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Resource partition among lacertid lizards in southern Europe

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(With 2 figures in the text)

Twenty-four species of lacertid lizards were examined at 31 sites in western Yugoslavia, Greece and Iberia. Comparative observations were made on over 4500 individual lizards, noting such features as times of activity, hunting methods, diet, micro- and macro-habitat, refuges used and body temperature. These data are used as a basis for assessing resource partition in related sympatric species, for finding out whether different systematic groups have characteristic types of niche, and for comparing community structure in the three peninsulas of southern Europe.

Contents

Introduction

Over three-quarters of the lizard species found in Europe west of the Black Sea, 38 out of 51, belong to a single family, the Lacertidae. They are the most prominent element in the reptile fauna of the region and, in many areas, are very conspicuous with up to seven species occurring in one place. In view of this it is surprising that few formal investigations of their compara-

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tive ecology have been made. There have, it is true, been a number of studies of single species (e.g. Martinez Rica, 1977; Palacios, Ayarzaguena, Ibañez & Escudero, 1974; Pérez Mellado, 1982; Peters, 1970) and of species pairs (e.g. Avery, 1978; Glandt, 1976, 1977, 1979; Marcuzzi, 1959; Pérez Mellado, 1981). But concerted attempts to find out how the members of larger European lizard communities differ ecologically are few, although Mellado, Amores, Parreño & Hiraldo (1975) and Mellado Camacho (1980) have reported on species associations in southern Spain.

Much anecdotal information and many general remarks about habitat differences are scattered through the literature (see, for example, Schreiber, 1875, 1912; Werner, 1894, 1907, 1938; Tomasini, 1894; Kopstein & Wettstein, 1921; Rollinat, 1934: Kramer & Mertens, 1938; Peaker & Peaker, 1968). While largely qualitative, a great deal of this comment seems to be accurate and gives some idea of the usual environments of the species concerned, but statements sometimes give a mistaken impression. For instance, because lacertids often bask in exposed positions where they are easily seen, observations may refer mainly to animals in this situation, even though they often conduct many of their other activities in places where they are much less obvious and may go largely unnoticed.

Another difficulty in interpreting anecdotal reports springs from the radical changes that have taken place in the European environment during the past few millennia. Deforestation, agriculture and urbanization have all greatly altered the vegetation and surface structure of Europe, especially in the Mediterranean region. Lizards frequently persist in such disturbed areas, although the composition of the fauna and the proportion of each species present may change substantially. Indeed, some environments modified by man often support higher populations of lizards than neighbouring, more natural ones. The widespread Mediterranean agricultural landscape with numerous dry-stone walls, stone piles and ditches separating gardens, vineyards and small fields appears to provide a 'supernormal' lizard habitat with great numbers of refuges and basking places and, probably, an enhanced food supply as well, especially in the form of dense arthropod populations associated with irrigation, human waste and growing crops. Predator pressures may be relatively low in such places, for raptors and snakes are often assiduously killed by man. It is in these greatly altered habitats that many published observations on lacertid ecology appear to have been made. They must be interpreted with care if some idea of the environments with which lizard species were originally associated is to be gained.

As a necessary preliminary to a study of the functional aspects of characters used in classifying lacertids (Arnold, 1970, 1973), I gathered data on their comparative ecology at first hand. Three main regions were chosen; all have a strong Mediterranean component, although they also include areas with climate and vegetation more typical of central Europe. They are western Yugoslavia, Greece and the Iberian Peninsula, with 11,10 and 12 species respectively. The faunas are substantially different: western Yugoslavia and Greece share only two species, western Yugoslavia and Iberia three and Greece and Iberia two. Consequently a maximum of 27 species could be compared, although in fact a few were not examined, or only cursorily. Areas with many sympatric species have the advantage that these can be contrasted directly in the same general environment. Their differences in ecology are likely to be more clearly displayed in this situation.

The main purpose of the study was to see if there is a correlation between taxonomic groups and the ecological characteristics of their members. In addition, an assessment was made of which ecological parameters are most important in defining niches of lacertids in southern Europe, and community structure in three geographical regions was compared.

Groups and species of lacertids present in southern Europe

All but three of the lacertid species found in Europe west of the Black Sea belong to a group of genera that appears likely to be holophyletic (that is, containing all the descendants of a single ancestral species). It comprises *Algyroides, Gallotia, Lacerta, Podarcis* and *Psammodromus* and has a total of about 70 species, nearly all confined to the South-west Palaearctic region. This assemblage has been reviewed elsewhere (Arnold, 1973). The main subgroups and the species present in southern Europe are listed below.

Lacerta part I, the green lizards: *L. agilis, L. lepida, L. schreiberi, L. trilineata, L. viridis.*

Lacerta part II. In Europe west of the Black Sea, the species of *Lacerta* part II fall into two morphological types that were formerly referred to separate subgenera: *Archaeolacerta* and *Zootoca.* These are no longer usually given formal standing but the names will be employed here as convenient vernaculars.

