relationship between the quantity of lipid deposits and snout-vent length in the whole population.

The rapid rate of growth of juvenile L.vivipara for six weeks after birth was consistent with the above explanation. The rate of growth of juvenile L.vivipara measured by Avery (1971) was similar to the rate measured here (24.9 mg g^{-1} day^{-1} v. 29.8 mg g^{-1} day^{-1}). The rate of increase of both weight and snout-vent length slowed later in the year. This was perhaps caused by deteriorating weather conditions.

There was some evidence to suggest that continental L.agilis may be larger than English L.agilis. Rashkevitch & Semenikhina (1974) working on L.agilis in Russia (for location see Figure 10.1) give the weights of two adults as 38 and 32 g, very much greater than the maximum weight found in this study (15.5 g).

Table 7.2 shows the mean snout-vent lengths of adult L.agilis from Continental Europe (data from Boulenger 1920) and from England (data from Boulenger and from this study). Although for L.agilis the mean snout-vent length of Continental lizards was greater than the mean snout-vent length of English lizards, only the difference between Continental males and English males (Boulenger) was significant ($p < 0.01$). If there is in fact a difference between the sizes of English and Continental L.agilis then

TABLE 7.2 MEAN SNOUT-VENT LENGTHS OF ADULT *L.agilis* AND *L.vivipara* IN CONTINENTAL EUROPE AND THE BRITISH ISLES

L.AGILIS

LOCATION	SEX	NUMBER OF SPECIMENS	MEAN SNOUT-VENT LENGTH	SOURCE OF DATA
Continental Europe	F	46	78.5	Boulenger (1920)
England	F	11	73.7	"
England	F	109	77.1	This study
Continental Europe	M	43	72.7	Boulenger
England	M	12	66.9	Boulenger
England	M	117	70.8	This study

L.VIVIPARA

Continental Europe	F	29	56.9	Boulenger
British Isles	F	57	57.8	"
Continental Europe	M	47	50.6	"
British Isles	M	21	50.1	"

it is likely that it could be caused by differences in the rate of growth of individuals. It was established in chapter 5 that individuals of L.agilis had the capacity to greatly increase their rate of food consumption in optimum conditions and they may therefore also be able to sustain much greater rates of growth at such times.

The mean snout-vent lengths of English and Continental L.vivipara are also given in Table 7.2 and these are very similar. Perhaps, therefore, individuals of L.vivipara are not capable of sustaining a greater rate of growth than that observed in England. This may be related to the fact that individuals have not the same capacity to increase their rate of food consumption as have individuals of L.agilis.

CHAPTER 8

HOME RANGE ECOLOGY OF LACERTA AGILIS

8.1 Introduction

The concept of home range was first distinguished from that of territory by Burt (1943). He defined home range as the "area traversed by the individual in its normal activities of food gathering, mating and caring for the young" but excluded occasional sallies outside the regularly used area. Most definitions of home range have been essentially similar to this. For instance, Jewell (1966) defined home range as "the area over which an animal normally travels in pursuit of its routine activities."

Noble (1939) defined territory as "any defended area." This is the simplest of several definitions that define territory in terms of the behaviour required to maintain it. A different type of definition of territory has been proposed by Pitelka (1959). He defines territory as an "exclusive area." This is an ecological rather than behavioural definition of territory. The ecological importance of territory lies in the degree in which the resources of the territory are used exclusively by the occupant, not in the behavioural mechanism required to maintain it. This definition therefore seems best for an ecological study and was also preferable as a working definition in this study because of the difficulties of observing the behaviour of *Lacerta agilis* and *Lacerta vivipara* in the field.

The measurement of home range as defined by Burt

(1943) or Jewell (1966) presents several problems. How are normal or routine activities defined? How is an occasional "sally" distinguished from a "normal" movement? Home range sizes may also vary with time, and descriptions of home range should also take into account differential utilization of different parts of the range (Hayne 1949). Some authors have identified areas within home ranges that are used very frequently while other areas are used only rarely (e.g. Ferner 1974).

In practice, the home range of an individual animal is usually calculated from recapture points of marked individuals. The two most common methods used to calculate home ranges of lizards from this type of data are those using recapture radii and those using polygon techniques.

The calculation of mean recapture radii was first proposed by Hayne (1949) and Dice and Clark (1953) and has since been used for lizards by Jorgensen and Tanner (1963) and Tinkle and Woodward (1967). One advantage of this method is that it does not suffer from bias caused by the number of observations. Home range is defined statistically in terms of a decreasing probability of capture from the geometric centre of the capture points. Unequal use of area within the home range is, to some extent, taken into account and definite home range boundaries which may be biologically unrealistic are not assumed. The main disadvantage of this method is that it assumes a circular home range. However, Jennrich & Turner (1969) have proposed a similar index of home range area which does not assume a circular home range.

Polygon methods have been used to calculate the home range area of many species of lizard (Tinkle, McGregor & Dana 1962; Hirth 1963; Brooks 1967; Boag 1973; Ferner 1974). The outermost points of capture are connected to form the smallest possible convex polygon (Southwood 1966). No assumptions need be made about the shape of the home range. The main problem when calculating home ranges using this method is that the estimate is biased by the number of observations used (Jennrich & Turner 1969). A convex polygon home range based on three observations is on average only about 3% of an estimate based on eighteen observations (Turner, Jennrich & Weintraub 1969). Boag (1973) found that home range sizes of _Podarcis muralis_ in Italy continued to increase until 170 observations were recorded. Jennrich & Turner (1969) have calculated correction factors from simulated distributions of capture points which adjust the convex polygon home range according to the number of observations made. This is necessary so that home range areas of different individuals captured an unequal number of times can be compared and also so that convex polygon home range sizes can be compared with those calculated from other methods such as recapture radii.

All methods of estimating home range size contain biologically unrealistic assumptions. The methods used can be considered as providing an index of home range size or alternatively home range size can be defined mathematically in terms of the method used to measure it, avoiding definitions such as those of Burt (1943) and Jewell (1966).

In general, there have been few studies of the home range ecology of the Lacertidae, most being of

New World lizards. Data on the home range size of *L.agilis* have been obtained in the U.S.S.R. (Tertyshnikov 1970; Rashkevitch & Semenikhina 1974). Buschinger & Verbeek (1971) have tracked *L.vivipara* in Germany using radioactive tantilum. Boag (1973) has made a detailed study of the home range ecology of *Podarcis muralis* in Italy. Weber (1957) has also looked at the home range ecology of *P.muralis* and Verbeek (1972) has made observations on the territorial behaviour of *P.sicula* and *L.vivipara*.

The interrelationships between home ranges of individuals is an important aspect of the social system of a species. Ferner (1974) defines the degree of home range overlap for lizards as the percentage of an individual home range that is shared by lizards of the same sex. The extent of home range overlap is closely related to other aspects of the social system, such as the degree of aggression between individuals and the type of mating system. For instance, Tinkle (1967) found that *Uta stansburiana* (Iguanidae) in Texas were highly territorial and aggressive and a monogamous mating system probably existed (Irwin 1965). In contrast, Ferner (1974) studying the rock lizard *Sceloporus undulatus* in Colorado found a high degree of home range overlap together with a probable social hierarchy and promiscuous mating system. The degree of home range overlap and the type of social system have also been found to vary intraspecifically; there was much more overlap between home ranges of *U.stansburiana* in a Colorado population than in the Texas population, and males were less aggressive (Tinkle and Woodward 1967). Stamps (1973), working on the lizard *Anolis aeneus* in the

Lesser Antilles, found that female social systems ranged from hierarchies to territories in different habitats.

There is clearly a close link between home range ecology and feeding ecology. In birds (Crook 1965) and primates (Crook & Gartlan 1966; Clutton-Brock & Harvey 1977) a variety of aspects of social organisation including home range size and overlap have been shown to be related to the distribution and abundance of food. Data on interspecific variation in home range size show that for mammals (McNab 1963), birds (Schoener 1968a) and lizards (Turner, Jennrich & Weintraub 1969), home range size increases with body weight and therefore with the energy requirements of individuals. For example the function relating home range size to body weight for herbivorous mammals was similar to that relating basal metabolism to body weight (McNab 1963). Intraspecific differences in home range size have been related to the food productivity of the habitat in birds (Stenger 1958) and lizards (Simon 1975). Simon showed that the territory size of the small iguanid lizard Sceloporus jarrovi was inversely correlated with food abundance within the territory. A large natural decrease in food abundance caused an increase in territory size and conversely territory size decreased when food was supplied artificially.

In this chapter, data are presented on the home range size of L.agilis on the study areas previously described. Some aspects of the utilization of the home range area by individual lizards are considered and data are presented concerning the degree of home range overlap between individual home range areas of L.agilis. The social system and its relationship to the home range ecology of L.agilis is also considered.

8.2 Methods

The lizards were caught in pitfall traps at the Soldiers Road study area and by hand at the Railway study area. Positions of capture were recorded and the lizards were marked and released. The pattern of dorsal markings of individual L.agilis was recorded by drawing. Some individuals could be recognised in the field from the pattern of these markings and by other characteristics such as breaks in and regeneration of the tail. Lizards were often seen more than once in the same place during one day, especially at the Railway site during April and May. In these cases only one observation was recorded.

Home range sizes were calculated using the convex polygon method (Southwood 1966) and corrected according to the number of observations as suggested by Jennrich & Turner (1969).

Observations on the movements of individual lizards were made at the Railway site in 1977. Individuals were followed from a distance of approximately 2-3 m.

8.3 Home Range Size

Home range sizes for individual L.agilis are shown in table 8.1. Both uncorrected and corrected home range size are shown. Data on the home range size of L.vivipara was not obtained because recaptures of marked individuals were not made.

TABLE 8.1 HOME RANGE AREA FOR L. agilis. THE NUMBERS USED TO DENOTE LIZARDS AT THE RAILWAY SITE ARE THE SAME AS THOSE USED IN FIGURES 8.4 AND 8.5. NOTE THAT AT SOLDIERS ROAD THE HOME RANGE AREA OF AN INDIVIDUAL LIZARD MAY BE GIVEN FOR 1975 AND 1976 SEPARATELY AND FOR THE TWO YEARS COMBINED. (AN ASTERISK DENOTES A SUB-ADULT INDIVIDUAL)

MALES

SITE	LIZARD	TIME PERIOD OVER WHICH OBSERVATIONS MADE	NUMBER OF CAPTURES OR SIGHTINGS	POLYGON HOME RANGE (m^2)	CORRECTED HOME RANGE (m^2)
Soldiers Road	A	June–Oct 1975	7	113	578
	B	Aug–Sept 1975	6	75	439
	C	June–July 1975	3	63	1454
	C	April–July 1976	14	775	2135
	D	April–Aug 1976	25	1155	2230
	E	April–Aug 1976	12	780	2400
	F	June–July 1976	3	161	3751
	G	May–July 1976	6	75	438
	H*	June–July 1976	6	325	1901
	C	June '75–July '76	17	950	2273
	F	June '75–July '76	5	478	3538
Railway	1	April–June 1976	16	1396	3455
	2	May–June 1976	6	150	879
	7	April–May 1976	12	161	495
	6	April–May 1976	10	904	3183
	9	April–July 1976	12	314	966
	5	April–July 1976	10	725	2553
	12	April–July 1976	6	675	2921
	11	April–May 1976	5	183	1356
	8	April–May 1976	7	41	210

FEMALES

SITE	LIZARD	TIME PERIOD OVER WHICH OBSERVATIONS MADE	NUMBER OF CAPTURES OR SIGHTINGS	POLYGON HOME RANGE (m^2)	CORRECTED HOME RANGE (m^2)
Soldiers Road	A	July–Aug 1975	9	384	1492
	B	May–Aug 1975	7	78	400
	C	July–Aug 1975	5	525	3890
	D*	May–July 1975	3	50	1163
	D	April–July 1976	5	169	1250
	A	April–July 1976	8	431	1866
	E*	June–July 1976	7	641	3309
	A	June–July 1976	17	654	1565
	D	July '75–July '76	8	233	1007
	F	July '75–June '76	4	63	679
	C	July '75–May '76	7	600	3060
Railway	1	May–June 1976	6	120	701
	3	May–July 1976	12	59	182
	8	May–June 1976	12	61	188
	11	May–June 1976	3	79	1843
	10	July '75–June '76	5	105	776
	9	April–May 1976	5	81	599

Uncorrected home range size increased greatly with the number of observations (Figure 8.1). This shows the necessity of using correction factors. A linear regression was fitted through the data for uncorrected home range size, data for the two sites being combined. The regression was significant ($F_{1,\ 35} = 31.8$, $p < 0.005$).

The effect of the correction factors on the data can be seen in Figure 8.2 where the correction factors have been used on the linear regression equation of Figure 8.1. The effect is strongest at low and high numbers of observations.

In cases where individuals were caught in 1975 and 1976, no changes were found in the position of the home ranges between the years. The continuation of observations on some individuals at the Railway study area in 1977 also indicated that the position of the home ranges of adults remained stable. The corrected home range size calculated using data from both 1975 and 1976 was in most cases no larger than the home range size calculated from one season's data (Table 8.1). This also indicates that the position of home ranges remains relatively stable.

Mean corrected home range sizes of male and female L.agilis are shown in Table 8.2. The means are calculated from the corrected home range sizes in Table 8.1, some estimates being excluded. The estimates excluded were firstly, those based on only three observations, both because the effect of correction factors was much greater than at higher numbers of observations (Figure 8.2) and because of the larger error associated with so few

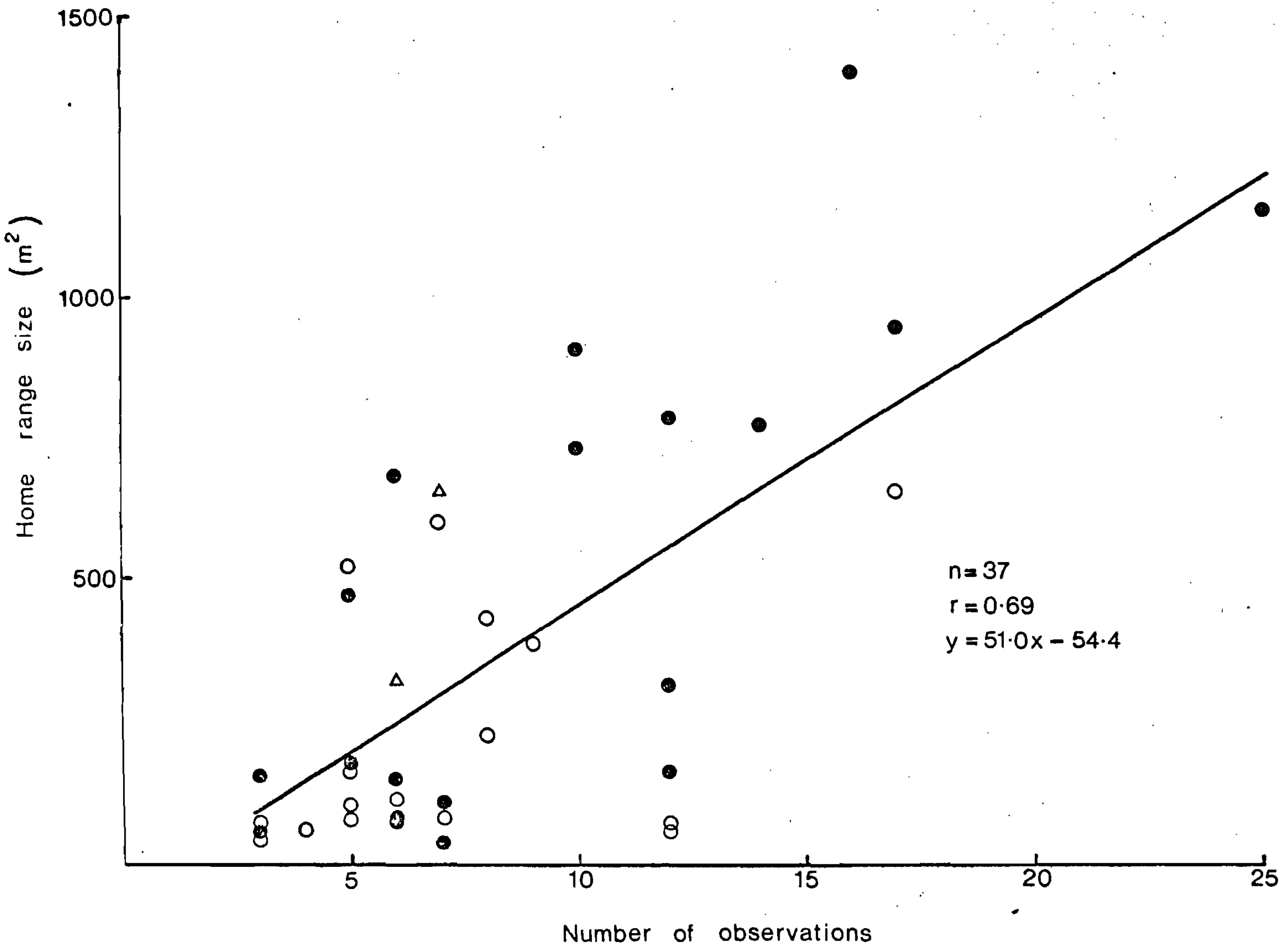

FIGURE 8.1 Regression of home range size (convex polygon) against the number of captures and sightings used to determine the home range size, for L.agilis. Closed circles, males; open circles, females; triangles, sub-adults.