Archaeolacertas: *L. bedriagae, L. graeca, L. horvathi, L. monticola, L. mosorensis, L. oxycephala.*

Zootocas: *L. praticola, L. vivipara.*

Podarcis, wall lizards: *P. bocagei, P. erhardii, P.filfolensis, P. hispanica, P. lilfordi, P. melisellensis, P. milensis, P. muralis, P. peloponnesiaca, P. pityusensis, P. sicula, P. taurica, P. tiliguerta, P. wagleriana.*

Algyroides: A.fitzingeri, A. marchi, A. moreoticus, A. nigropunctatus.

Psammodromus: P. algirus, P. hispanicus.

The three lacertids in southern Europe that do not belong to the South-west Palaearctic generic group are *Acanthodactylus erythrurus, Eremias arguta* and *Ophisops elegans.* Information on distribution, size and identification of European lacertids can be found in Arnold & Burton (1978).

General ecological characteristics of European lacertids

The lacertids found in Europe are relatively small lizards with snout-vent measurements of adults varying from about 3.5 cm to 20 cm. They are all diurnal and heliothermic, basking to maintain body temperatures that are often substantially higher than that of the ambient conditions and usually fall between about 30°C and 39°C in active animals with access to sunlight. Activity through the day varies with season and locality but there is often a main period of activity in the morning and another less pronounced one in the late afternoon. This bimodal pattern is most marked in summer and in warm areas; at cooler times of year and in generally cool places, the distribution of activity may be unimodal, peaking in the middle of the day. In many regions, all or most lacertids undergo at least a short period of hibernation.

Diet consists largely of arthropods, although other invertebrates may be taken and large species occasionally consume even small vertebrates. A certain amount of soft vegetable food may also be eaten, particularly by the bigger forms and by populations on small Mediterranean islands with impoverished faunas (see for example Eisentraut, 1949). As will be seen, European lacertids hunt much of their prey actively.

With the exception of most populations of *Lacerta vivipara*, which produce fully formed young, all European lacertids lay eggs. Clutches vary in size from one in the smallest species to more than 20 in the largest and often more than one clutch is produced each year. The young usually emerge in the summer and, at this time, three main size classes can be distinguished in many populations: hatchlings, animals about a year old and adults. However, some southern species such as *Psammodromus hispanicus* and *Podarcis milensis* on Milos seem to mature in a year or less and some of the large forms may take more than two years, even in southern Europe.

Lacertids are preyed on by a variety of birds and snakes and to a lesser extent by small mammals and even other lizards. Anti-predator responses are varied: all species can shed the tail, as a means of escape and of distracting attackers, and they habitually make use of secure refuges such as holes and crevices. Coloration is often cryptic, although this is not always immediately apparent, especially if only basking animals are seen. This is because, as previously stated, many species bask and hunt in different environments and colouring tends to match the hunting areas, possibly because it is more important for the lizard to be cryptic when it is concentrating on foraging than when it is merely basking and has time to watch for predators. Also, a good colour match with the hunting environment may act as aggressive camouflage, concealing the lizard from its prey.

Methods

In most lizard communities, the main factors in niche differentiation are diet (kind and size of food items), hunting method, time of activity and microhabitat. Some idea of dietary differences was gained by examining stomach contents and faeces of various species and hunting methods were assessed by incidental observation in the field. Times of activity and microhabitats were studied by going to areas with more than one species and walking slowly through as many habitat types as possible, examining lizards with 7 x 35 binoculars and recording a number of parameters for each individual seen. Localities were surveyed only once and, where feasible, species were observed at more than one place. A photographic record was made of the different habitats investigated. As many of the following parameters as possible were noted for every specimen encountered.

1. Time of day.

2. Sex and maturity (adult, immature or hatchling).

3. Substrate. The actual surface on which the lizard was first seen. Substrates were divided into the following categories:

(a) Rock: including natural continuous faces, boulders down to about 15 cm across, and concrete and road surfaces.

(b) Stones: mineral objects from about 15 cm down to 3 cm across.

(c) Earth: smaller particles than stones. Both stones and earth may include sparse plants.

(d) Vegetation: used for lizards climbing in twigs etc., and for those on grass and amongst dense plants close to the ground.

(e) Timber: boles and branches of standing trees, and fallen trunks and branches more than 5 cm in diameter.

(f) Other: various usually artificial surfaces, such as pieces of tin-plate and corrugated iron, plastic sheeting and paper.

4. Height above the ground. Lizard species often differ in their tendency to climb and the easiest way of assessing this is to record their height above the ground when first seen. This parameter has frequently been used by workers on the iguanid lizard genus *Anolis* (see, for instance Rand, 1964; Schoener, 1968; Schoener & Gorman, 1968). Here it is fairly unequivocally applied because these lizards are mainly arboreal and it is usually not difficult to decide where ground level is in woodland. Lacertids, on the other hand, occur quite frequently on sloping surfaces, such as rock pavements, and decisions about ground level here may be harder. To simplify assessments, extensive slopes of less than 45° were regarded as being at ground level, while lizards on steeper inclines were recorded in relation to the nearest piece of level ground.