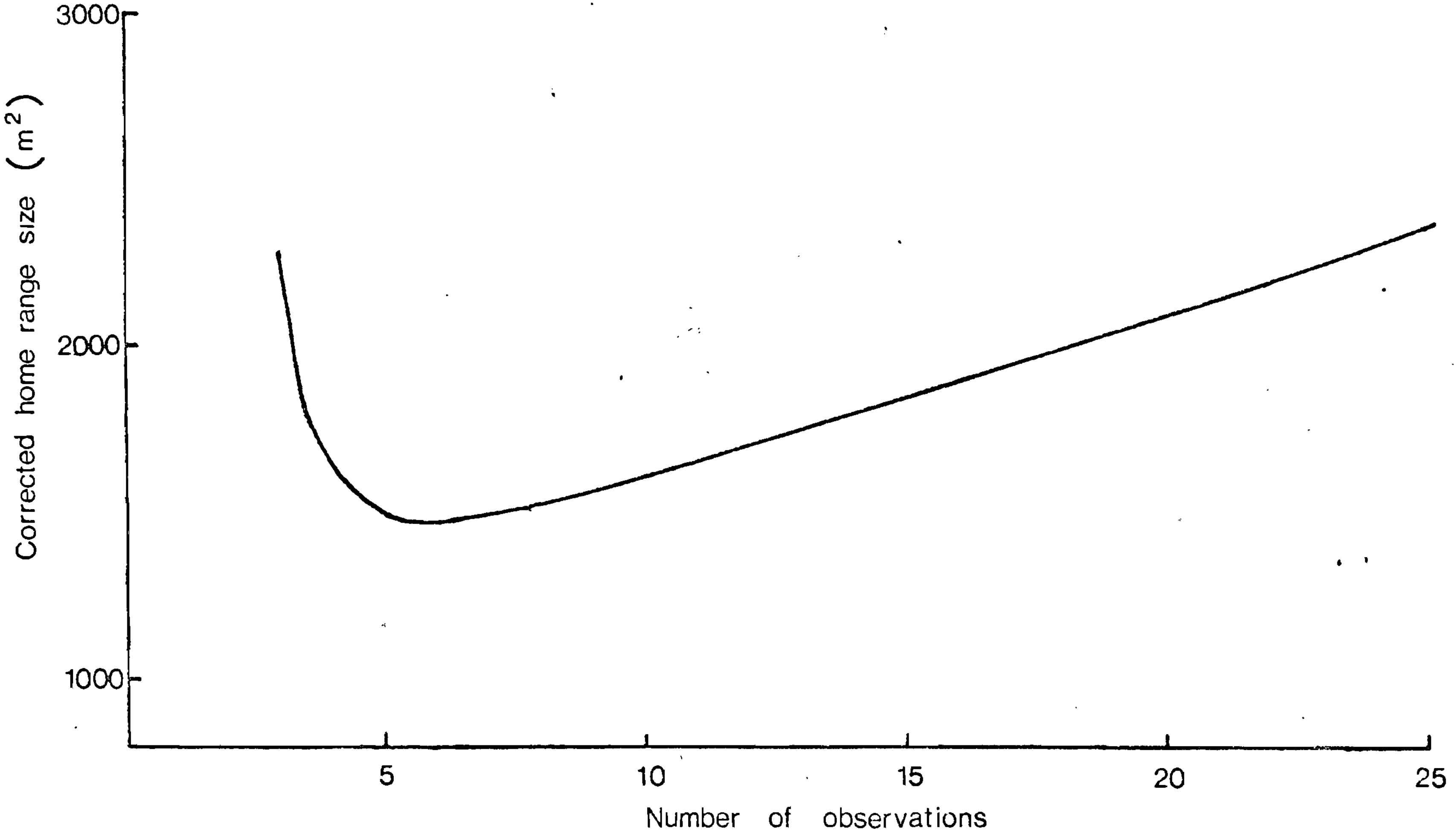

FIGURE 8.2 The corrected home range size, calculated by using correction factors (see section 8.3(i)) on the linear regression equation of Figure 8.1, plotted against the number of observations used to determine home range size.

TABLE 8.2 MEAN CORRECTED HOME RANGE SIZES OF <u>L.agilis</u> AT THE TWO STUDY AREAS

Study area	Sex	Number of individuals	Mean home range size (m^2)
Railway	♂	9	1780
"	♀	5	489
Soldiers Road	♂	6	2130
"	♀	5	1924

observations, and secondly, those estimates based solely on data collected in 1975 at Soldiers Road, because of the small area covered by the traps in that year. Where data were available from two years on an individual lizard, the home range size used was based on both years' data.

The difference between the mean corrected home range size of males and females was not significant at Soldiers Road ($t = 0.32$, $p = 0.8$) but was at the Railway ($t = 2.97$, $p < 0.05$). Mean corrected home range size for females was significantly smaller at the Railway compared with Soldiers Road ($t = 2.61$, $p < 0.05$) but the difference for males at the two sites was not significant ($t = 0.63$, $p = 0.5$).

8.4 Utilization of the home range area

It was not possible to follow individual lizards throughout their daily activity period because of their habit of foraging under dense vegetation. However, observation of individual lizards for shorter periods of time were made at the Railway study area. One male was followed as he moved 43 m alongside the disused railway track, this movement taking 29 minutes.

Details of the home range of this male are shown in Figure 8.3. This lizard used the same overwintering site (probably a burrow in the bank) during three consecutive winters (1975-76, 1976-77 and 1977-78). Observations of this lizard, who could be recognized by his dorsal markings, were made in two separate areas, in the vicinity of his overwintering site and in an area of coarse grass at the eastern end of the study area

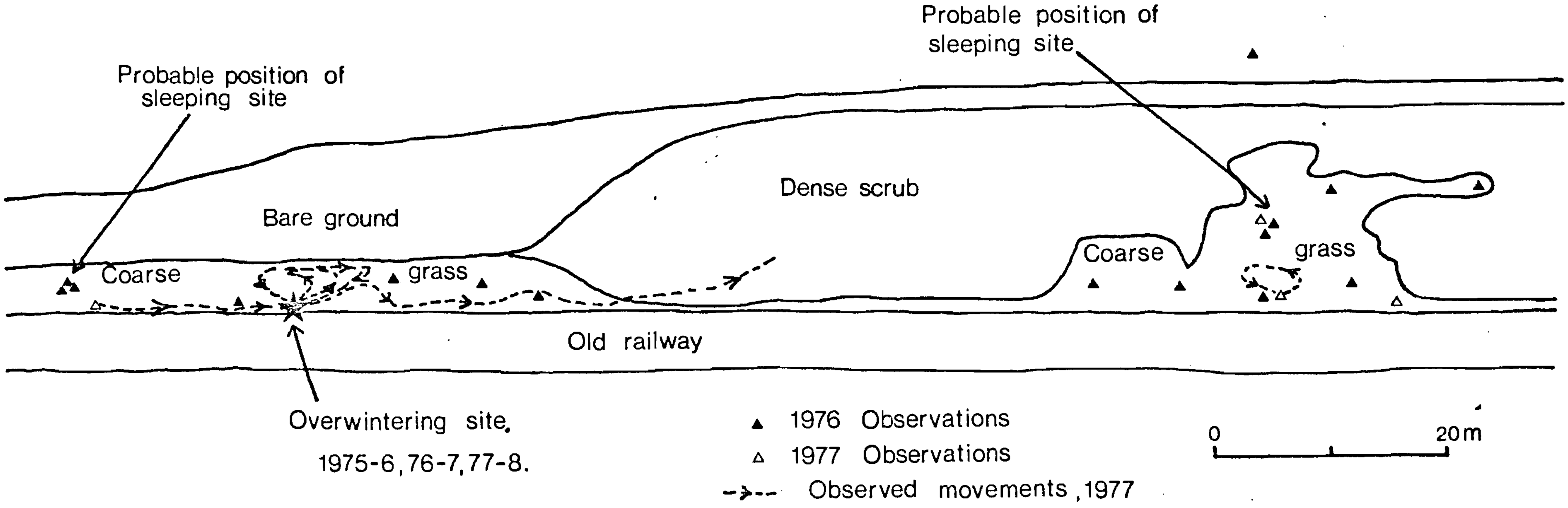

FIGURE 8.3 Details of the home range of an individual male L.agilis at the Railway site in 1976 and 1977.

(Figure 8.3). In both 1976 and 1977 this individual spent much time during April basking close to his overwintering site, where he retreated at night or when disturbed. He was observed to make short foraging movements in the immediate vicinity of the overwintering site (Figure 8.3), usually returning to a basking site close to his burrow.

In the spring of both 1976 and 1977 this male moved from the vicinity of his overwintering burrow to the eastern end of his home range. This occurred between the 17 and 20 April 1976 and on 4 May 1977. Several sightings were then made in this new area during May; when using this part of his range the male used a different overnight site. On 10 June 1976 he was again observed in the vicinity of his overwintering site. Several other individuals also used more than one overnight site.

It was not possible to identify area used with greater than average intensity at Soldiers Road. However, at the Railway home ranges often consisted of patches of intensively used habitat separated by areas of bare ground.

8.5 Interrelationships between home ranges

It was evident at both study areas that any one area was utilized by several different lizards of both sexes. The term home range overlap is usually applied specifically to describe overlap between the ranges of individuals of the same sex (Ferner 1974). Thus in 1975 at Soldiers Road overlap between female home ranges was evident, although not between male or sub-adult ranges

(Figure 8.6). Overlap between male ranges at Soldiers Road, however, was evident in 1976 (Figure 8.7). At the Railway site in April and May 1976 considerable overlap existed between both male and female home ranges (Figures 8.4 and 8.5). The grass strip at the centre of the site was within the range of at least six males at this time.

The degree of home range overlap (that percentage of an individual range shared by lizards of the same sex; Ferner 1974) should ideally be estimated for each individual lizard. However, this can only be done if the exact boundaries of the home range are known. The only method which actually defines home range boundaries is the convex polygon method but the boundaries drawn are not biologically realistic. Also, polygon estimates are too small unless based on a very large number of captures. If a convex polygon home range was taken as a true home range, home range overlap would be underestimated.

An index of the degree of home range overlap within a population can be calculated if density and mean home range size are known and it is assumed that the lizards distribute their home ranges evenly over the site, so that the home range overlap between ranges is minimised and equal for each lizard. For males at Soldiers Road in 1976 with a density of five males per 4000 m^2 and a home range size of 2000 m^2 the degree of home range overlap was 75%.

The high degree of home range overlap is illustrated by the use of the same overnight site by different lizards at different times. One overnight site was observed to be used by nine different individuals during 1976. Preferred

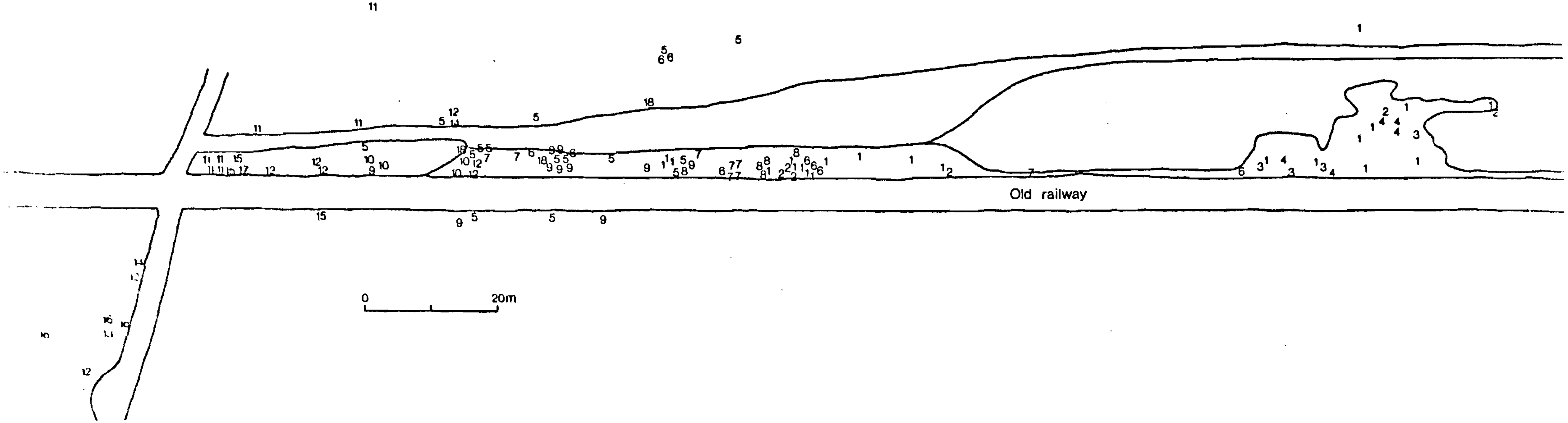

FIGURE 8.4 Captures and sightings of known individual male <u>L.agilis</u> at the Railway site in 1975 and 1976. Each number refers to an individual lizard (total of eighteen individuals). For details of the site see Figure 2.2.

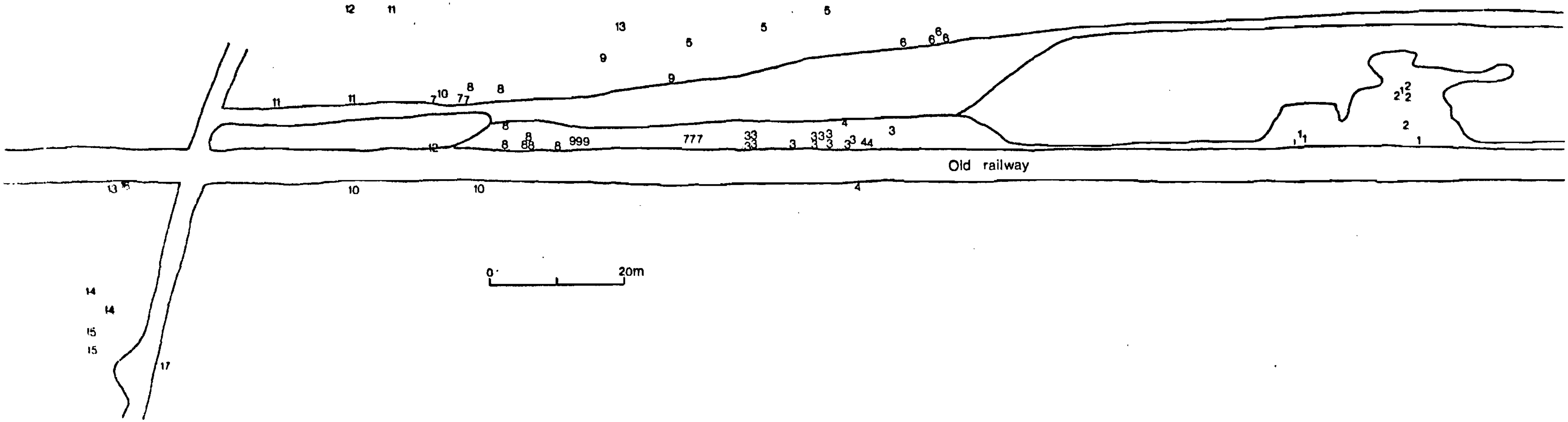

FIGURE 8.5 The same as Figure 8.4 but for females (total of seventeen individuals).

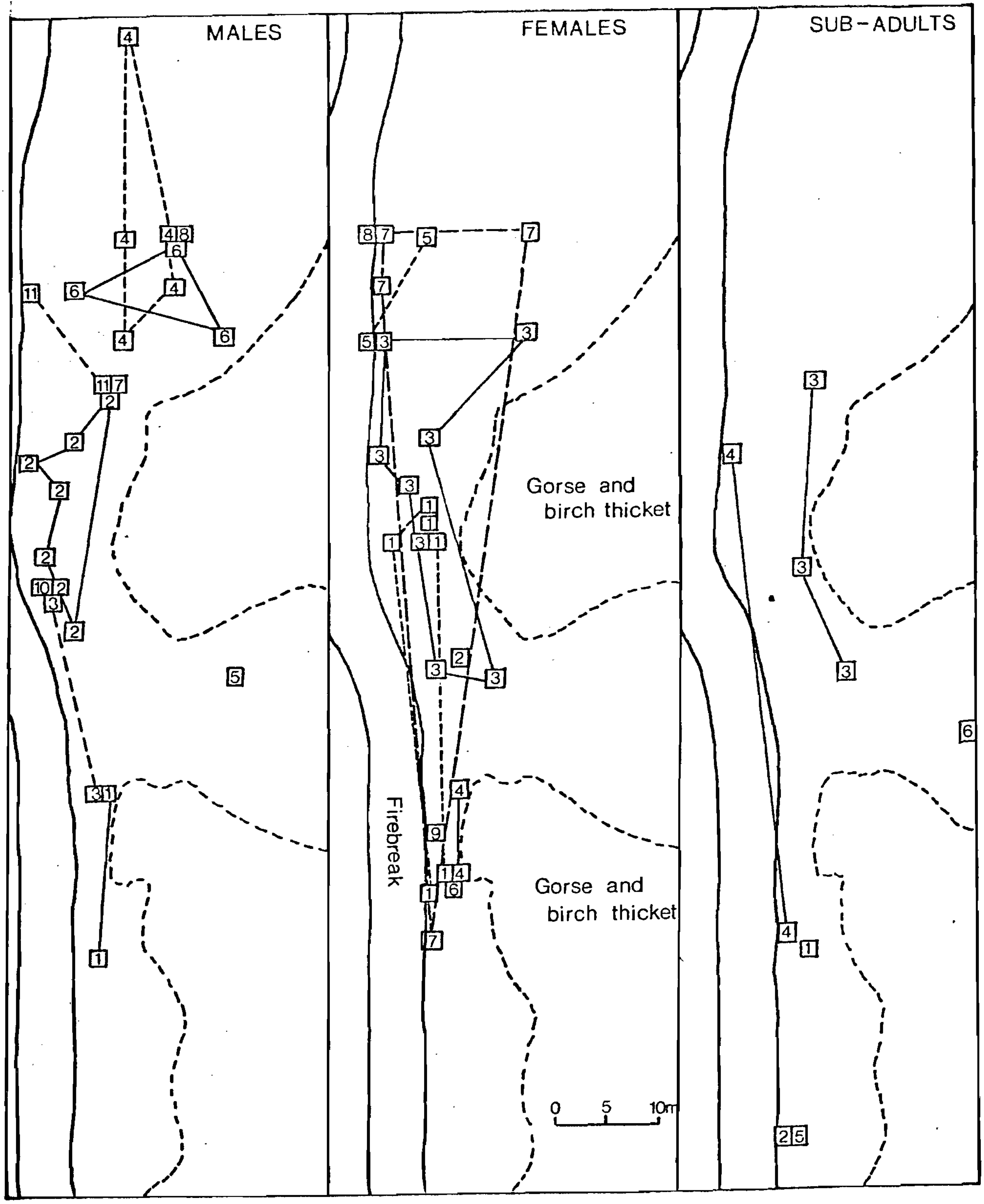

FIGURE 8.6 Captures of male, female, and sub-adult L.agilis at Soldiers Road in 1975. Each number refers to an individual lizard; capture points have been connected for clarification and do not represent home ranges.

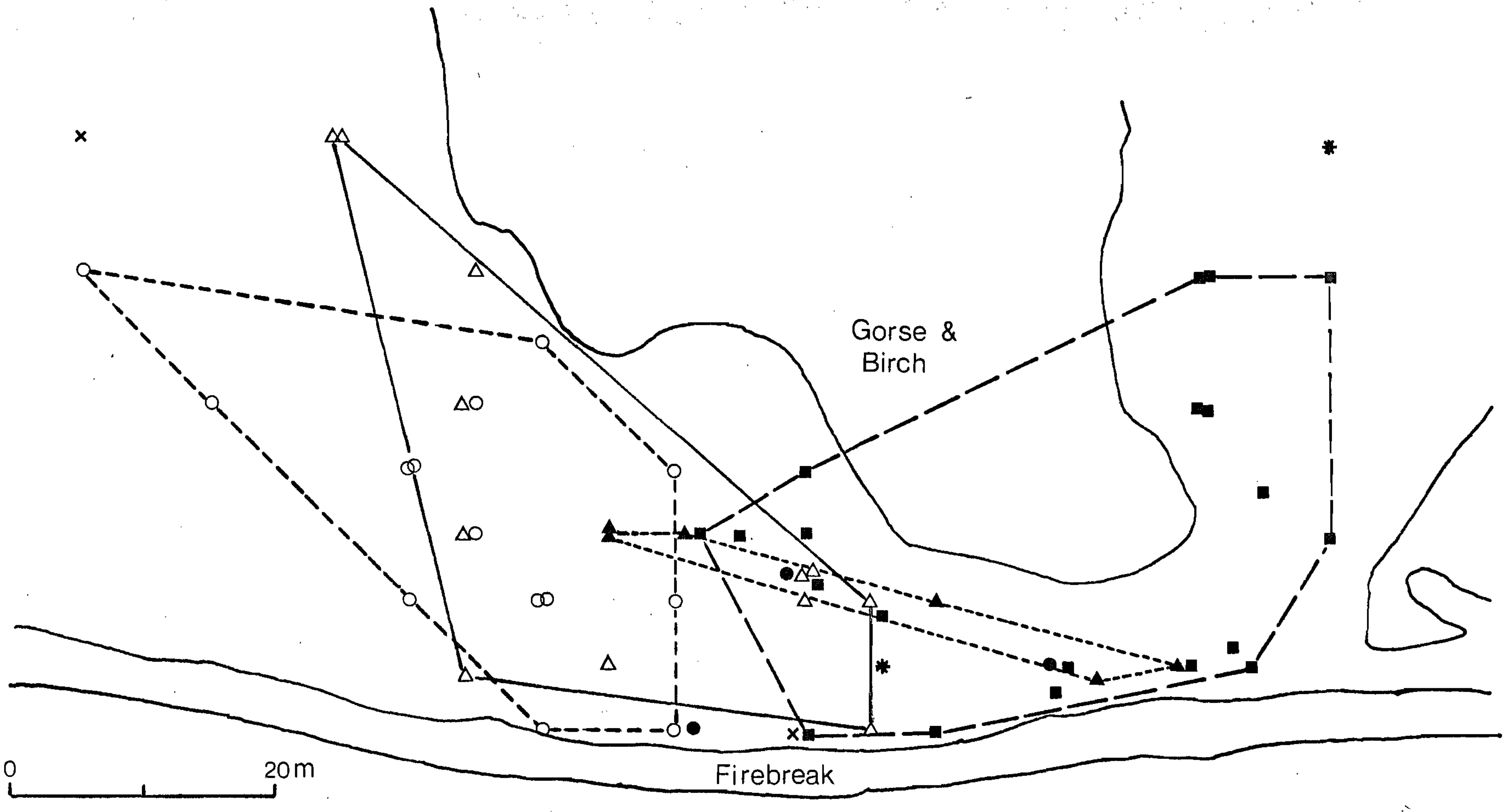

FIGURE 8.7 The capture points of seven individual male <u>L.agilis</u> (each lizard represented by a different symbol) at the Soldiers Road site in 1976. Convex polygon home ranges have been drawn for four individuals.

basking areas, often near overnight or overwintering sites were also used by several different individuals at different times during the year.

8.6 Social Behaviour

Observations of interactions between male L.agilis in April and May 1976 and 1977 at the Railway site suggested that a social hierarchy (some individuals consistently dominate other individuals, some individuals are consistently dominated, Hinde 1970) existed amongst males (Table 8.3). All the interactions observed between males were quickly terminated by the withdrawal of one individual. The hierarchy seems to be based mainly on size differences between individuals (Table 8.3). Fighting between males (described by Smith (1951)) was not observed but there was evidence that it occurred as many males caught during April and May showed bruising under the chin, which is caused when one male grasps the head of the other in his jaws. Bruising was not observed at other times of year. Social interaction between females was not observed in the field.

There was no evidence of any behaviour that could be interpreted as having the purpose of territorial defence. Conflicts appeared not to be settled by prior occupancy of space. On one occasion a male was observed to enter a burrow in the evening which was already occupied by another male. The first lizard was displaced. In both encounters observed between males in 1977 (Table 8.3) the same lizard was dominant although one encounter took place at a basking site frequently used

TABLE 8.3 SOCIAL INTERACTIONS AMONGST INDIVIDUAL *L.agilis* AT THE RAILWAY STUDY AREA

(a) Male-male interaction

	Dominant lizard	Snout-vent length (mm)	Subordinate lizard	Snout-vent length (mm)
1976	Hec.	77	Ern.	75
	Hec.	77	Ern.	75
	Hec.	77	Bob.	60
	Rus.	66	Tho.	69
	Tan.	78	Zon.	76
	Tan.	78	Zon.	76
	Alf.	76	Gor.	58
1977	Hec.	81	Tho.	77
	Hec.	81	Tho.	77

(b) Mating Pairs Observed: Male x Female

Male	Female
Gre.	Mat.
Geo.	Mat.
Stu.	Hel.
Stu.	Bel.

by the subordinate lizard and only one metre from his overwintering burrow.

Although copulation was not observed courtship (Smith 1951) was observed between some pairs. Identification of the individuals involved suggested a promiscuous mating system (Table 8.3).

8.7 Discussion

The estimates of home range size for individual lizards were subject to several sources of error. The two different methods used for catching lizards at the two sites had different sources of error associated with them.

At the Railway, where lizards were caught by hand, there was probably a bias towards seeing lizards in certain places, such as frequently used basking sites, often near burrows, where individuals basked in the early morning and late evening. Basking lizards were much easier to see than lizards which were foraging under dense vegetation, although some foraging lizards were caught. It is possible that the distribution of basking sites did not reflect the true home range.

This type of error may also have occurred at Soldiers Road where it was not possible to place traps under the dense gorse and birch thicket. However, in general this type of error can largely be overcome by using pitfall traps since, in contrast to hand capture, the traps caught foraging lizards rather than basking lizards. This seems a major advantage of using pitfall traps to measure home range size.

The pattern of utilization of the home range area at the Railway may also have affected the result of the measurement of the home range area. Some observations made on individual lizards suggested that individuals may use a small area within their home range for several days before moving to another area. It is possible that the small home range size of some individuals at the Railway (Table 8.1) was due to observations being made on the individual in only a part of the total home range area.

The uncorrected home range size of individual lizards calculated by the convex polygon method was strongly related to the number of observations made to determine it. The number of observations made was insufficient to determine the point at which the increase in home range size begins to level off. This problem was overcome by using correction factors which were computed using simulated home ranges by Jennrich & Turner (1969). However, the capture points in the simulated home ranges had a bivariate normal distribution so if the capture points of the individual lizards do not approximate to this distribution another source of error is introduced.

The mean home range size of males at the Railway and Soldiers Road was similar despite the different methods used. The difference between the home range sizes of females at the two sites may reflect a difference in the distribution of the capture dates. At Soldiers Road, only 16% of the observations were made in April and May whereas at the Railway, 79% were made in April and May. Observations on gravid females made during May showed that some individuals tended to bask for long periods in one place. One gravid female did not move from the immediate vicinity (she was not observed more than 0.5 m away) of her overwintering burrow until 4 June 1977 when she moved away. She spent long periods basking outside her burrow and shuttling between the shade of the burrow and the sunshine outside. Simms (1970) also notes that gravid females of L.agilis become increasingly restricted to small favourable areas. Males at this time move over a wide area.

It is possible that gravid females are at a greater risk from predation. One way to lessen this risk may be to restrict their movements. Alternatively, perhaps the low density of prey at this time of year (see chapters 4 and 5) means that the energetic cost of foraging widely is not balanced by an equivalent return in terms of increased food consumption. The function of the larger male home range in the spring may therefore be to find mates. At this time of year males lose weight but females do not (section 5.3(i)). Later in the year, the apparent similarity in the home range size of males and females suggests that the density and distribution of the same resource, probably food, is determining the home range size.

In many studies of the home range ecology of other species of lizard it has been found that the home ranges of males were larger than those of females (Hirth 1963; Jorgensen & Tanner 1963; Brooks 1967; Tinkle 1967; Ferner 1974) but the phenomenon has never been adequately explained. A disparity would suggest that different factors were important in determining the size of the home range in each case. Stamps (1977), working on the tropical territorial lizard Anolis aeneus, has found that females defend food resources whereas males defend mates. Where home range size differs between sexes these may be the two resources which are important. In the Lacertidae, Boag (1973) found that female Podarcis muralis occupied areas of approximately the same size as males and Tertyshnikov (1970) could not discover a difference between the home range sizes of the two sexes.

The home range sizes of individual L.agilis were much larger than those measured by Tertyshnikov (1970) and Rashkevitch & Semenikhina (1974) in the U.S.S.R. (For location see Figure 10.1) (Table 8.4). Tertyshnikov used a different method to measure home range size; he followed individuals using binoculars. Home range sizes were calculated from a maximum of six days observation on one individual but not corrected according to the time period of the observations. However, even uncorrected home range sizes in England were greater than home range sizes in the U.S.S.R. so it seems likely that there is a real difference. The home ranges in the U.S.S.R. were also consistently smaller in three different habitats than those in two habitats in England so the factors causing the disparity seem to act independently of habitat differences in each place.

There also appear to be differences in other aspects of the home range ecology of individuals between the two places. In the study areas in England there was a high degree of home range overlap which precluded the possible existence of territories. Territorial behaviour was not observed. Female lizards appeared tolerant of each other whereas a social hierarchy probably existed amongst males at least in the spring. Individual lizards appeared to use more than one overnight site in their home range area and the same overnight sites and preferred basking areas were used by several different individuals during the year. This contrasts with the observations of Tertyshnikov (1970) for more southerly populations of L.agilis in the U.S.S.R. "The lizards defend their refuges and preferred foraging-places from invasion by other individuals. If far from their burrow and foraging-places the lizards treat each other tolerantly but near them they are very aggressive. It was noted that the 'residents' even attacked larger individuals and, grasping them by the head, tried to turn them onto their backs. The conflict was discontinued as soon as one withdrew. In all cases the 'residents' were the victors." The lizards used only one refuge (overnight site) which was permanent and used throughout the season.

There therefore seems to be a distinct difference between the home range ecology in England, where individuals have large, overlapping home ranges and are not territorial, and that in southern U.S.S.R. where there are smaller home ranges and some territoriality seems to exist.

This is similar to the difference found between populations of Uta stansburiana in Texas (southern population) and Colorado (northern population) (Tinkle & Woodward 1967; Tinkle 1969a). In Colorado there was less social interaction between individuals than in Texas, more home range overlap and individuals were less aggressive. Texas lizards were strongly territorial whereas in Colorado a social hierarchy, with older individuals dominant, probably existed. Tinkle (1969a) explains this by the following reasoning. In Texas there is strong selection for aggression because aggressive individuals can hold territories and reproduce whereas less aggressive individuals are prevented from mating or forced into sub-optimal areas. In Colorado there is less selection for aggressive behaviour because some less aggressive animals are able to increase their fitness by extending their reproduction over a longer period, behaving submissively and perhaps therefore, being less exposed to predation.

Although this explanation may also be important in explaining the apparently similar discrepancy between populations of L.agilis in England and in southern U.S.S.R., it is also possible to explain the apparent differences in social structure by starting from the difference in home range size. In England the large home range size of individuals means that it is physically impossible for a lizard to defend its home range area from the intrusions of other individuals. Thus, as with the Colorado population of Uta stansburiana but for slightly different reasons, there will be little selection for aggressive behaviour since aggression may merely drive an intruder into another part of the home range of the resident. The high degree of home range overlap and the social structure of the population may, therefore, be a result of the requirement of individuals for a large home range area because of the distribution and density of resources in the habitat. In the populations in southern U.S.S.R. the smaller home range size allows some territoriality to exist.

Interspecific differences in the home range ecology of the Lacertidae are listed in Table 8.4. The small wall lizards Podarcis muralis and Podarcis sicula are both strongly territorial (Verbeek 1972; Boag 1973) and the territories of P.muralis in Italy are approximately seventy times smaller than the home ranges of L.agilis in England.

It was not possible to measure the home range size of L.vivipara because no recaptures of marked individuals were obtained. Buschinger & Verbeek (1971) followed individual L.vivipara tagged with radioactive tantilum in West Germany and found that males may cover an area of more than 60 m in diameter in one day. The home range area of one male, calculated by the convex polygon method from data in Buschinger & Verbeek (1971), was 1300 m^2 (Table 8.4). As this result was based on only three days continuous observations on one individual, actual home range sizes are likely to be considerably larger than this. Therefore it appears that the home range size of L.vivipara may be at least as great or greater than that of L.agilis. Moreover, the difficulty in obtaining recaptures of this species, which has also been experienced by R. Avery (pers. comm.), suggests that home ranges of this species may be much larger than those of L.agilis. This is contrary to what might be expected from consideration of the difference in size and therefore energy requirements, between the two species.

Direct information could not be obtained on home

TABLE 8.4 HOME RANGE ECOLOGY OF LACERTID LIZARDS

Species	Location	Habitat	Home range size	Home range overlap	Territorial behaviour	Authority
Lacerta vivipara	West Germany	Dense herbs, scattered trees	$> 1300\ m^2$*	? (probably a high degree of overlap)	No territorial behaviour Males fight sometimes Females tolerant	Buschinger & Verbeek (1971) Verbeek (1972)
Lacerta agilis	England	Heathland & grass/scrub habitat	see Tables 8.1 & 8.2	75%	No territorial behaviour, males have dominance hierarchy and fight in spring. Females tolerant	This study
Lacerta agilis	U.S.S.R.	Steppes & wooded belts	$190-250\ m^2$	?	Some lizards use permanent burrows	Rashkevitch & Semenikhina (1974)
Lacerta agilis	U.S.S.R. 45°N	Fescue wormwood steppes	$181\ m^2$	Considerable overlap which depends on the density of the population	Individuals (males and females) have permanent burrows and foraging areas which they defend	Tertyshnikov (1970)
		Grassy steppes	$148\ m^2$			
		Wooded belts	$108\ m^2$			
Eremias arguta	U.S.S.R. 45°N	Desert steppes	$122\ m^2$	?	Defend preferred foraging areas but do not have permanent burrows	Tertyshnikov (1970)
		Grassy steppes	$38\ m^2$			
Podarcis muralis	?	Dry stone wall	♂ $15\ m^2$ ♀ ?	? (probably little overlap)	Males defend territories Females have no territories	Weber (1957)
Podarcis muralis	Italy (Naples)	Walled garden	♂ $26\ m^2$ ♀ $23\ m^2$	♂ 8% ♀ 18%	Males and females defend territories	Boag (1973)
Podarcis sicula	Northern Yugoslavia	Island with low shrubs	Radius < 3 m (= area $< 26\ m^2$)	? (probably little overlap)	Males defend territories	Verbeek (1972)

* Calculated from data in Buschinger and Verbeek (1971) (based on three days' continuous observation on one male).

range overlap of L.vivipara for the same reason. However, considering that twenty-six individuals were caught at the Soldiers Road study area and given the probable large home range for the species, the degree of overlap must be very great.

The social behaviour of a species is related to the pattern of home range overlap. For example, from the interrelationships of home ranges in a Texas population of Uta stansburiana, Tinkle (1967) inferred a monogamous mating system because, in practice, owing to the strong territorial system each male was only in contact with one female. In contrast, a promiscuous system would be expected from the high degree of home range overlap of L.agilis and observations suggested this was the case. A social hierarchy rather than a territorial system would also be expected from the amount of overlap and observations were consistent with this.

In summary, it is suggested that the high degree of home range overlap and lack of territoriality that was characteristic of the populations of L.agilis studied results from the requirement of individuals for a large home range which it is not possible for individuals to defend.