5. Refuges. When disturbed, lacertids will usually run to some sort of cover which often varies with the species concerned. In order to gather data on these differences, each lizard observed was pursued to see where it would hide. Possible shelter is provided by a wide range of objects but to facilitate comparison refuges were divided into three main classes.

(a) Crevices. These include any openings which allow the lizard concerned considerable lateral movement but restrict it in its vertical plane, either at their entrances or further inside. Most refuges assigned to this category were fissures in large sections of rock, but physically similar cavities in dry-stone walls and narrow caps in piled timber were also included.

(b) Holes. Like crevices this category was restricted to cavities in solid objects or between them. Holes differ from crevices in that they appear to restrict lizards no more vertically than laterally. Included here are the interstices between piled stones and in scree, cavities among tree roots, and burrows dug by other animals or the lizards themselves.

(c) Vegetation. Included here are all plants which produce a three-dimensional system of openings through which a lizard can run or climb, that is, bushes and herbage rather than tree trunks and branches. Often lizards appear to depend only on the density of such vegetation for their protection, but in some cases they may use burrows or holes secreted in it. It is therefore likely that some animals scored as hiding in vegetation should really be recorded as utilizing holes.

6. Distance fled. The distance individual lizards fled when chased was noted. This involved difficulties as, in most species, the distance travelled depends on how scared the lizards are. Paradoxically, the more obviously disturbed ones frequently run shorter distances, for in some habitats refuges are numerous and lizards can often find some sort of shelter very quickly if necessary. But, when not closely pressed, many will travel further away, running from the vicinity of one refuge to that of another. Consequently records were only made when lizards ran to the nearest obvious cover.

7. Humidity and shade. It was apparent that some species differ in the humidity of their microhabitat, or possibly in other factors often associated with humidity such as relative shadiness or coolness. In such cases, no precise assessment could be made but proximity to water or presence of richer vegetation were noted as indirect indicators of such differences and the relative shadiness of the microhabitat was noted.

8. Body temperature. Body temperature readings of active lizards were gathered using Schultheiss thermometers with bulbs approximately 2 mm in diameter which were inserted into the cloaca. This was only done with naturally active animals that could be caught rapidly without initial disturbance, usually by noosing. Temperatures that took longer than 15 s to obtain from the time of capture were rejected.

All except the last of these parameters were recorded for more than 4500 lizards and cloacal temperatures were taken of over 500 of them, the data being summarized in Appendix 1 (Tables IV-VII) and Appendix 3 (Tables XI and XII). Localities investigated and the dates they were visited are listed in Appendix 2 (Tables VIII-X). A total of 131 days were spent in the field.

In the case of four species found in western Yugoslavia, field observations were supplemented by habitat choice observations in the laboratory (p. 749).

Potential factors in niche differentiation

Time of activity

No evidence was found of marked differences in time of activity between sympatric species.

Hunting methods

Foraging strategies of lizards have been divided into two main types: active and 'sit and wait' (see for instance Schoener, 1971). Observation suggests that lacertids in southern Europe are substantially active hunters and individuals are often seen moving through the environment searching for prey. Sit-and-wait foraging is, however, occasionally seen in many species. Basking animals will run forwards to snap up a passing insect and rock-dwelling forms like *Lacerta horvathi* sometimes leap from crevices to catch flies. This suggests considerable flexibility in feeding behaviour and there may well be differences in emphasis and detail between species and perhaps even between sexes and age groups as well. The initial division of feeding strategies into two main types has been elaborated by Regal (1978, 1983): among the more active hunters he recognizes intensive foragers, which search largely for hidden food, and cruising foragers, which move about scanning the environment for exposed prey. Both these techniques are used by European lacertids and are often seen in the same species. Ground-dwellers in vegetation and litter frequently seem to forage intensively, while rock-climbing forms, which take a relatively high proportion of flying insects (p. 782), often adopt a cruising strategy.

Foraging behaviour in European lacertids clearly deserves more detailed investigation, but incidental observations made during the study of microhabitats give the impression that differences between syntopic species are not radical and there is no clear differentiation between active and sit-and-wait specialists such as is found in many desert communities (Pianka, 1966, 1973; Arnold, 1984).

Diet

See Appendix 4. All European lacertids that have been checked eat a wide range of prey types. Differences in dietary composition between species certainly exist but, to a large extent, they seem to reflect differences in availability between microhabitats rather than active selection by the lizards themselves, although this undoubtedly takes place to some degree.

Substantial variation in mean prey size exists and correlates with differences in body, and especially head size, of the lizards concerned. In particular, green lizards (*Lacerta* part I) take larger prey when adult than do other forms. This reduces potential competition for food in some cases: for instance, where the large *Lacerta lepida* forages in the same environments as the very small *Psammodromus hispanicus* (Mellado *et al.*, 1975). But, in general, green lizards have their own specific microhabitats and their large mean prey size is only likely to be important in niche separation where these border environments that are occupied by smaller species.