CHAPTER 9

PITFALL TRAPPING AND LIZARD ACTIVITY

9.1 Introduction

Pitfall traps have been used as a method of catching lizards in several ecological studies in the U.S.A. (Jorgensen & Tanner 1963; Spoecker 1967; Parker 1972). Sometimes they have been used in conjunction with drift fences (Blair 1960; Bostic 1965).

Both Spoecker (1967) and Parker (1972) have used the rate of capture of lizards in pitfall traps as an index for comparing the activity of different sex and age classes within a population. In theory, capture rates are dependent on the rate of exposure to traps which is itself dependent on a combination of the density and activity of individuals. Thus within a sex or age class where short-term changes in density are likely to be small, short-term variation in the number of individuals caught is likely to be caused by changes in activity. Furthermore, daily variations in the number of lizards caught are likely to be caused in part by the effect of environmental conditions on activity. In the case of *Lacerta agilis* and *Lacerta vivipara* activity is likely to consist largely of foraging. Thus environmental conditions may affect the time available for foraging by determining the time taken to raise body temperature to preferred levels and the rate of cooling during foraging or, in other words, the proportion of time spent basking.

This chapter is therefore largely concerned with the influence of weather on the rate of capture of lizards in the pitfall traps. First, however, some general data from the pitfall trapping is given and seasonal variations in the rate of capture of male, female and sub-adult L.agilis are examined. Differences in the success between individual traps are also considered. Methods relevant to this chapter are given in chapter 3.

9.2 Rates of capture and recapture

During 1975, seventy-two lizard captures (including recaptures) were made, sixty-four of L.agilis and eight of L.vivipara (Table 9.1). Trapping rates were 1.4 lizards per 100 trap days for L.agilis and 0.1 lizards per 100 trap days for L.vivipara. The ratio of first captures to recaptures was 0.64 for L.agilis; all the captures of L.vivipara were of different individuals (Table 9.1). The maximum number of times any individual of L.agilis was caught was nine, fifteen individuals were caught more than once and five more than once in the same trap.

In 1976, 137 lizard captures were made, 119 L.agilis and eighteen L.vivipara (Table 9.1). Thus 13% of captures were L.vivipara compared with 11% in 1975. The ratio of first captures to recaptures was 0.34, lower than in 1975, and again no recaptures of L.vivipara were obtained.

9.3 Activity

Figure 9.1 shows the monthly catch rate of male, female and sub-adult L.agilis in the traps in 1975 and 1976. No juveniles were captured in the traps.

A decline in number of males, females and sub-adults

TABLE 9.1 PITFALL TRAPPING DATA FOR *L.agilis* AND *L.vivipara*

	1975	1976
Total number of trap days	4832	11550
Number of captures of *L.agilis*	64	119
Number of individual *L.agilis* caught	25	30
Number of captures of *L.vivipara*	8	18
Number of individual *L.vivipara* caught	8	18

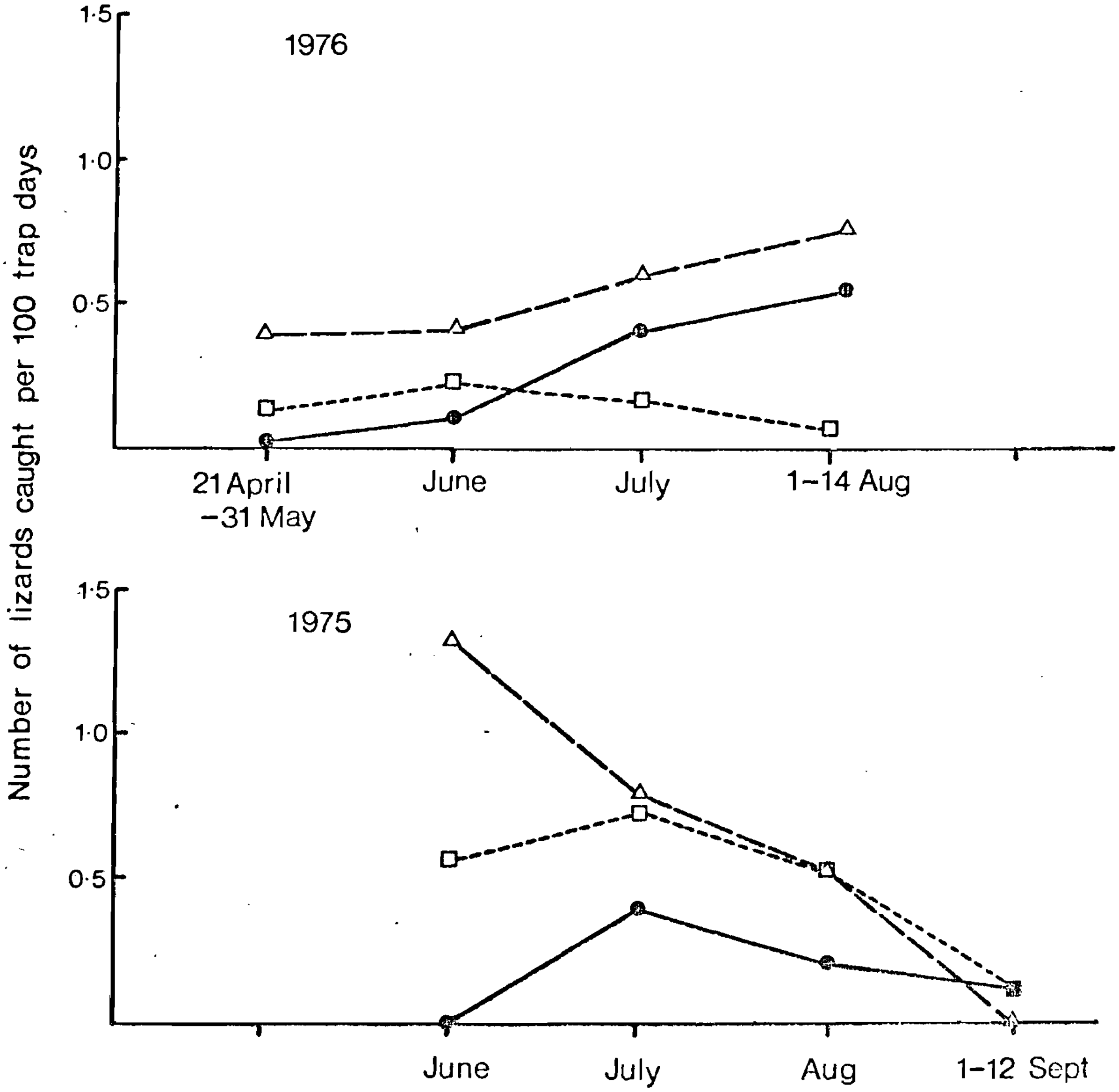

FIGURE 9.1 Rates of capture of male (triangles), females (squares) and sub-adults (circles) in the pitfall traps at Soldiers Road.

caught can be seen between July and September 1975. Few lizards were caught in September and trapping was discontinued because of this. Weather conditions in September were cool and overcast and this was probably the main reason. There was also a marked difference in the number of individual L. agilis caught between the first and second halves of August, 1975, 87% of lizard captures being made on or before August 16, so the decrease in catch rate between July and August is caused by a sharp decline in numbers caught in the latter half of August.

During 1976, the rate of capture of females was much less than for males, in contrast to 1975. In both years, however, there was a marked increase in the number of sub-adults caught between June and July. Trapping in 1976 was prematurely brought to a halt by the destruction of the study site by fire.

The number of lizards caught was examined in relation to two environmental variables, maximum temperature and total daily net solar radiation. Figure 9.2 shows frequency histograms of the number of days in different temperature and radiation classes. Days are also classed as either successful (at least one lizard caught) or unsuccessful (no lizards caught) for each species. The number of days in different classes is very variable. For L. agilis the proportion of successful days increases with both temperature and radiation but for L. vivipara no such increase is discernible although at the lowest temperature and radiation levels few individuals were caught.

In Figure 9.3 the mean number of lizards caught per

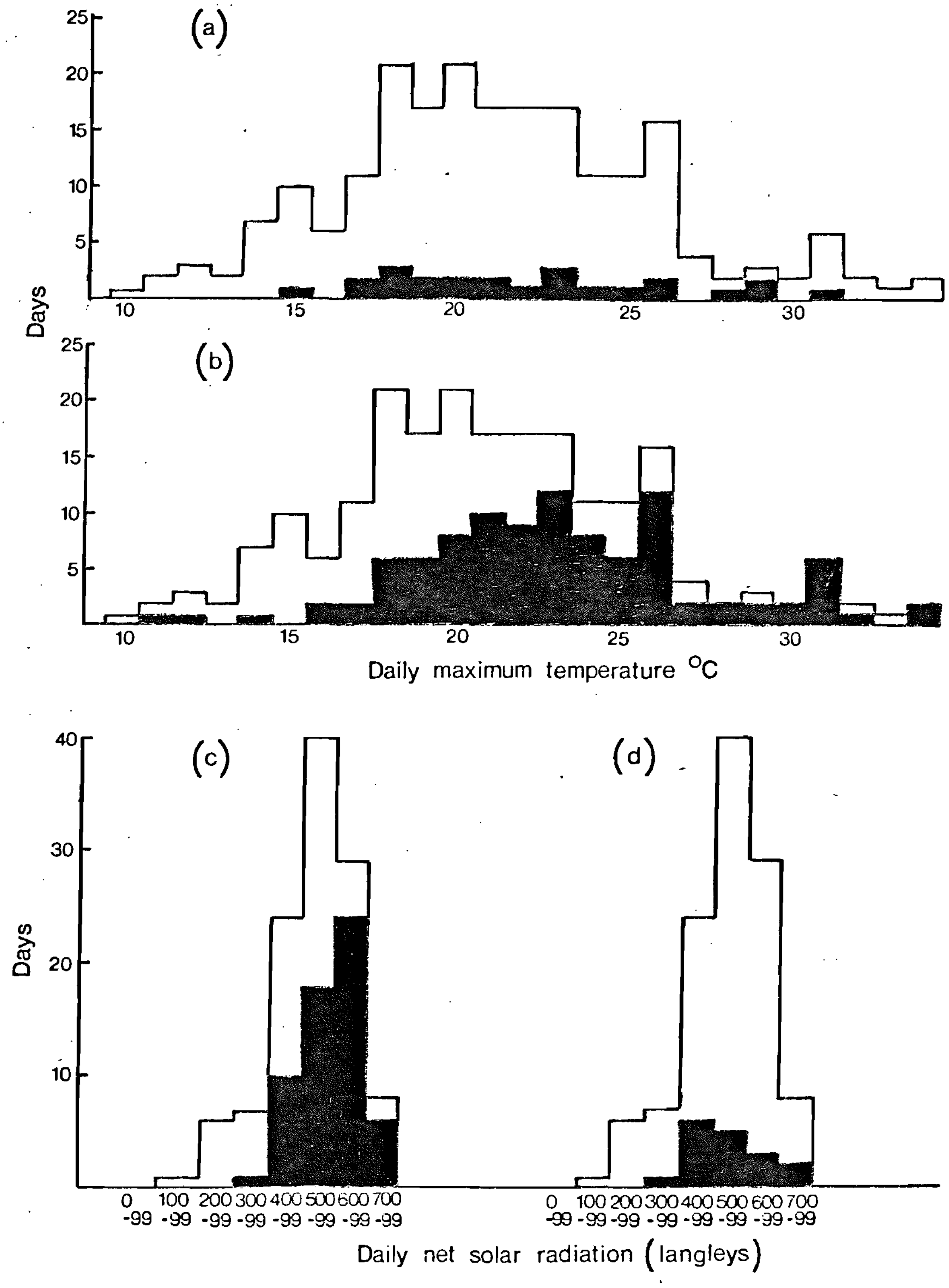

FIGURE 9.2 Frequency distributions of the number of days in daily maximum temperature and net daily solar radiation categories during pitfall trapping. Days are divided into those successful (shaded) and unsuccessful (unshaded) at catching lizards, for L.agilis (b & c) and L.vivipara (a & d). Temperature data are for 1975 and 1976 combined, radiation for 1976 only.

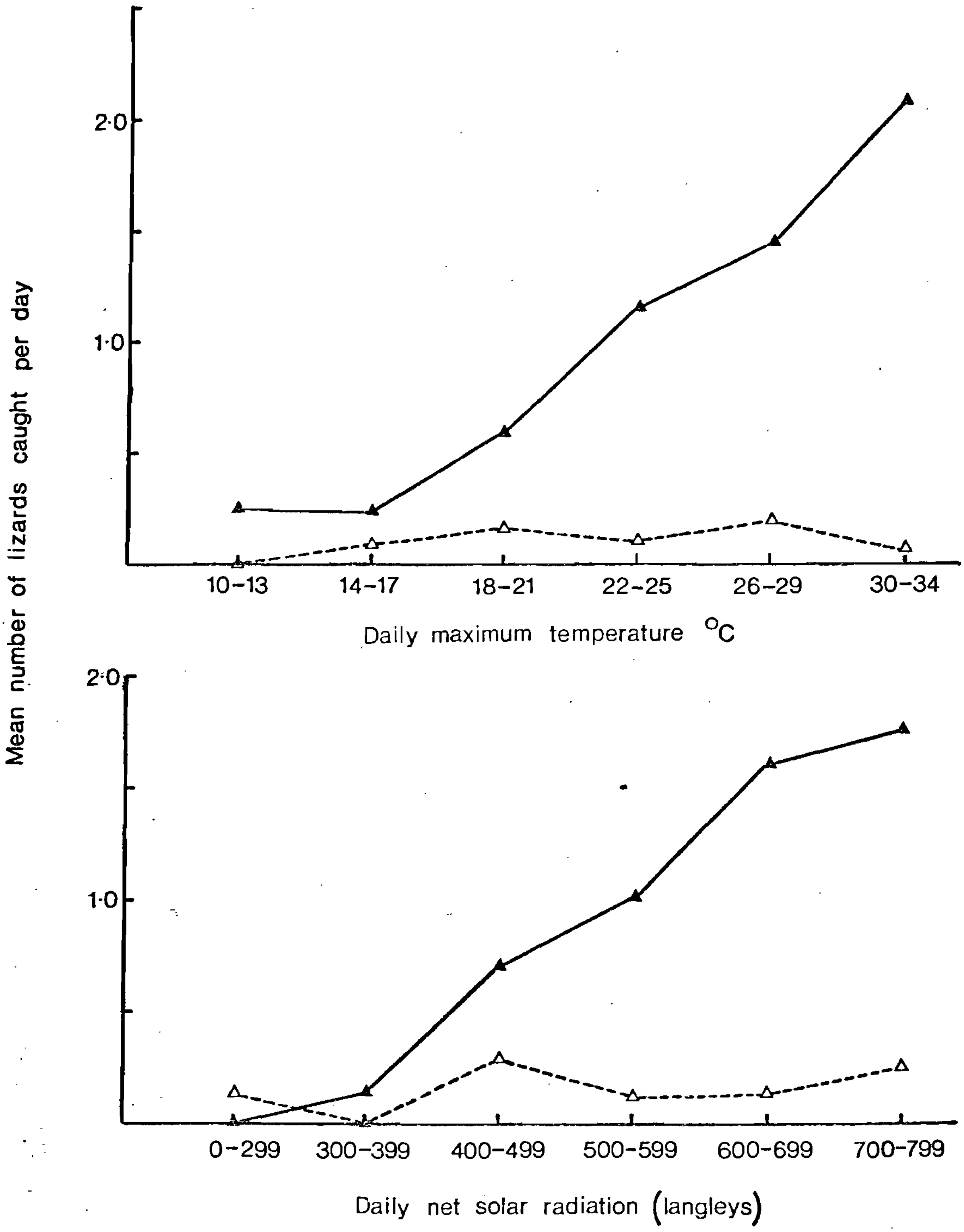

FIGURE 9.3 The mean number of individuals of L.agilis (solid line) and L.vivipara (broken line) caught per day in the pitfall traps in relation to daily maximum temperature (1975 and 1976) and net daily solar radiation (1976 only).

day is shown for different temperature and radiation categories. Numbers of L.agilis caught rise steadily with temperature and radiation, whereas numbers of L.vivipara do not show any similar trend, remaining low even at the highest temperature and radiation levels.

Whilst the upward trend for L.agilis is clear it is possible that a similar trend existed for L.vivipara but was not apparent because of the low numbers caught. To test whether there was a real difference between the two species in their response to the two environmental variables, the mean temperature and radiation for captures of each species was calculated (i.e. the mean of the daily temperature and solar radiation values for every lizard capture). These are shown in Table 9.2. Both means of temperature and radiation were significantly greater for L.agilis captures than for L.vivipara captures (temperature, $t = 2.33$ $p < 0.025$; radiation, $t = 2.08$ $p < 0.05$). Also shown in Table 9.2 are the mean temperature and radiation levels for unsuccessful days for both species. For L.agilis mean values for temperature and solar radiation were significantly greater for lizard captures than for unsuccessful days (temperature, $t = 9.03$, $p < 0.001$; radiation, $t = 5.82$, $p < 0.001$). These differences were not significant for L.vivipara).

9.4 Differences in success rate between traps

There was considerable variation in the number of lizards caught in different traps. In 1975, the most successful trap caught five lizards during the season; many traps did not catch any lizards. It appeared that

TABLE 9.2 MEAN DAILY MAXIMUM TEMPERATURE AND TOTAL SOLAR RADIATION FOR LIZARD CAPTURES AND FOR UNSUCCESSFUL DAYS (NO LIZARDS CAUGHT)

	Mean daily max. temp. for lizard captures (°C)	Mean daily solar radiation for lizard captures (langleys)	Mean daily max. temp. for unsuccessful days (°C)	Mean daily solar radiation for unsuccessful days (langleys)
L.agilis	24.2	589.3	19.6	480.4
L.vivipara	22.1	532.0	21.3	533.3

individuals of L.agilis were captured both in traps sited in dense Calluna and those in relatively bare ground.

A frequency distribution of the number of lizards caught per trap in 1975 is shown in Figure 9.4. If each trap had an equal chance of catching a lizard then a Poisson distribution would be expected. The observed distribution is compared with the expected Poisson distribution, calculated from the mean number of lizards caught per trap, in Figure 9.4. Although more traps than expected caught no lizards and fewer than expected caught one, the departure from the Poisson distribution was not significant (chi^2 test $p = 0.1$). Therefore, the hypothesis that each trap had an equal chance of catching a lizard cannot be rejected.

9.5 Discussion

No consistent pattern in the activity of male and female L.agilis was observed between 1975 and 1976. In both years, however, numbers of sub-adults caught increased greatly between June and July. There seem to be two possible explanations for this. Firstly, it may represent a rise in the activity of sub-adults. At the end of June sub-adults measure on average 53 mm in snout-vent length and at this time, individuals are beginning to take an increasing proportion of harder and larger prey, characteristic of the diet of adults (see chapter 4). These changes could be accompanied by a transition to adult activity patterns and larger home ranges. The second possibility is that females at the Soldiers Road site do not lay their eggs on the study area and the

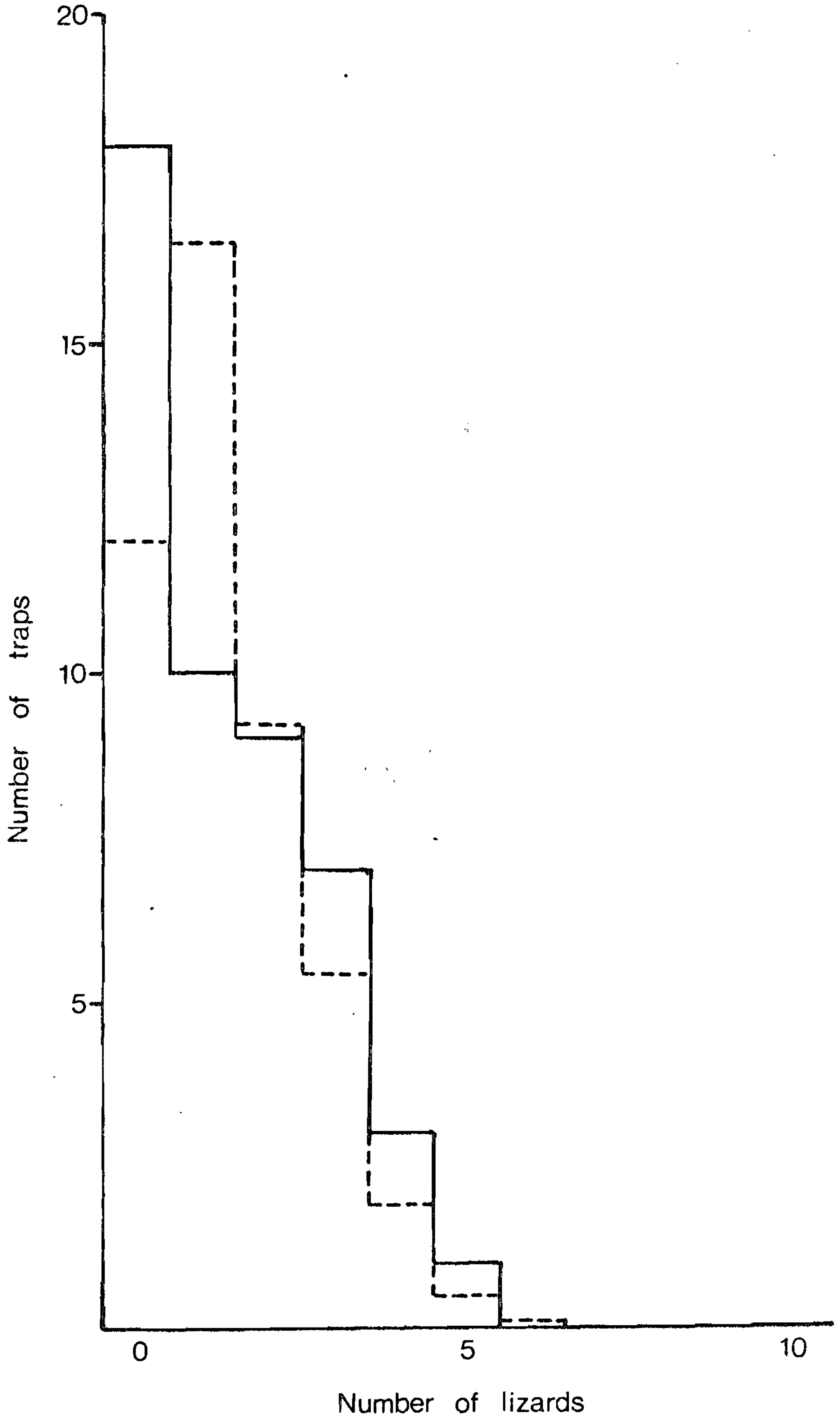

FIGURE 9.4 Frequency distributions of the number of lizards caught per trap. Solid line observed distribution. Broken line expected distribution if each trap has an equal chance of catching a lizard.

increase represents a dispersal of sub-adult lizards from other areas. At the Railway one female was observed egg-laying 130 m from her normal home range area (section 6.4). No egg-laying activity was observed on the Soldiers Road study area and no juveniles were seen or caught in traps. Gravid females were not caught in traps during the egg-laying period. The rise in the number of sub-adults caught could therefore represent a dispersal from the vicinity of the egg-laying sites to new areas. The nearest known egg-laying site was 120 m from the study area. These two possibilities are not mutually exclusive; a dispersal of sub-adults is likely to be accompanied by an increase in their activity.

A notable result from pitfall trapping was that a far greater number of L.agilis were caught than L.vivipara. The difference was consistent over two years. There are several possible explanations, the most obvious being a disparity in densities between the two species. It was not possible to measure the density of L.vivipara because no recaptures of marked individuals were made, so densities of the two species could not be directly compared. However, observations of the two species on the study areas suggested that the densities were not as different as the ratio of their numbers in the pitfall traps (Table 9.1) suggested. Therefore it would seem that other reasons besides density are also needed to account for the difference.

One possibility could be a behavioural difference between the two species. It seems unlikely that L.vivipara learnt to avoid the traps as this was not the case with L.agilis. Behavioural differences such as any difference in microhabitat preferences could lead to a difference in the rate of exposure to the traps. However, evidence from the diets of the two species (section 4.8) suggested that if there was any difference in microhabitat preference it was not one that would cause L.agilis to be more exposed to traps than L.vivipara.

Another possibility is that individuals of L.vivipara are less active than individuals of L.agilis and so exposed less to the traps. Attempts to quantify the energy expended on activity of lizards in natural conditions have been beset with difficulties. These attempts have usually been made by multiplying a basal or resting metabolic rate, measured by oxygen consumption in the laboratory, by a factor to account for activity (Dawson & Bartholomew 1956; Alexander & Whitford 1968; Mueller 1970; Tinkle & Hadley 1975). Factors between 1.5 and 3 have been suggested and Dutton, Fitzpatrick & Hughes (1975) have calculated the effect on the energy budget of Sceloporus olivaceus of using different values for these factors. These factors are derived from laboratory studies where oxygen consumption of lizards stimulated to activity is compared with basal or resting rates (Licht 1965; Bennett & Licht 1972; Bennett & Gleeson 1976; Dm'iel & Rappeport 1976). However, activity in the laboratory often bears little relation to behaviour in the field. The situation is further complicated by the fact that several lizard species studied have been found to have little potential for increasing aerobic metabolism during activity; activity is supported primarily by anaerobic metabolism (Moberly 1968; Bennett 1972; Bennett & Dawson 1972; Bennett, Dawson & Bartholomew 1975; Bennett & Gleeson 1976; Dm'iel & Rappeport 1976). Lizards therefore rapidly become exhausted as lactic acid levels rise and an oxygen debt is accumulated.

Because of these and other difficulties, energetic costs of normal activities such as prey catching, foraging, thermoregulatory behaviour, escape from predators, and social behaviour are not, in general, known. It is therefore also not known whether there are significant differences in the energy expenditure on activity between lizard species. Recently however, a new method of measuring the energy expenditure of lizards in the field, involving the use of radioisotopes, has been used successfully (see Congdon, Ballinger & Nagy 1979) and this technique should solve some of the problems concerned with the energetics of lizard activity.

Values of between 53 and 81% have been calculated for the expenditure of energy on respiration as a percentage of the total annual energy expenditure of small lizards (Iguanidae) in the U.S.A. (Mueller 1970; Dutton, Fitzpatrick & Hughes 1975; Tinkle & Hadley 1975). Using factors of between 1.5 and 3 to adjust basal or resting metabolic rates to active rates; energy expenditure on activity was therefore between 24 and 41% of the total budget of these lizards. It can be seen that the potential for saving energy in this area is large.

Avery (1976) has argued that individuals of

L.vivipara in southern England have less 'spare' time and energy than more southerly species such as Podarcis muralis and Podarcis sicula in Italy. They therefore cannot afford, in terms of time and energy, to engage in "non-essential" activities. It would therefore be expected that adaptations which resulted in energy being saved would be particularly favoured for L.vivipara. Avery (1978) calculated that the lower preferred body temperature of L.vivipara compared with P.muralis resulted in a considerable saving in terms of energy expenditure and also suggested that there may be a difference in the metabolic expenditure on activity.

Thus it is tempting to argue that individuals of L.vivipara practise a considerable degree of economy in their energetic expenditure on activity compared with other lizard species, causing the low rates of capture in the traps. The economy could take the form of reducing the distance travelled each day whilst foraging by reducing the time spent foraging or speed of movement while foraging. At this stage, however, it is not possible to dismiss other equally plausible explanations for why few L.vivipara were caught in the traps. Nevertheless, the very different response of the trapping rate of each species as temperature and solar radiation levels rose suggests that activity may have something to do with the low numbers of L.vivipara caught.

Considering first the case of L.agilis, the numbers of L.agilis caught per day showed a steady rise with maximum daily temperature and mean daily solar radiation. This can be interpreted as a rise in the activity of individual L.agilis. In other studies where pitfall trapping has been used for catching lizards it has not been possible to relate numbers caught daily with environmental variables as the traps were not checked daily.

The steady rise in the numbers of L.agilis caught is predictable from the pattern of thermoregulatory behaviour shown by the species. Individuals forage widely, travelling long distances (chapter 8). Foraging takes place usually in the shade, or semi-shade, but in cooler conditions individuals seem to forage more in the open. Foraging is interrupted by periods of basking: basking lizards were observed feeding when suitable prey passed within sight but, generally, basking lizards did not select basking sites so they could observe large areas for the presence of potential prey as many sit-and-wait lizard predators do (Pianka 1969). They also did not appear alert when basking, sometimes shutting their eyes. Most activity and most feeding, then, seems to take place in the shade or semi-shade, lizards often being observed foraging under dense vegetation. As temperature and solar radiation levels rise L.agilis needs to spend less time basking in order to raise its body temperature to its preferred level and also rates of cooling will be slower in the intervals between basking. The percentage of time spend basking will therefore diminish and for L.agilis this will result in an increase in activity.

The dependence of the behaviour of small heliothermic lizards on weather conditions is well known. For example, Spellerberg (1972) has demonstrated the decrease in the percentage of time spent basking with increasing surface temperatures for species of the Sphenomorphus species complex in Australia. Avery (1978) divided the behaviour of the lizards Podarcis muralis and Podarcis sicula into four categories depending on weather conditions. These ranged from periods when no lizards were seen to periods of uninterrupted sunshine when basking was minimal and large numbers of lizards were seen. The results for L.agilis suggest a steady rise in activity within these categories. There was no observable levelling off of activity even at the highest temperature and radiation levels. A bimodal activity pattern has been demonstrated for species of Acanthodactylus lizards in Israel and Spain (Busack 1976) and Simms (1970) has observed that L.vivipara sometimes retreat into burrows or under stones in hot weather. Avery (1978), however, found that Podarcis muralis and Podarcis sicula did not show a bimodal activity pattern. The situation is not clear for L.agilis. Few individuals were observed during the hottest parts of hot days (maximum temperatures > 24° C). However this was probably, to a large extent, caused by activity taking place in dense vegetation where it was difficult to observe the lizards. Temperatures recorded under deep Calluna on the hottest days during the study period (maximum temperatures 30-34° C) were little higher than 30° C although temperatures under Calluna where the canopy was less dense were much higher (pers. obs.). During these days, therefore, it is not unlikely that individuals are active under very dense vegetation but in practice it is difficult to distinguish between this and the other possibility that the lizards retreat down burrows. As the temperatures under deep Calluna on these hottest days was very close to the preferred body temperature of L.agilis of approximately 30°C (Liberman & Pokrovskaja 1943; Spellerberg 1976) individuals would not need to bask at all during much of the day. There is no suggestion of a bimodal activity pattern from the pitfall trapping results as a levelling off of activity at the highest temperatures was not found. A monophasic period of activity has been shown for L.agilis in Europe (Marx & Kayser 1949; St. Girons 1971).

The pattern of the variation in the numbers of L.vivipara caught with temperature and solar radiation was very different from that of L.agilis. The numbers caught did not increase significantly with increasing temperature and radiation levels. Thus there appears to be a difference in the relative activity of the two species in relation to temperature and solar radiation, L.agilis being relatively more active at higher temperatures. It seems relevant that the centre of the distribution of L.agilis is further south than that of L.vivipara. Possibly the activity pattern of L.agilis represents the usual pattern for small heliothermic lizards and that of L.vivipara is an adaptation to low levels of solar radiation and temperature. Other adaptations of reptiles to cold climatic conditions have been reviewed by Spellerberg (1976).

The relative difference between the two species could be caused either by the activity of L.agilis being depressed at low temperatures or by that of L.vivipara being depressed at high temperatures, or any combination of the two. Considering the first possibility, it may be that at low temperatures the larger L.agilis has to spend more time basking than the smaller L.vivipara. However, it seems unlikely that the difference in body size could have a large effect on the proportion of time spent basking.

Considering now the second possibility, Avery (1971) has shown that the rates of food consumption of L.vivipara in the field in sunny weather are not significantly different from rates of ad libitum food consumption in the laboratory; during good conditions in the field individuals were apparently feeding at their maximum rate, this rate being set physiologically or by stomach volume (Avery 1973, 1978). Perhaps, at high temperatures individuals are unable to raise their food consumption in order to support higher levels of activity but can still feed at their maximum rate with activity levels similar to those at lower temperatures. It seems relevant that individuals of L.vivipara kept in the laboratory and allowed to thermoregulate for 5 hours every day remained healthy whereas those allowed to thermoregulate for 8 hours a day lost weight and eventually died (Avery 1978). In contrast L.agilis having a bigger stomach and much higher rate of maximum food consumption (chapter 5) will presumably gain benefits in terms of increased food consumption which will at least compensate for the increase in activity at higher temperatures.

CHAPTER 10

THE DISTRIBUTION OF LACERTA AGILIS IN RELATION TO CLIMATE

10.1 Introduction

Climate is clearly of particular importance for ectothermic animals such as lizards. In the previous chapter the influence of temperature and solar radiation on the activity of Lacerta agilis and Lacerta vivipara was examined. Furthermore, for an oviparous species such as L.agilis, climatic variables will obviously directly affect the conditions experienced by the eggs during their development. The importance of solar radiation in raising the temperature of the eggs and so presumably accelerating their development was demonstrated in chapter 6. Thus, because an ectothermic species is so directly dependent on weather, it is not unlikely that climatic factors may be of overriding importance in determining the limits of its distribution.

It is the relationship between climate and the distribution of L.agilis that is examined in this chapter. In particular, the relationship between climatic factors and the northern limits of the species is investigated, the southern limits are then examined and finally, the distribution of L.agilis in England is considered. These investigations are carried out using climatic data from meteorological stations and of course, these records are not exactly equivalent to the conditions experienced by the lizards. Nevertheless, for the purposes of this investigation, they probably adequately measure differences in conditions experienced by lizards in different locations.

10.2 Methods

Data from meteorological stations both within and outside the range of L.agilis are given in Appendix VI. The locations of these stations are shown in Figure 10.1, each number referring to a station listed in Appendix VI. All data were taken from 'Tables of temperature, precipitation and climate for the world' (H.M. Stationery Office, 1972). Most of the records were based on 25 years' data although some of the sunshine records for the U.S.S.R. were based on only five years' data. The statistical procedure of two group multiple discriminant analysis was carried out using a computer program.

10.3 Winter Temperatures

January average daily minimum temperature varied greatly within the range of L.agilis (Appendix VI) from 1.8°C in Rennes to -20.4°C in Ufa. In England January temperatures were high compared with the rest of the range. Temperatures at stations outside the northern limits of the distribution were no lower than those at many stations well within the range. L.agilis, therefore, is able to tolerate extremely cold conditions during winter submergence and winter temperatures are unlikely to impose any limits on the distribution.