Microhabitat

As indicated elsewhere (Arnold, 1973) and as Mellado *et al.* (1975) found in a lizard community in southern Spain, spatial separation appears to be the main factor differentiating the niches of European lacertids. It is discussed below.

Differences in microhabitat

(see Appendix 1)

Western Yugoslavia

Lacerta horvathi

A lizard essentially endemic to north-west Yugoslavia which is found from the Julian Alps to the Velebit mountains but does not extend much lower than an altitude of 600 m.

Méhely (1904) states that *L. horvathi* is present in mainly wooded areas of Croatia in the company of *Podarcis muralis* and *Lacerta vivipara, b*ut does not say how these lizards differ in habitat. However, he does indicate that he found *L. horvathi* in open, rocky situations. The three localities I visited were quite extensively wooded and again *L. horvathi* was strictly confined to exposed rock surfaces such as precipitous limestone outcrops, steep road cuttings and limestone cliffs and pavements that usually had only very sparse vegetation. It climbed extensively on these, rarely descending to the ground, and nearly always took refuge in crevices when disturbed.

On Mount Učka, *L. horvathi* occurred between about 1100 m and 1300 m in an area of beech forest. Here it was found alone, although *Podarcis muralis* was present at lower altitudes. Nearly all sightings were on cliffs and road cuttings that were often 15-20 m high and nearly vertical or even overhanging. In spite of there being no potential competitors in contiguous microhabitats, *L. horvathi* did not seem to enter them. The mean height above the ground at first sighting was 1 .91 m.

At Plitvice and the Soča valley, this lizard was encountered in similar habitats among more open deciduous woodland but was not altitudinally separated from *Podarcis muralis* which occurred on less precipitous but more broken areas, such as road-side screes and banks. It used crevices as refuges less frequently than *L. horvathi* and did not climb so high, the mean height above the ground at first sighting at Soca being 0.57 m compared with 2.08 m for *L. horvathi;* at Plitvice the heights were 0.52 m and 1.42 m respectively.

Lacerta oxycephala

This lizard, endemic to south-west Yugoslavia, occurs from Šibenik south to the Albanian border and reaches a number of off-shore islands. It ranges from sea level to about 1600 m.

Like the previous species, *L. oxycephala* is largely found on rocky surfaces but also occurs extensively on their man-made analogues such as field walls, fortifications, bridges and buildings. It is a more agile climber than other rock-dwelling lizards in southern Europe and is frequently seen on very open and precipitous faces, sometimes on bare exposures 15 m or more from the ground. At all localities, *L. oxycephala* climbed higher than syntopic lacertids, mean heights above the ground at first sighting varying from 0.84 m to 1.55 m. In such towns as Korčula, Ston, Mostar and Dubrovnik, its ability to live on the walls of buildings enables this lizard to penetrate far into built-up areas. In all places its usual refuge consists of crevices and sometimes the interstices of screes and stone piles. Although most time is spent on open faces, foraging *L. oxycephala* will descend into vegetation close to the base of cliffs and walls. While not generally confined to moist places, this lizard may be absent from very dry environments and, in the lowlands where *Lacerta mosorensis* is not found, it seems to be most abundant where there is water nearby.

Lacerta mosorensis

Another lizard endemic to south-west Yugoslavia with a range that is somewhat smaller than that of *L. oxycephala.* Unlike this species it does not appear to occur below an altitude of 550 m.

Lacerta mosorensis and *L. oxycephala* are the only European archaeolacertas west of the Black Sea that are sympatric, so their comparative ecology is of particular interest. Werner (1907) states that near Gacko he saw *L. mosorensis* mainly on rock faces, like *L. oxycephala,* but that it did not climb so high as this species and appeared to be confined to moister areas. My own observations around Gacko confirm Werner's impression. The majority of *L. mosorensis* that I saw occurred on limestone exposures or large boulders, as did *L. oxycephala,* but the height distribution was different: only 22% of *L. mosorensis* were higher than 0.6 m when first sighted compared with 54% of *L. oxycephala* and only 4% above 1.2 m compared with 26%. The mean height above the ground at first sighting was 0.55 m compared with 1.26 m in *Lacerta oxycephala. L. oxycephala* often occurred on exposed, sunny, frequently south-facing rock outcrops and limestone pavements whereas *L. mosorensis* was largely confined to areas with more shade. At the west end of the Ključ valley near Gacko, *L. oxycephala* was common on open pavement while *L. mosorensis* was most abundant in open oak woods. Here it lived on low rock outcrops but foraged on the wood floor to some extent and occasionally climbed on tree boles and among twiggy vegetation. Where the woods bordered limestone pavement, *L. mosorensis* was mainly seen on the edges of these, although a few occurred away from the periphery. These, however, were not on the open surface but were in deep solution holes and big fissures characteristic of karst limestone formations. Such hollows are shady and have an essentially woodland flora of *Cyclamen* etc. Similar habitat differentiation between the two archaeolacertas was also noted at 1400 m on the nearby mountain of Baba Planina and at Nevesinje.