10.4 The northern limits of the range

The aim of this section was to see if the position of the northern boundary of the range of L.agilis was consistent with changes in climatic variables. Summer

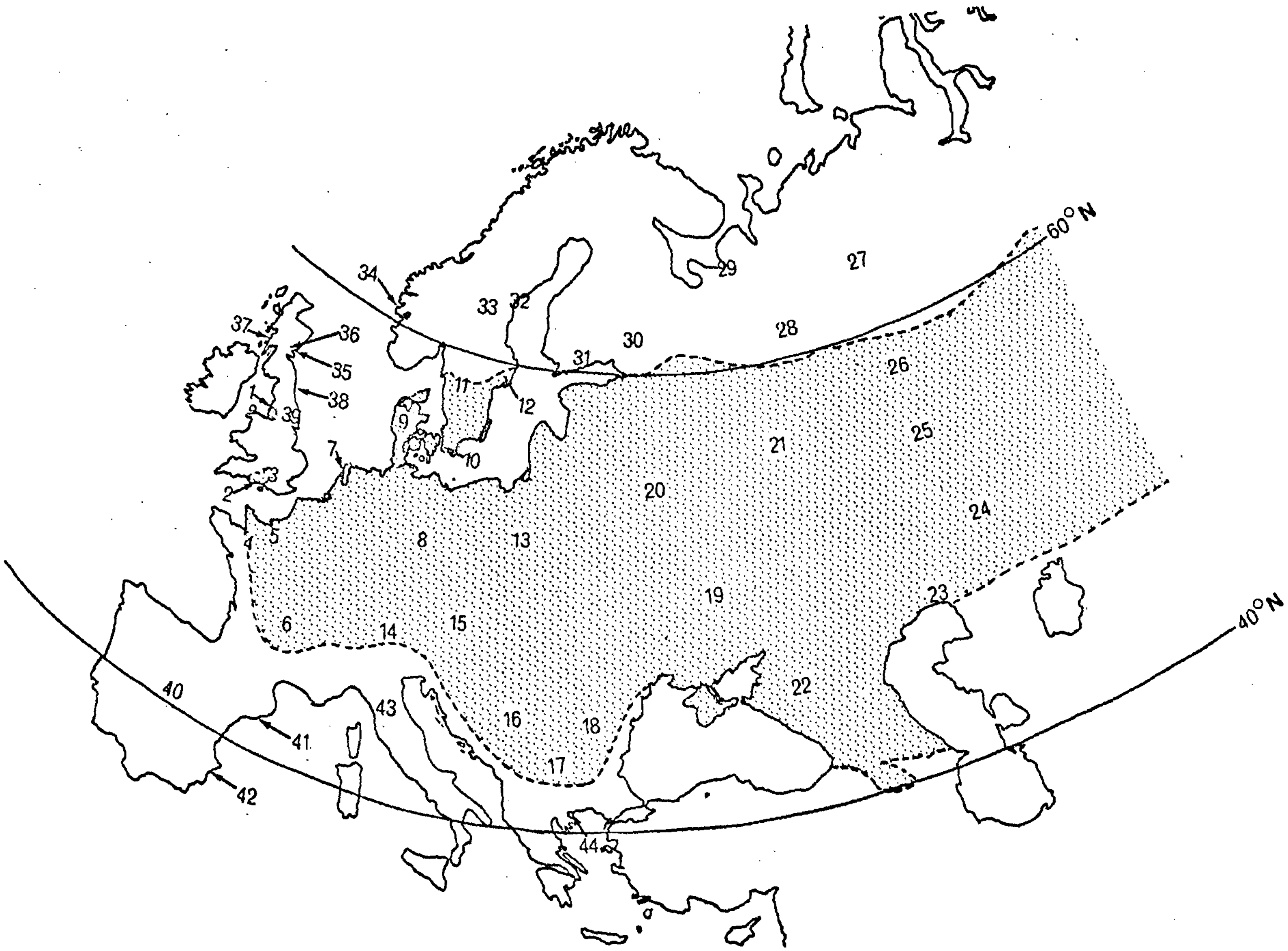

FIGURE 10.1 Location of Meteorological stations and the distribution of L.agilis in Europe. Numbers refer to stations listed in appendix VI. The work of Tertyshnikov (1970) and Rashkevitch & Semenikhina (1974) took place close to station 22.

temperatures and levels of solar radiation, and the length of the summer, were considered likely to be most important.

Three variables were selected, total sunshine hours (April - September), mean daily maximum temperature (May - September, average of the five monthly values), and number of months with mean daily maximum temperature greater than 13°C. The last was chosen as indicative of the length of the season. These variables are subsequently termed X_1, X_2 and X_3.

Using these variables, a two group multiple discriminant analysis was carried out in order to examine the position of the northern boundary of the range. Thirty-five stations were chosen for the analysis, twenty-two within the range and thirteen outside the northern boundary. The analysis finds the weighted linear combination of variables which is the best discriminator between the two groups, in this case the presence or absence of L. agilis, and thus determines how well the presence or absence can be predicted from a linear combination of the variables used.

As a means of assessing the discriminatory power of each variable separately and of variables in combination the statistic $\frac{D}{2}$ (where D = Mahalonobis distance between the two groups) is shown in table 10.1. The higher D, the better the discrimination.

Of the three variables taken singly, X_2 is the best discriminator. From $\frac{D}{2}$ the probability of misclassification can be obtained from tables; for X_2 alone it is about 25%. Addition of X_1 or X_3 to X_2 did little to improve its discriminatory power. X_1 and X_3 together were almost as good as X_2 and much better than either X_1 or X_3 singly.

TABLE 10.1 THE MAHALOBIS DISTANCE (D) FOR THE THREE VARIABLES USED IN THE DISCRIMINANT ANALYSIS TAKEN SINGLY AND IN COMBINATION. THIS DISTANCE MEASURES THE DISCRIMINATORY POWER OF EACH VARIABLE OR COMBINATION. CORRELATION COEFFICIENTS BETWEEN VARIABLES ARE ALSO SHOWN.

Climatic variable	D/2	correlation coefficient (r)
X_1 (Total sunshine)	0.425	-
X_2 (Mean temperature)	0.938	-
X_3 (Length of season)	0.677	-
$X_1 + X_2$	0.940	0.51
$X_1 + X_3$	0.924	0.01
$X_2 + X_3$	0.984	0.65
$X_1 + X_2 + X_3$	1.022	-

combination of all three variables although the best of all combinations was not significantly better than X_2 by itself. The discrimination using all three variables was highly significant ($F_{3, 31} = 10.7$ $p < 0.005$).

The reasons for these results appear to be as follows. Total summer sunshine (X_1) is high outside the northern boundary of the range in U.S.S.R. and Sweden and it is therefore not a good discriminator by itself. Likewise, length of season (X_3) is not good by itself because many stations within the range in the U.S.S.R. have only 5 months over 13°C, the same value as many of the stations outside the northern boundary. Mean temperature (X_2) is best by itself and is not greatly improved by sunshine or length of season probably because it is correlated with these two. Although sunshine totals were generally low in Britain, and lower in northern England and Scotland than anywhere else, it is possible to explain the absence of lizards in northern Britain by temperature alone, the most important factor in other parts of the range. This does not mean that these low sunshine totals were unimportant, only that sunshine did not increase the discriminatory power of mean temperature.

The individual discriminant scores for each station based on all three climatic variables are shown in table 10.2. The analysis predicts that at stations with discriminant scores above the critical mid-point (21.3) lizards should be present and for scores below the mid-point lizards should be absent. Six stations were misclassified and these were mostly stations near the northern boundary of the range, wrongly classified as having lizards absent. If these discriminant scores

TABLE 10.2 DISCRIMINANT SCORES FOR STATIONS USED FOR THE DISCRIMINANT ANALYSIS. DISCRIMINANT SCORES WERE COMPUTED USING THREE CLIMATIC VARIABLES TO GIVE THE BEST DISCRIMINATION BETWEEN THE TWO GROUPS (+ OR - L.agilis)

Station	Discriminant score	Presence + or absence of L.agilis	
Belgrade	27.9	+	
Armavir	27.0	+	
Clermont-Ferrand	26.7	+	
Aktyubinsk	26.1	+	
Kharkov	26.0	+	
Innsbruck	24.8	+	
Rennes	24.5	+	
Liepzig	24.3	+	
Rouen	23.8	+	
Ufa	23.3	+	
Reading	23.3	+	
Bournemouth	23.2	+	
Warsaw	22.5	+	
Gorkiy	22.4	+	
Smolensk	21.6	+	
Stockholm	21.5	+	
Malmo	21.4	+	
Helsinki	21.3	-	
			CRITICAL MID-POINT
Den Helder	21.2	+	
Perm	21.1	+	
York	21.0	-	
Harnosand	21.0	-	
Studsgard	20.9	+	
Kotlas	20.8	+	
Blackpool	20.7	+	
Jonkoping	20.3	+	
Sortavala	20.0	-	
Sveg	19.7	-	
Perth	19.2	-	
Dundee	18.8	-	
Bergen	18.5	-	
Oban	18.0	-	
Troitsko-Pechorskiy	17.3	-	
Archangel	17.2	-	
Tynemouth	17.0	-	

are taken as a measure of the 'suitability' of the climate for L.agilis it would appear that the two stations in southern England are not borderline cases, but are as suitable as many places in continental Europe, and better than some stations within the range in Scandinavia and the U.S.S.R.

The discriminatory analysis shows that it is possible to predict the approximate position of the northern boundary of the range from consideration of three climatic variables. The absence of L.agilis from northern England and Scotland, although at a lower latitude than parts of the range in Scandinavia and the U.S.S.R., is also predictable. The most important of the three variables seems to be temperature but this is not entirely clear as although temperature was the best individual discriminator, sunshine and length of season combined were as good.

10.5 The Southern Limits

The most striking feature about the distribution of L.agilis in southern Europe is its absence from regions with a Mediterranean climate. Several generalizations can be made about differences between stations with this type of climate and stations within the southern part of the range. Although Mediterranean summers were very warm mean summer maximum temperatures were no higher than some of the warmest stations within the range (Guryev, Armavir, Aktyubinsk, Bucharest, Belgrade). More distinctive differences are the comparative warmth of the Mediterranean winters and the much longer summers, shown by more months over 13°C.

Using discriminant coefficients calculated from the discriminant analysis, it is possible to obtain discriminant scores for new stations not included in the original analysis. This was done for several new stations in the Mediterranean and southern part of the range (Table 10.3). These scores are therefore based on the same linear combination of variables that was found to be the best discriminator for the northern stations.

Scores for the stations outside the southern limit of the range were in all cases higher than stations within the range, suggesting that the same combination of the three variables is important in southern Europe as northern Europe except, of course, that in southern Europe, when values of temperature, sunshine and length of season are high then L.agilis is absent. This occurs despite the fact that the situation in the south is complicated by the presence of a greater number of other lizard species.

10.6 Distribution in Britain

The distribution of L.agilis in England is shown in Figure 10.3. Stations in central and southern England where L.agilis is absent were not included in the discriminant analysis because the analysis was concerned with the range in general, not with particular irregularities which may be caused by factors other than climate. However, to see how the lizard distribution in England relates to the discriminant analysis in more detail, discriminant scores for

TABLE 10.3 DISCRIMINANT SCORES OF STATIONS NEAR THE SOUTHERN BOUNDARY OF THE RANGE OF *L.agilis*

Weather station	Discriminant score	Presence or absence of *L.agilis*
Alicante	36.4	-
Thessaloniki	33.2	-
Barcelona	32.3	-
Zaragoza	32.2	-
Florence	31.6	-
Madrid	30.8	-
Guryev	30.7	+
Bucharest	29.0	+
Belgrade	27.9	+
Sofia	27.0	+
Armavir	27.0	+

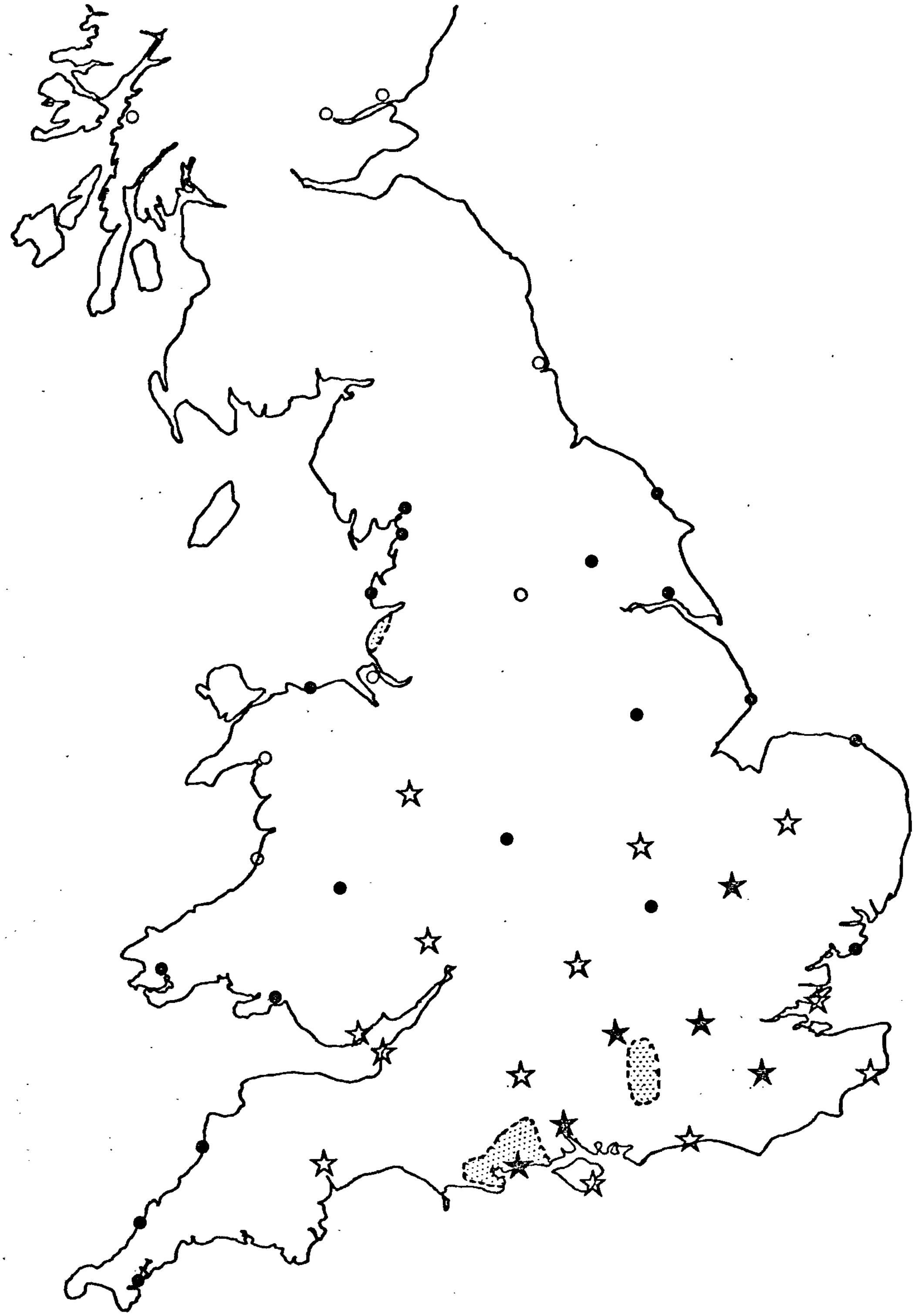

FIGURE 10.2 The distribution of L.agilis in Britain and discriminant scores for Meteorological stations. Stations are classed according to their discriminant scores (see text). Stars are stations above the critical mid point (21.3), circles stations below the mid point. Closed stars score > 23.0, open stars 21.4 - 22.9, closed circles 20.0 - 21.3, open circles < 19.9.

thirty-nine new stations in England and Wales were computed in the same way as the new Mediterranean stations, using the discriminant coefficients from the original analysis. The results are summarized in Figure 10.3 where stations are classed according to their scores.

The distribution in southern England falls within the area of highest scores. In contrast, the few lizards in north-west England do not correspond with any area of high scores. There are many parts of southern England with scores over the critical mid-point where L.agilis is absent. Other factors must be the cause of this: these may or may not be climatic. Possibly, the low sunshine amounts in England compared with the rest of the range may be important. The effect of sunshine in the discriminatory analysis may have been obscured by the effect of temperature. Jackson (1978) has recently attempted to explain the apparent decline in number of L.agilis in north-west England by a corresponding decline in the amount of sunshine in May.

10.7 Discussion

The position of the northern limit of the range of L.agilis was, to a large extent, consistent with variation in three climatic factors. These same factors may also be important in determining the southern limits. Although these are the kind of factors which would be expected to limit the distribution of an ectothermic animal such as L.agilis, the relative importance of the different ways in which they could affect lizard populations is not known.

In England, the distribution is centred on the area which appears to be the most suitable climatically. This area seems to be just as suitable as many areas in Continental Europe. In contrast, there were no apparent climatic reasons for the existence of L. agilis in north-west England. L. agilis is absent from many areas in England which appear climatically suitable; the possible reasons for this have been discussed by Beebee (1978).

CHAPTER 11

GENERAL DISCUSSION

This final discussion concentrates on the comparison between Lacerta agilis and Lacerta vivipara. First, differences in macrohabitat preferences between the species are discussed. Second, in cases where populations of the two species share the same habitat the way resources are partitioned is considered. Third, differences and similarities between the two species in their adaptation to the environmental conditions of southern England are discussed and finally, some possibilities for further work are considered.

In Dorset populations of L.vivipara are found in a wide variety of plant communities such as heathlands, chalk downland and limestone grassland, hedgerows, roadside verges and woodland edges. In contrast, populations of L.agilis are largely restricted to areas of heathland, particularly dry heathland.

In spite of this association of populations of L.agilis with heathland, individuals can utilize a wider range of habitats in cases where these border the heath. Thus at the Railway site, the home ranges of many adults consisted of areas of coarse grass, scrub and bog. Individuals appeared to use all of these different types of habitat in an opportunistic way. It seemed that they could meet all their ecological requirements in these habitats except that of egg-laying (females overwintered, mated and became gravid there). These observations suggest that the primary reason for the restriction of populations of L.agilis to heathlands in Dorset is concerned with the hatching and survival of the juveniles.