Lacerta mosorensis was seen in more open situations, but only on a north-east facing slope with scattered hawthorn bushes *(Crataegus)* and restricted insolation. Here it was the dominant species, 47 individuals being observed compared with only eight *L. oxycephala,* but where bushes were fewer and the slope curved so that it faced east and received more sun, *L. oxycephala* was the only archaeolacerta present, 61 being counted. All the *L. mosorensis* microhabitats that I came across appeared to be more humid overall than those occupied by *L. oxycephala.* Like the latter species, *L. mosorensis* typically used crevices as refuges.

It seemed possible that the habitat difference between *L. mosorensis* and *L. oxycephala* might be reflected in the body temperatures of normally active animals: *L. mosorensis,* occupying shadier and moister places as it does, might be expected to operate at lower average temperatures. Forty *L. mosorensis* checked in August had a mean temperature of 34.0±1.15°C with over 80% of individuals within 2°C. of the mean. Unfortunately, *L. oxycephala* in the region were very shy (Tomasini, 1894, found this too) and only 10 could be caught. These showed no significant difference in temperature from the *L. mosorensis* sample. Nor did a much bigger number of *L. oxycephala* caught a few days later at another locality, Boračko Jezero, 70 km away. Here 80 *L. oxycephala* had a mean temperature of 34.1±1.5 °C with 75% of individuals within 2 °C of the mean.

Although *L. mosorensis* may occur in fairly bare habitats, these are often degraded woodland and within them it occupies microhabitats that conform most closely to woodland conditions. It consequently seems likely that this lizard was primarily associated with open wooded environments when these were more extensive in south-western Yugoslavia.

Podarcis melisellensis

This wall lizard is confined to the east Adriatic region, occurring from Istria to northern Albania. It is found on many islands but extends not more than 160 km inland and usually far less; nearly all populations are below 1000 m.

Podarcis melisellensis differs sharply from the three archaeolacertas discussed above in climbing far less, in not being largely restricted to rocky surfaces and in taking refuge in holes and vegetation rather than crevices. It is typically found in quite dry habitats and usually occupies irregular, sometimes sloping surfaces. Thus it may be encountered on stony hillsides, path-side banks and discontinuously rocky ground. All habitats where it was seen had at least some bushy or herbaceous vegetation in which it hunted and often hid. Plant cover varied considerably in extent and *P. melisellensis* occurred in situations ranging from open dry woodland and degraded woodland, with small grazed bushes or tree stumps with secondary growth, to open slopes with patches of long grass. Specimens observed off the ground tended to be most often in plants or on steep banks rather than on rock faces, although they were sometimes seen on flattish boulders and on the tops of low walls bordering fields, especially in the absence of *P. muralis. P. melisellensis* penetrates substantial distances into towns like Mostar, but only where there are parks and gardens.

Podarcis muralis

Although widespread in western Yugoslavia, this species is absent from the Mediterranean region south of about Senj. The most broadly distributed member of *Podarcis,* it is found over much of south and central Europe and in north-west Asia Minor as well.

Where *P. muralis* occurs in sympatry with archaeolacertas and with *P. melisellensis* it frequently occupies situations that are intermediate between these forms. Thus it often lives in less rocky, lower places than the archaeolacertas, while being more scansorial and more often found on rocks than *P. melisellensis.* It is in fact a much more adept climber than the last species but appears to be excluded from more precipitous habitats by the presence of archaeolacertas. At Opatija, where the latter are absent, *P. muralis* climbs significantly higher than at other Yugoslav localities examined (p. 767). In the Šištica gorge at Boracko Jezero, *P. muralis* and *L. oxycephala* occur together with significant spatial overlap, judged by height and substrate type. But the latter species forages much more on rock faces and the mean body temperature of normally active animals is about 1.8 °C lower than in *P. muralis* (Table XI).

The ecological separation of *P. muralis* and *P. melisellensis* is not entirely based on the mechanical properties of their environment. Like *L. mosorensis* and *L. oxycephala,* they too appear to be influenced by relative humidity. Usually, *P. muralis* is found in apparently moister situations than *P. melisellensis.* For instance, at Boracko Jezero, *P. melisellensis* occurs mainly on arid stony ground with low shrubs on the valley floor, but is largely replaced by *P. muralis* in areas of open beech wood and in the comparatively moist Šištica gorge. In intermediate areas, where both forms exist, substantial separation still occurs based on habitat type and height above the ground in the way described above. The influence of relative humidity is also apparent at Gacko and at Jablanica, near the Mostar road, where *P. muralis* occurred within about 30 m of small streams that pass under the highway, but not in the intervening areas of degraded oak woodland where *P. melisellensis* was found. The few body temperature readings available for the latter species suggests that it does not differ much from *P. muralis* in this parameter, so it seems unlikely that their habitats reflect different preferred temperatures.

Podarcis sicula

In Yugoslavia, a species that is confined to parts of the Adriatic coast and islands. It is widespread in Italy and on nearby islands and has isolated colonies elsewhere in the Mediterranean region.

Podarcis sicula is typically associated with open terrestrial habitats in Yugoslavia, at least on the mainland and larger islands. It also tends to occupy quite fertile areas. Around Trogir and Split, *P. sicula* occurred on arable land, such as vineyards, tomato fields and ploughed ground, and on sparse pasture. The lizards foraged in such places but ran swiftly when disturbed to hide in the interstices of dry-stone walls and in hedges. They climbed well here and also used such structures for basking after the main morning feeding period. Compared with most other small Yugoslav lizards, *P. sicula* is a strong runner on open ground and covers significantly greater distances when fleeing to cover. Out of 138 individuals checked, 17% ran over 3 m to a refuge compared with less than 7% of *L. oxycephala, L. mosorensis, P. melisellensis* and *P. muralis* (see also p. 776).

Podarcis sicula was seen in open meadows on the island of Krk and again fled long distances to their periphery. It frequently enters towns, particularly along open ground by roads and at Zadar was present on the sloping overgrown walls of the fortifications. Where they occur together, *P. sicula* is replaced by *P. melisellensis* in typically less fertile areas of more broken and often more overgrown ground. This sort of difference was noted by Nevo, Gorman, Soule, Yung Yang, Clover & Jovanovic (1972) on two small islands and is probably responsible for the observation of Kramer & Mertens (1938) that, in Istria, *P. sicula* occurs along the borders of large roads whereas *P. melisellensis* is found along country paths.

Lacerta vivipara

A lizard confined to humid mountain areas in western Yugoslavia, but widespread in the rest of Europe outside the Mediterranean region.

This species was only encountered at Gacko on Gatačko Polje, a large, partly cultivated grassy plain. Here it was limited to the moister areas around drainage ditches, where it occurred among lush grass and rushes *(Juncus).* Lizards scarcely climbed and usually retreated into vegetation when disturbed. In Britain *L. vivipara* is more catholic in its habitat, but again is largely terrestrial and most abundant in non-arid places with lush vegetation.

Lacerta agilis

A species found mainly in temperate montane areas in western Yugoslavia but widely distributed in much of the rest of Europe outside the Mediterranean regions.

Like *L. vivipara,* this lizard was found at Gacko on the polje and Werner (1907) also recorded it from the grassy areas on the summit of the nearby Baba Planina. It differed from *L. vivipara* in inhabiting the drier parts of the plain, occurring in hayfields, on the edges of patches of corn, in mixed grass and low, spiny leguminous plants, and on closely grazed pasture among small hawthorn bushes *(Crataegus* sp.) dwarfed by browsing animals. Specimens were also seen in the latter type of habitat on Mount Ucka. Retreat was usually into small bushes or into burrows either of rodents or apparently dug by the lizards themselves. *L. agilis* was not seen away from dry meadowland in Yugoslavia and it did not penetrate neighbouring, usually more rocky country where archaeolacertas and species of *Podarcis* were found. The separation of this species from *L. vivipara* based on humidity differences between their habitats is also recorded by Glandt (1976, 1977, 1979) in West Germany. In Britain, *L. agilis* is found in rather different places, typically on sand dunes and heaths, where it may climb in dense heather and again conceals itself among dense vegetation or in burrows.

Lacerta viridis

Although widespread in central and southern Europe, this lizard is absent from many Mediterranean areas including much of the coastal region of Yugoslavia, southern Greece and most of Iberia.

While most conspicuous when basking on walls or rock exposures, *L. viridis* spends most of its time in and around dense, bushy vegetation. It is commonly associated with bramble patches *(Rubus* sp.) but occurs about other often quite spiny plants as well, such as grazed hawthorn *(Crataegus).* Such vegetation provides hiding places and *L. viridis* also forages in it but frequently makes sallies into nearby grassland and other open areas to feed. When hunting among plants this lizard often climbs quite high among the stems, its very long tail being used to spread its weight.

Lacerta viridis was encountered at Soca, Plitvice, Gacko, Boracko Jezero and Jablanica. At Gacko it occurred in less flat, more sheltered situations than *L. agilis*.

Lacerta trilineata

In western Yugoslavia, a species that is confined to the Mediterranean lowlands and nearby islands. It is more widely distributed in the southern Balkan peninsula, including much of mainland Greece and the Aegean islands.

Lacerta trilineata replaces the similar *L. viridis* in drier, warmer areas. Its behaviour is much the same, although the dense vegetation that it occupies is often more widely separated from similar clumps by open ground. Again, bramble is a common habitat.

It was observed at Opatija, Krk, Zadar, Split and Mostar.