Glandt (1976) has studied the habitat preferences of L.agilis and L.vivipara in the region of the lower Rhine in West Germany. He summarized these habitat preferences in terms of the occurrence of each species along the two gradients of substrate humidity and vegetation cover. In West Germany pure populations (one species without the other) of both L.agilis and L.vivipara occur, as well as mixed populations (both species together). Glandt suggested that pure L.vivipara populations tend to be found in biotopes within areas of considerable vegetation cover (i.e. continuously, sometimes densely forested areas, so such a biotope would be a forest clearing), whereas pure L.agilis populations are found in open, treeless areas. The transitional zones between these closed and open habitats support mixed populations. He also suggested that pure L.agilis populations tend to be found on dry substrata , pure L.vivipara populations on wet substrata , and mixed populations in intermediate areas.

Casual observations of the two species in Dorset suggested that L.vivipara was found more often than L.agilis in areas of wet heathland and bog. However, in general Glandt's interpretation of the habitat preferences of the two species in West Germany is not particularly helpful in understanding the habitat preferences of the two species in England.

The results of the present work were concerned with cases where populations of L.agilis and L.vivipara share the same habitat. It was difficult to obtain direct observations on the use of microhabitat by the two species because individuals usually foraged beneath dense vegetation. The few casual observations made on foraging lizards did not suggest any obvious differences in the use of microhabitat. The data from the diet of the two species which related to microhabitat gave inconclusive results. There is therefore a need for more evidence on this subject. It is probable that there is a large degree of overlap in the use of microhabitat between the two species, and that any differences are more likely to be related to thermoregulatory activities than to resource partitioning.

Two factors were important in the partitioning of food resources, prey size and prey hardness. Most of the differences in prey taxonomy between the species were probably related to these two factors, particularly prey hardness. The prey size and prey hardness differences between adult L.agilis and L.vivipara, when taken together, constitute a high degree of separation of food resources. It is therefore probably unnecessary for there to be any significant degree of resource partitioning along any other dimensions.

The degree of overlap of food resources was much greater between L.vivipara and juvenile L.agilis. However, juvenile L.agilis tend to remain largely near to the bare sand where they hatched (chapter 6) so it is possible that there is some separation by macrohabitat between L.vivipara and juvenile L.agilis.

It is not possible to reach any definite conclusions about competition between the two species solely from data on resource overlap, for one also needs information about whether resources are in short supply. Prey was least abundant in the spring so it is at this time, if any, that competition between the two species for food could be important. Juveniles of L.agilis hatch at the time when food is most abundant so competition with L.vivipara is unlikely to be significant.

The question of how L.agilis and L.vivipara are adapted to the environmental conditions of southern England is of particular interest. First, what are these conditions and how do they affect the lizards? Avery (1976) has shown how the relatively low summer temperatures and small amounts of summer solar radiation lead to an increase in the proportion of time spent basking by L.vivipara compared with P.muralis in southern Europe, and consequently a reduction in the time available for feeding. It is also possible that food resources may be less abundant in England, but this would have the same effect of lowering food consumption.

L.vivipara and L.agilis appear to cope with these effects on food consumption in different ways. L.agilis overcomes the problem by being able to utilize locally and seasonally abundant prey, and probably by storing large quantities of fat to enable it to survive periods of food shortage. Energy expenditure on growth, reproduction, and perhaps activity remain higher than a species from southern Europe such as P.muralis.

In contrast, L.vivipara seems to accept lowered rates of food consumption and compensates by reducing energy expenditure. The smaller size of individuals means that the energy requirements of individuals are less, and energy expenditure on reproduction, growth, and perhaps activity are less than for *L.agilis*.

There are also many similarities between the two species in their mode of adaptation to the environmental conditions of southern England. The life history strategies of both species are characteristic of K strategists (delayed maturity, low annual adult mortality), the most important factors leading to selection for this strategy probably being low levels of predation, and environmental unpredictability (chapter 6). Viviparity in lizards is usually associated with species having a late maturing, single brooded reproductive strategy (Tinkle, Wilbur & Tilley 1970) and for *L.vivipara* is most simply seen as an adaptation to quicken the development of the embryo. Both species have large, overlapping home ranges (chapter 8). The large home range size compared with species in southern Europe (see Table 8.4) is probably not caused directly by the reduced time available for feeding in England, but would be expected if there was a difference in the levels of food resources.

The work on the food consumption of *L.agilis* suggested that the rate of food consumption of individual lizards was sensitive to changes in prey density. Thus low prey densities could have serious consequences for individual lizards, such as a failure to lay a clutch or to lay the normal number of eggs, a failure to deposit sufficient fat before the winter, a decrease in the rate of growth, or death from starvation. It is not known which, if any, of these possible consequences of food shortage are important in natural populations of L.agilis, but it is by such means that food abundance could limit population size. A detailed population study which would identify the extent and causes of mortality at different stages of the life history is needed before the role of food or other factors in limiting populations of L.agilis can be assessed. This is the most important area in which further work is required but the practical difficulties are enormous. Further research could also fill in many gaps in the present work, such as the prey of juveniles of L.agilis, the food available to L.agilis and L.vivipara (the practical difficulties of investigating this are great and only a very detailed study would be valuable), the growth of juvenile L.agilis and adult L.vivipara, and the home range ecology of L.vivipara. Lipid deposition in L.agilis is of particular interest but it is difficult to see a way of approaching the problem without sacrificing lizards. The problems of the absence of hard-bodied prey in the diet of L.vivipara, and of the variation between different faecal samples of L.agilis, were also of interest. The investigation of these problems, perhaps by laboratory studies, could have more general importance for optimal foraging theory.

The reproductive ecology of L.agilis was only superficially examined, and there is clearly great scope for further studies in this area. Such studies would be of particular importance in the context of the conservation of L.agilis in England. The general applications to conservation of the results presented in this thesis will be left for those concerned with conservation to consider and not discussed here, but it is hoped that this work will help conservationists to understand better the ecology of L.agilis in England.

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APPENDIX I LIST OF SPECIES IDENTIFIED FROM FAECAL SAMPLES

(a) LIST OF SPECIES OF COLEOPTERA IDENTIFIED FROM FAECAL SAMPLES OF *Lacerta agilis*. NOMENCLATURE FOLLOWS KLOET & HINCKS (1977)

Carabidae

Carabus problematicus Herbst.
Notiophilus palustris (Duftschmid)
Pterostichus cupreus (L)
Pterostichus nigrita (Paykull)
Pterostichus lepidus (Leske)
Olisthopus rotundatus (Paykull)
Calathus erratus Sahlberg or *fuscipes* (Goeze)
Amara aenea (Degeer)
Amara plebeja (Gyllenhal)
Harpalus rufipes (Degeer)

Sphaeriidae

Sphaeridium scarabaeoides (L)

Silphidae

Silpha sp.

Staphylinidae

Staphylinus compressus Marsham

Scarabaeidae

Aphodius sp.
Onthophagus sp.
Serica brunnea (L)

Coccinellinae

Coccinella septempunctata L.

Tenebrioniidae

Cylindrinotus laevioctostriatus (Goeze)

Cerambycidae

Alosterna tabacicolor (Degeer)

Chrysomelidae

Donacia sp.
Oulema melanopa (L)
Calomicrus circumfusus (Marsham)

Curculionidae

Strophosomus sus Stephens
Phyllobius pyri (L)
Sitona regensteinensis (Herbst)

(b) LIST OF SPECIES OF ARANEAE IDENTIFIED FROM FAECAL SAMPLES OF *Lacerta agilis* AND *Lacerta vivipara*. NUMBERS OF EACH SPECIES IDENTIFIED ARE ALSO SHOWN. NOMENCLATURE FOLLOWS LOCKET, MILLIDGE & MERRETT (1974)

	Lacerta agilis	*Lacerta vivipara*
Gnaphosidae		
Drassodes cupreus (Blackwall)	1	1
Zelotes praeficus (L. Koch)	3	
Clubionidae		
Cheiracanthium erraticum (Walckenaer)	1	
Zora spinimana (Sundevall)	4	1
Zora sp.	10	5
Thomisidae		
Xysticus cristatus (Clerck)	7	1
Xysticus erraticus (Blackwall)	1	1
Xysticus sp.	5	11
Oxyptila trux (Blackwall)	1	
Oxyptila atomaria (Panzer)	1	
Oxyptila sp.	2	
Philodromus cespitum (Walckenaer)	4	
Philodromus aureolus (Clerck)	2	
Philodromus histrio (Latrielle)	1	
Tibellus oblongus (Walckenaer)	4	
Salticidae		
Heliophanus flavipes C.L. Koch	1	
Euophrys frontalis (Walckenaer)		1
Unidentified Salticids	8	4
Lycosidae		
Pardosa nigriceps (Thorell)	17	7
Pardosa pullata (Clerck)	1	1
Pardosa amentata (Clerck)	1	
Pardosa sp.	30	16
Trochosa terricola Thorell	4	3
Trochosa sp.	5	3
Alopecosa pulverulenta (Clerck)		1
Arctosa leopardus (Sundevall)	1	
Pirata hygrophilus Thorell	1	

	Lacerta agilis	*Lacerta vivipara*
Pisauridae		
Pisaura mirabilis (Clerck)	2	
Theridiidae		
Crustulina guttata (Wider)	2	
Episinus truncatus Latrielle	12	
Steatoda phalerata (Panzer)	1	
Theridion bimaculatum (L)	2	
Enoplognatha ovata (Clerck)	8	1
Araneidae		
Araneus sp.	1	
Linyphiidae		
Linyphia furtiva O.P.-Cambridge	6	
Linyphia clathrata Sundevall	1	
Linyphia triangularis (Clerck)	11	
Lepthyphantes tenuis (Blackwall)		1
Unidentified Linyphids	11	1
TOTAL	182	59

(c) SPECIES IDENTIFIED FROM FAECAL SAMPLES OF L.agilis - OTHER GROUPS

Opiliones (Martens 1978)

Phalangium opilio L.
Paroligolophus agrestis (Meade)
Rilaena triangularis (Herbst)

Hymenoptera (Kloet & Hincks, 1945)

Formicidae

Lasius sp. (Lasius niger (L) or Lasius alienus (Foerster); queens)
Tetramorium caespitum (L); workers

Lepidoptera (Kloet & Hincks 1972)

Saturniidae
Saturnia pavonia (L) (emperor moth larva)

Orthoptera (Kloet & Hincks 1964)

Acrididae
Chorthippus brunneus (Thunberg)

Heteroptera (Kloet & Hincks 1964)

Pentatomidae
Picromerus bidens (L)
Rhacognathus punctatus (L)
Alydidae
Alydus calcaratus (L)
Berytinidae
Neides tipularius (L)
Nabidae
Nabis ericetorium Scholtz

Homoptera (Kloet & Hincks 1964)

Ulopa reticulata (Fabricius)

Dictyoptera (Kloet & Hincks 1964)

Pseudomopidae
Ectobius pallidus (Olivier)
Ectobius panzeri Stephens

APPENDIX II LINEAR REGRESSION EQUATIONS OF LENGTH (l) AGAINST OTHER ANATOMICAL DIMENSIONS FOR DIFFERENT INVERTEBRATE GROUPS, OBTAINED FROM MEASUREMENTS ON THE REFERENCE MATERIAL. THESE RELATIONSHIPS WERE USED TO CALCULATE PREY LENGTH FROM THE PARTS FOUND IN THE FAECAL SAMPLES. ALL MEASUREMENTS ARE IN mm.

Diptera: wing length (W_D)

$l = 1.17\ W_D - 0.38$ ($n = 50$, $r = 0.98$)

Bees: wing length (W_B)

$l = 1.09\ W_B + 0.64$ ($n = 28$, $r = 0.94$)

Ichneumonidae: wing length (W_I)

$l = 1.42\ W_I - 0.90$ ($n = 20$, $r = 0.98$)

Lepidoptera larvae: head capsule size (h_L) (head length + head width)

$l = 6.00\ h_L - 2.84$ ($n = 33$, $r = 0.96$)

Lepidoptera larvae: mandible size (m_L) (length + width)

$l = 24.6\ m_L - 4.53$ ($n = 35$, $r = 0.96$)

Isopoda: mandible length (m_I)

$l = 10.74\ m_I + 0.88$ ($n = 30$, $r = 0.94$)

Moths: head size (h_M) (head length + width)

$l = 3.67\ h_M + 0.74$ ($n = 20$, $r = 0.94$)

Opiliones: chelicera length (c_o)

$l = 3.74\ c_o + 0.39$ ($n = 20$, $r = 0.94$)

Orthoptera: femur length (f_o)

$l = 1.76\ f_o + 0.30$ ($n = 16$, $r = 0.97$)

APPENDIX III(a) MEAN PREY LENGTH IN RELATION TO SNOUT-VENT LENGTH FOR *L.agilis*.

SV length	Number of prey items	Mean prey length (mm)	Variance
31	37	5.1	8.7
37–45	22	6.2	27.4
47–51	35	8.3	55.4
54–57	56	7.5	24.4
59–62	118	9.0	62.2
66–68	103	10.5	95.5
72–74	128	10.7	81.8
80–85	161	10.2	57.4

APPENDIX III(b) MEAN PREY LENGTH IN RELATION TO SNOUT-VENT LENGTH FOR *L.agilis* (DATA FOR PREY LENGTH LOG TRANSFORMED)

Snout-vent length (mm)	Number of prey items	Mean log prey length (mm)	Variance
31	37	3.84	0.39
37	3	3.10	0.64
43	6	3.25	0.30
44	8	5.46	0.61
45	5	5.53	0.40
47	6	5.56	0.20
48	5	5.19	0.10
50	15	7.43	0.47
51	9	4.50	0.66
54	15	6.30	0.39
55	12	5.51	0.68
56	25	5.42	0.26
57	4	5.41	0.37
58	6	8.69	0.25
59	26	5.30	0.32
60	47	6.92	0.54
61	22	5.85	0.23
62	32	6.64	0.41
64	58	7.16	0.26
66	28	6.20	0.17
67	32	5.99	0.18
68	66	8.06	0.49
70	53	6.57	0.54
72	86	8.94	0.48
73	31	8.28	0.21
74	52	5.95	0.28
75	63	7.67	0.20
79	68	8.95	0.43
80	49	10.34	0.32
81	92	6.09	0.29
82	17	8.98	0.58
84	14	7.34	0.32
85	21	10.90	0.58

APPENDIX III(c) MEAN PREY LENGTH IN RELATION TO SNOUT-VENT LENGTH FOR L.vivipara (DATA FOR PREY LENGTH LOG TRANSFORMED)

Snout-vent length	Number of lizards	Number of prey items	Mean log prey length (mm)	Variance
38	1	5	1.22	0.049
41	1	11	1.09	0.22
42	2	10	1.27	0.46
43	1	3	1.23	0.062
46	2	5	1.11	0.096
48	2	5	1.56	0.019
49	1	8	1.23	0.31
50	2	12	1.29	0.13
52	2	17	1.41	0.28
53	3	20	1.42	0.41
55	3	4	2.00	0.29
56	2	8	1.72	0.20
57	3	9	1.50	0.17
58	2	9	1.72	0.30
59	1	5	1.72	0.070
62	1	2	2.00	0.30
69	1	17	2.06	0.44

APPENDIX IV PREY CATEGORIES IDENTIFIED FROM FAECAL SAMPLES OF INDIVIDUAL *L.agilis* WHERE LARGE NUMBERS OF ITEMS WERE FOUND IN *ONE* SAMPLE ($N > 17$)

Female 10.5.76

Curculionidae	15
Araneae	1
Lepidoptera larvae	1
TOTAL	17

Female 24.5.77

Curculionidae	10
Cylindrinotus laevioctostratus (Coleoptera)	3
Ichneumonidae	3
Symphyta	1
Isopoda	1
Araneae	1
Diptera	1
Lepidoptera larvae	1
TOTAL	21

Male 15.7.77

Isopoda	5
Carabidae	3
Symphyta	3
Araneae	3
Orthoptera	2
Curculionidae	2
Heteroptera	2
Other Hymenoptera	1
Lepidoptera larvae	1
Opiliones	1
TOTAL	23

Male 15.7.77

Staphylinidae	5
Ichneumonidae	4
Heteroptera	2
Lepidoptera adult	1
Orthoptera	1
Apoidea	1
Diptera	1
Carabidae	1
Alosterna tabacicolor (Coleoptera)	1
Homoptera	1
Araneae	1
Unidentified larvae	1
TOTAL	20

Female 18.7.77

Calomicrus circumfusus (Coleoptera)	14
Curculionidae	10
Staphylinidae	3
Diptera	3
Araneae	3
Lepidoptera larvae	2
Ichneumonidae	2
Other Hymenoptera	2
Apoidea	1
Heteroptera	1
Isopoda	1
TOTAL	42

Female 26.7.77

Araneae	7
Curculionidae	3
Cylindrinotus sp. (Coleoptera)	2
Dictyoptera	1
Unidentified larvae	1
Homoptera	1
Nabis ericetorium (Heteroptera)	1
Dermaptera	1
Other Hymenoptera	1
Lepidoptera adults	1
TOTAL	19

Female 29.7.75

Formicidae queens (*Lasius* sp.)	4
Opiliones	3
Carabidae	2
Other Hymenoptera	2
Ichneumonidae	1
Araneae	1
Lepidoptera larvae	1
Lepidoptera adults	1
Curculionidae	1
Cantharidae (Coleoptera)	1
TOTAL	17

Female 30.7.77

Staphylinidae	7
Diptera	3
Orthoptera	2
Lepidoptera larvae	2
Lepidoptera adults	2
Unidentified larvae	1
Curculionidae	1
TOTAL	18

Female 1.8.75

Formicidae queens (*Lasius* sp.)	13
Rhacognathus punctatus (Heteroptera)	3
Other Hymenoptera	1
Tetramorium caespitum worker (Formicidae)	1
TOTAL	18