Algyroides nigropunctatus

A species with a distribution similar to *Podarcis melisellensis,* but it occurs less widely on the Yugoslav islands and extends further south, to western Macedonia, north-western Greece and the Ionian islands.

At Opatija, a few individuals were seen on the boles of olive trees *(Olea europaea)* but *A. nigropunctatus* was more conspicuous on semi-shaded, often partly overgrown rock faces. On Krk, this quite scansorial lizard was often observed on dry-stone field walls and, as at Opatija, was usually close to vegetation, in contrast to climbing *Podarcis* species, and was never seen very far from trees and bushes. More singularly on Krk, *A. nigropunctatus* was occasionally encountered climbing in Bay *(Laurus nobilis)* and Kermes oak *(Quercus coccifera)* bushes. F. A. Winnal (pers. comm.) has also noted this species in bushes on Krk and observed it up to 4 m from the ground. He suggests that it might in fact be commoner in bushes than on walls and rocks, although this is not easy to judge as the sombre, brownish lizard is much harder to see in bushes than against the pale grey limestone of the area which is used for walling. Bruno (1980) records *A. nigropunctatus* from walls with bushy vegetation and from the trunks of *Quercus pubescens* on Krk and Cres islands. Lilge & Wicker (1972) also report it from overgrown walls.

Cage observations of ***Algyroides nigropunctatus*** *and other Yugoslavian lacertids*

Habitat choice observations were made of captive individuals of four Yugoslav species including *Algyroides nigropunctatus* to see if this lizard really was more prone to climb in bushes than the others. The lacertids used had been collected in late August and early September, maintained on a 12 h light/12 h dark regime and fed on a variety of insects. Observations were made in late October and November and conducted in a large glass-fronted cage 100 cm high x 65cm x 65 cm. This contained a potted Holm oak bush (*Quercus ilex)* almost as tall as the cage; the floor was covered with a mixture of turf and stones and numerous refuges were provided. Heating lamps were placed above the bush and close to the cage floor as well, so that the lizards did not have to climb to warm themselves. Screens prevented them from seeing the observer.

TABLE I

*Percentage of time spent in bush by captive lizards of four species from western Yugoslavia; for further explanation see text. Differences between **Algyroides nigropunctatus** and the other three forms are significant at the* P= <0.001 *level (x^2 test), as are those between **Lacerta oxycephala** and the rest.*

	Dav					
Species	**1**	**2**	**5**	**9**	**10**	**11**
Algyroides nigropunctatus	**27**	**46**	**56**	**69**	**74**	**75**
Lacerta oxycephala	**2**	**1**	**4**	**6**	**7**	**9**
Podarcis muralis	**40**	**29**	**27**	**25**	**16**	**25**
Podarcis melisellensis	**40**	**37**	**34**	**11**	**24**	**36**

Each species was tested separately. Eight individuals of each, four males and four females, were introduced into the cage and their positions noted every 15 min over a period of 6.5 h. This was repeated on the second, fifth, ninth, tenth and eleventh days after introduction. The process was then repeated with another species. The results, given in Table I, are expressed as:

$$\frac{\text{total number of observations of lizards in bush}}{\text{total number of observations of lizards not in refuges}}\ 100$$

The differences between *A. nigropunctatus* and the *Lacerta* and *Podarcis* species over the last three days of observations are significant at the $P = < 0.001$ level.

It will be seen that the four species differed considerably in their behaviour. The normally rock-dwelling *Lacerta oxycephala* scarcely climbed at all, and all lizards of this species observed in the bush were less than 20 cm from the cage floor. The *Podarcis muralis* climbed immediately they were put in the cage, but afterwards spent most of their time on its floor. This behaviour is in keeping with the 'personality' of this species which is inquisitive and typically explores a new cage very thoroughly. *P. melisellensis,* which often lives around bushy vegetation, also climbed considerably more than *L. oxycephala*. The *A. nigropunctatus* began by spending most of their time on the cage floor but climbed progressively higher into the bush until, in the last three days of their stay in the cage, they spent an average of between 69% and 75% of their time there. Assuming that adults of the species are rather conservative in exploring new environments, these observations support the case for *A. nigropunctatus* passing significant amounts of time in bushy vegetation. The species is discussed further on p. 751.

Greece—Corfu

Podarcis taurica

A widely distributed form in south-eastern Europe, except western Yugoslavia.

This is a ground-dwelling lizard that scarcely climbs. Most sightings were from flat, fairly dry areas, often with prickly, low vegetation. They included gravel and dunes near the sea partly overgrown with spiny plants, grass and rushes, sparse pastures, shallow grassy ditches and arable land. Hunting and basking habits on Corfu were similar to those observed in southern Greece (p. 753).