Sub-adult female 3.8.77

Araneae	8
Opiliones	3
Lepidoptera larvae	2
Oulema melanopa (Coleoptera)	1
Unidentified Coleoptera	1
Lepidoptera adults	1
Homoptera	1
Neuroptera	1
Orthoptera	1
Unidentified larvae	1
TOTAL	20

Sub-adult female 9.8.77

Araneae	4
Curculionidae	3
Orthoptera	3
Lepidoptera larvae	3
Homoptera	2
Nabis ericetorium (Heteroptera)	1
Isopoda	1
Diptera	1
Lepidoptera adults	1
Other Hymenoptera	1
Calomicrus circumfusus (Coleoptera)	1
TOTAL	21

Female 10.8.75

Opiliones	7
Araneae	4
Picromerus bidens (Heteroptera)	1
Rhacognathus punctatus (Heteroptera)	1
Tetramorium caespitum worker (Formicidae)	1
Curculionidae	1
Dictyoptera	1
Lepidoptera larvae	1
TOTAL	17

Female 15.8.77

Coccinellidae	7
Araneae	3
Apoidea	2
Formicidae queens	2
Diptera	2
Ichneumonidae	1
Dictyoptera	1
Isopoda	1
TOTAL	19

Female 15.8.77

Diptera	7
Araneae	4
Carabidae	2
Homoptera	2
Opiliones	1
Orthoptera	1
Unidentified larvae	1
Heteroptera	1
TOTAL	19

Male 9.9.77

Diptera	3
Araneae	3
Lepidoptera larvae	2
Unidentified larvae	2
Formicidae queens	2
Curculionidae	2
Picromerus bidens (Heteroptera)	1
Opiliones	1
Apoidea	1
Carabidae	1
Other Hymenoptera	1
TOTAL	19

Male 10.9.77

Araneae	3
Diptera	3
Apoidea	2
Formicidae queens	2
Coccinellidae	2
Carabidae	1
Staphylinidae	1
Sphaeridium scarabacoides (Coleoptera)	1
Nabis ericetorium (Heteroptera)	1
Lepidoptera adults	1
Juvenile lizard	1
TOTAL	18

Female 15.9.77

Diptera	12
Apoidea	5
Carabidae	1
Heteroptera	1
Lepidoptera larvae	1
TOTAL	20

Female 15.9.77

Formicidae queens	5
Carabidae	4
Apoidea	4
Diptera	4
Araneae	4
Nabis ericetorium (Heteroptera)	1
Homoptera	1
Lepidoptera larvae	1
Dictyoptera	1
Isopoda	1
TOTAL	26

APPENDIX V GROWTH OF INDIVIDUALS OF <u>L.agilis</u>

(a) RAILWAY STUDY AREA

LIZARD	SEX	DATE OF CAPTURE	SNOUT-VENT LENGTH(mm.)	WEIGHT(g)	ESTIMATED YEAR OF BIRTH
NOI	F	27.7.75	78	11.4	1972
		27.8.75	79	13.0	
		12.7.76	84	12.2	
		3.8.76	85	14.0	
ELE	F	31.7.75	76	10.4	1972
		6.5.76	81	12.2	
		8.5.76	82	12.3	
		18.5.76	81	11.3	
		27.5.76	83	14.0	
		15.4.77	82	12.6	
		23.6.77	86	14.0	
		20.7.77	85	11.6	
MRS	F	2.9.75	78	10.7	1972
		17.9.75	79	11.3	
		20.4.76	80	10.8	
		23.5.76	82	12.2	
		12.5.77	85	12.8	
VEN	F	18.8.75	79	11.3	1972
		26.4.76	83	10.3	
		18.5.76	84	10.8	
		5.7.77	85	11.0	
MAG	F	26.4.76	74	8.6	1973
		17.5.76	75	9.3	
		20.6.77	80	11.1	
ALI	F	18.5.76	81	11.3	1972
		26.7.76	82	11.0	
		22.6.77	83	12.1	
		18.7.77	81	9.8	
010	F	29.7.75	76	9.4	1972
		13.4.77	89	12.9	
FLO	F	24.8.75	73	10.3	1972
		20.4.76	74	10.0	
		20.5.76	78	12.5	
		17.5.77	85	14.3	
ART	M	12.4.76	78	10.5	1972
		16.4.76	78	11.0	
		21.4.76	77	10.8	
		17.5.76	78	10.4	
		6.7.76	81	13.0	
		4.4.77	80	11.5	

LIZARD	SEX	DATE OF CAPTURE	SNOUT-VENT LENGTH (mm)	WEIGHT (g)	ESTIMATED YEAR OF BIRTH
HEC	M	3.4.76	76	11.0	1972
		12.4.76	77	11.2	
		20.4.76	79	11.5	
		3.5.76	78	11.2	
		22.5.76	78	10.6	
		10.6.76	79	10.2	
		4.4.77	83	-	
		30.6.77	83	11.0	
THO	M	12.4.76	68	6.6	1973
		6.5.76	69	7.1	
		26.5.76	70	7.5	
		4.4.77	78	10.5	
JON	M	3.5.76	65	6.4	1974
		6.5.76	64	6.1	
		4.5.77	73	9.2	
TAN	M	11.5.76	78	10.4	1972
		13.4.77	80	10.2	
BOB	M	15.6.76	62	5.1	1974
		13.4.77	70	7.5	
EDW	M	3.8.76	72	8.0	1973
		4.4.77	73	9.3	
		10.5.77	73	9.6	
100	M	12.6.76	51	2.5	1975
		4.4.77	67	6.5	
		27.4.77	66	5.7	

(b) SOLDIERS ROAD STUDY AREA

LIZARD	SEX	DATE OF CAPTURE	SNOUT-VENT LENGTH (mm)	WEIGHT (g)	ESTIMATED YEAR OF BIRTH
004	F	25.6.76	51	2.5	1975
		29.6.76	55	3.0	
		1.7.76	54	2.9	
		25.7.76	58	3.9	
		27.7.76	57	3.6	
010	M	28.5.76	43	1.5	1975
		5.6.76	45	1.7	
		29.6.76	48	2.0	
503	M	6.8.75	55	4.6	1974
		5.9.75	57	4.6	
		7.5.76	61	5.4	
		15.6.76	65	6.4	
		27.6.76	68	7.0	
		31.7.76	70	6.9	
		4.8.76	-	6.9	
140	M	7.6.75	71	-	1972
		16.7.75	73	10.2	
		21.6.76	77	9.7	
		2.7.76	77	11.3	
		4.7.76	78	10.3	
141	M	1.7.75	70	7.9	1972
		16.7.75	71	8.4	
		12.8.75	70	9.4	
		23.4.76	72	7.7	
		7.5.76	72	8.3	
		9.5.76	72	8.4	
		13.5.76	73	-	
		24.5.76	72	8.2	
		8.6.76	73	8.1	
		6.7.76	74	9.2	
520	M	21.4.76	67	6.5	1973
		22.4.76	66	6.3	
		17.5.76	66	6.0	
		29.6.76	70	8.2	
		10.7.76	72	7.5	
		20.7.76	71	8.5	
		22.7.76	71	7.9	
		25.7.76	71	8.4	
		5.8.76	72	9.0	
510	M	8.6.75	61	5.7	1973
		29.6.75	63	5.7	
		8.7.75	65	-	
		10.5.76	67	6.0	
		13.7.76	71	7.5	

LIZARD	SEX	DATE OF CAPTURE	SNOUT-VENT LENGTH (mm)	WEIGHT (g)	ESTIMATED YEAR OF BIRTH
025	F	7.6.75	-	9.7	1972
		4.7.75	71	6.5	
		8.7.75	71	7.6	
		10.7.75	72	8.1	
		26.7.75	73	7.7	
		28.7.75	72	7.8	
		31.7.75	73	8.0	
		22.4.76	-	7.5	
		9.5.76	74	8.8	
		24.5.76	76	9.1	
		29.5.76	76	9.3	
		7.6.76	78	8.6	
		29.6.76	80	10.3	
		4.7.76	79	9.8	
		25.7.76	81	10.7	
034	F	10.6.75	70	7.8	1972
		16.6.75	70	7.6	
		7.6.76	80	9.6	
		3.7.76	79	8.4	
501	F	9.7.75	67	7.2	1973
		8.8.75	70	7.7	
		26.4.76	74	7.0	
		28.6.76	79	9.5	
401	F	3.8.75	68	5.7	1973
		6.8.75	69	6.3	
		7.8.75	69	6.2	
		10.8.75	70	7.4	
		7.9.75	70	7.4	
		7.5.76	74	7.3	
		5.6.76	74	6.8	
402	F	7.9.75	71	7.7	1973
		25.7.76	79	9.5	
205	F	30.7.75	54	3.2	1974
		31.7.75	54	3.1	
		3.8.75	54	3.9	
		13.5.76	61	4.6	
		14.6.76	65	5.4	
		25.6.76	68	6.2	
		30.6.76	68	5.7	

APPENDIX VI (a) CLIMATIC DATA FOR STATIONS WITHIN RANGE OF <u>L.agilis</u>

				MEAN DAILY TEMPS. ° C Min. JAN	Max. APR	Max. JUL	Max. SEP	SUNSHINE HOURS APR	JUL	SEP	TOTAL HOURS SUNSHINE APR-SEP	NO. MONTHS MEAN DAILY MAX.>13° C	MEAN DAILY MAX. TEMP. MAY-SEP
ENGLAND													
1. Blackpool	53°46'N	3°02'W	10 m.	1.7	11.9	19.0	17.2	178	192	123	1112	6	17.6
2. Bournemouth	50°43'N	1°54'W	42 m.	1.7	13.4	21.1	18.7	185	213	150	1202	7	19.5
3. Reading	51°27'N	0°58'W	69 m.	1.0	13.9	22.1	19.2	166	191	136	1079	7	20.3
FRANCE													
4. Rennes	46°04'N	1°43'W	35 m.	1.8	15.0	23.4	20.8	190	231	163	1244	7	21.5
5. Rouen	49°23'N	1°03'E	68 m.	0.2	14.6	23.0	20.1	182	199	154	1131	7	21.0
6. Clermont-Ferrand	45°48'N	3°09'E	329 m.	-1.1	15.9	25.4	22.1	178	262	178	1297	8	23.1
NETHERLANDS													
7. Den Helder	52°58'N	4°45'W	4 m.	0.7	10.2	19.5	17.9	179	214	149	1208	6	17.8
EAST GERMANY													
8. Leipzig	51°19'N	12°25'E	141 m.	-3.0	13.7	23.8	20.0	177	223	174	1139	7	21.7
DENMARK													
9. Studsgard	56°05'N	8°55'E	54 m.	-3.4	10.6	21.1	17.3	185	221	167	1219	5	19.0
SWEDEN													
10. Malmö	55°36'N	13°03'E	8 m.	-3.0	10.3	21.7	17.4	177	253	172	1349	5	19.2
11. Jonköping	57°46'N	14°11'E	92 m.	-5.8	9.4	21.4	16.0	152	218	125	1147	5	18.4
12. Stockholm	59°21'N	18°04'E	44 m.	-5.1	8.3	21.9	15.3	208	295	174	1535	5	18.2
POLAND													
13. Warsaw	52°13'N	21°03'E	110 m.	-5.5	11.8	22.9	19.0	158	219	158	1246	5	21.6
AUSTRIA													
14. Innsbruck	47°16'N	11°24'E	582 m.	-6.5	15.5	24.8	20.8	163	210	180	1128	7	22.7
15. Vienna	48°15'N	16°22'E	203 m.	-3.8	14.5	24.6	20.1	184	266	159	1383	7	22.1
YUGOSLAVIA													
16. Belgrade	44°48'N	20°28'E	132 m.	-3.2	17.5	28.3	24.3	191	295	229	1478	7	25.8

APPENDIX VI (a) cont.

					MEAN DAILY TEMPS. °C Min. JAN	Max. APR	Max. JUL	Max. SEP	SUNSHINE HOURS APR	JUL	SEP	TOTAL HOURS SUNSHINE APR-SEP	NO. MONTHS MEAN DAILY MAX.>13°C	MEAN DAILY MAX. TEMP. MAY-SEP
BULGARIA														
17.	Sofia	42°42'N	23°20'E	550 m.	-4.0	15.8	27.1	22.1	179	320	222	1511	7	24.1
RUMANIA														
18.	Bucharest	44°30'N	26°05'E	92 m.	-7.0	17.9	29.8	25.3	191	326	233	1565	7	27.1
U.S.S.R.														
19.	Kharkov	49°56'N	36°17'E	152 m.	-11.8	13.7	26.7	21.0	187	309	215	1512	6	24.1
20.	Smolensk	54°45'N	32°04'E	241 m.	-14.9	9.1	21.9	16.2	148	271	185	1342	5	19.5
21.	Gorkiy	56°13'N	43°49'E	82 m.	-17.0	9.8	22.9	16.1	193	266	164	1484	5	20.0
22.	Armavir	44°59'N	41°07'E	208 m.	-6.1	17.4	29.6	24.5	201	308	243	1602	7	26.7
23.	Guryev	47°07'N	51°51'E	-	-11.9	16.9	32.6	24.0	266	333	264	1786	7	28.9
24.	Aktyubinsk	50°17'N	57°09'E	226 m.	-18.6	12.3	29.1	21.0	242	303	242	1657	5	25.3
25.	Ufa	54°45'N	56°00'E	197 m.	-20.4	10.1	25.3	17.6	226	265	170	1485	5	21.6
26.	Perm	58°01'N	56°18'E	161 m.	-20.3	8.5	23.7	14.1	209	248	133	1307	5	18.9
				MEAN	-6.4	13.0	24.3	19.5	188.3	255.8	179.3	1351.8	6.15	21.8
				VARIANCE	46.8	8.66	11.25	8.75	656.9	1898.2	1458.3	35888.02	0.98	9.31

APPENDIX VI (b) CLIMATIC DATA FOR STATIONS OUTSIDE THE RANGE OF <u>L.agilis</u>

					MEAN DAILY TEMPS. °C				SUNSHINE HOURS			TOTAL HOURS SUNSHINE	NO. MONTHS MEAN DAILY	MEAN DAILY MAX. TEMP.
					Min. JAN	Max. APR	Max. JUL	Max. SEP	APR	JUL	SEP	APR-SEP	MAX.>13° C	MAY-SEP
U.S.S.R.														
27.	Troitsko-Pechorskiy	62°42'N	56°12'E	107 m.	-25.6	5.3	22.4	11.6	168	269	114	1241	3	16.4
28.	Kotlas	61°14'N	46°38'E	69 m.	-21.1	7.5	22.3	13.6	164	273	107	1323	5	18.2
29.	Archangel	64°35'N	40°30'E	13 m.	-20.4	5.0	20.0	11.9	178	278	103	1306	3	15.8
30.	Sortavala	61°43'N	30°43'E	18 m.	-16.9	5.6	20.0	13.5	163	269	114	1337	5	16.8
FINLAND														
31.	Helsinki	60°12'N	24°55'E	46 m.	-8.5	6.4	21.6	15.0	184	295	152	1546	5	17.8
SWEDEN														
32.	Harnosand	62°38'N	17°57'E	8 m.	-9.8	7.1	22.2	15.4	204	273	148	1391	5	18.2
33.	Sveg	62°02'N	14°25'E	360 m.	-15.3	6.8	21.0	13.6	167	228	132	1159	5	17.3
NORWAY														
34.	Bergen	60°24'N	5°19'E	43 m.	-0.5	9.2	18.8	15.2	156	179	98	983	5	16.5
U.K.														
35.	Dundee	56°28'N	2°56'W	45 m.	0.0	11.4	19.4	16.5	146	158	125	919	5	17.3
36.	Perth	56°24'N	3°27'W	23 m.	-0.8	12.2	19.9	16.8	147	163	120	932	5	17.9
37.	Oban	56°25'N	5°30'W	69 m.	1.5	10.9	17.1	15.4	142	137	108	897	5	16.1
38.	Tynemouth	55°01'N	1°25'W	33 m.	2.2	10.4	17.9	15.9	152	169	124	948	4	15.9
39.	York	53°57'N	1°05'W	17 m.	0.8	12.8	21.0	18.0	142	174	122	974	6	19.0
				MEAN	-8.80	8.51	20.3	14.80	162.5	220.4	120.5	1150.5	4.69	17.17
				VARIANCE	92.8	7.05	2.62	3.27	306.4	3065.5	242.4	44388.7	6.67	0.94
SPAIN														
40.	Madrid	40°25'N	3°41'W	660 m.	1.5	18.4	30.8	25.0	236	366	257	1830	8	26.7
41.	Barcelona	41°24'N	2°09'E	93 m.	6.3	18.2	27.9	25.0	221	314	200	1556	11	25.5
42.	Alicante	38°22'N	0°30'W	81 m.	5.9	21.3	31.1	29.0	262	362	252	1847	12	28.9

APPENDIX VI (b) cont.

				MEAN DAILY TEMPS. °C				SUNSHINE HOURS			TOTAL HOURS SUNSHINE	NO. MONTHS MEAN DAILY	MEAN DAILY MAX. TEMP.
				Min. JAN	Max. APR	Max. JUL	Max. SEP	APR	JUL	SEP	APR-SEP	MAX.>13° C	MAY-SEP
ITALY													
43. Florence	43°46'N	11°15'E	51 m.	1.9	18.8	30.0	25.7	205	346	219	1697	9	27.1
GREECE													
44. Thessaloniki	40°37'N	22°57'E	25 m.	1.9	19.7	32.4	27.7	227	367	253	1778	9	29.3
			MEAN	3.50	19.28	30.44	26.48	230.2	351.0	236.2	1741.6	9.8	27.5
			VARIANCE	4.54	1.29	2.21	2.57	355.0	399.2	514.2	11337.0	2.16	2.0