Algyroides nigropunctatus

On Corfu, this species climbed far more than *Podarcis taurica* and occurred in a wide range of habitats. In contrast to its behaviour in western Yugoslavia, it enters built-up areas where it is conspicuous on the pale dry-stone walls of gardens and on parapets and fortifications. In central and southern Europe it is common for at least one small lacertid in an area to enter villages and often at least the outskirts of towns. In many regions *Podarcis muralis* does this but, where it is absent, other species do so. Thus, where it occurs in western Yugoslavia, in Istria and the inland mountain areas, *P. muralis* is the common peri-urban lizard. But on Krk and at Zadar, Trogir and Split it is *P. sicula* and, at Mostar, Ston, Korcula, Dubrovnik and Kotor, *Lacerta oxycephala.* As already stated, *P. melisellensis* is also present in Mostar but does not extend into such completely built-up areas as *L. oxycephala* does. Where there is a variety of lizards in the surrounding countryside, it is one of the more scansorial species that extends farthest into towns and villages. This is presumably because their natural spatial niche conforms most closely to the walls and other vertical structures of human settlements. It is consequently not entirely surprising that on Corfu, where the only other small lacertid is the virtually non-climbing *Podarcis taurica, Algyroides nigropunctatus* should be the species to enter towns.

It is presumably on the basis of such behaviour on Corfu and Cephalonia as well, that some authors (for instance Werner, 1894, and Mertens, 1961) regard *A. nigropunctatus* as a 'Kulturfolger', that is, a species closely associated with human environments. However, this is certainly not necessarily so elsewhere in its range and on Corfu this lizard is widely distributed in more natural environments as well. Here it occurs on rocky overgrown banks and field walls but a very substantial proportion of animals were associated with timber. Many were seen on tree boles, especially of large old olives, up to 5 m from the ground and on fallen and logged cypress trunks *(Cupressus sempervirens),* as well as among piles of brush wood. Of 166 animals observed 74 were in such wood-associated situations. As in western Yugoslavia, *A. nigropunctatus* was usually seen in or quite close to shade. Body temperatures of 12 normally active animals averaged 32.3°C in May. This is considerably lower than summer temperatures of active *Podarcis* and *Lacerta* species (Table XI).

Association of this species with bushes and trees in the south of its range has been noted by other authors: Corfu (olives—Cyrén, 1909), Albania (bushes and olives up to 5 m from the ground—Kopstein & Wettstein, 1921), Ithaca (old olives—Cyrén, 1941).

It seems probable that *A. nigropunctatus* was originally mainly associated with woodland habitats and particularly with tree boles, twiggy vegetation whether dead or alive and fallen timber. This is supported by direct observation in such habitats, especially on Corfu, the tendency of the species to stop close to shade, its apparently low body temperature when active, the fact that its rough scaling and sombre dorsal coloration are most cryptic against bark, and its behaviour in captivity (p. 749). That this association is not immediately obvious in many areas is partly because *A. nigropunctatus* on bushes and timber are far less conspicuous than ones on walls and other human structures. Also, unlike Corfu, Mediterranean Yugoslavia has lost most of its natural woodland through felling and overgrazing. What is left is often degraded and old trunks and fallen timber are usually removed for firewood. Although *A. nigropunctatus* survives in this region, it is usually in greatly modified environments.

Lacerta viridis

This species was encountered at only one locality on Corfu, in dense brambles near water.

Lacerta trilineata

As in western Yugoslavia, *L. trilineata* occurred in and around brambles and dense bushes. It was nearly always in situations drier than those where *L. viridis* was found.

Greece—Peloponnese

Lacerta graeca

An archaeolacerta that is endemic to the Peloponnese and commonest in montane regions, although it also occurs at lower altitudes.

At Sparti, this lizard was associated with rock and rock-like surfaces in mountain areas. These were often partly shaded and included outcrops and boulders in deciduous woodland, road-side cuttings and stone-faced embankments, retaining walls and parapets. Such sites were frequently close to water and usually damper than surrounding areas, at least in the spring. *L. graeca* did not confine its foraging to such hard surfaces but also descended to the ground to search in vegetation at the bases of outcrops and in leaf litter, and even occasionally climbed the boles of olive trees. These excursions, however, rarely extended much more than 3 m from rocky structures.

At Lake Stymphalia, *L. graeca* was encountered on steep rock exposures above the lake and on large boulders on its shore. As at Sparti, the lizard occupied relatively damp microhabitats here, but it climbed higher than at that locality and did not wander so far from rocky surfaces.

Podarcis peloponnesiaca

Like *Lacerta graeca,* this lizard is endemic in the Peloponnese

Werner (1938) states that *P. peloponnesiaca* is a marked ground-dweller, but this does not seem to be so. Certainly it is not almost entirely restricted to the ground in the way that *Podarcis taurica* is. Most animals observed were quite close to some climbable surface, if not actually on it, although it might be quite modest in extent. Around Sparti, the lizard often occupied sloping rocky or stony ground, the vicinity of low walls between orange groves and fields, rocky road-side banks, the bases of olive trees and the ruins of buildings. Foraging took place on such structures and on more level surfaces close by, which were usually open or with sparse low vegetation. Occasional animals were seen quite high on the boles and main branches of small trees. At Stymphalia, *P. peloponnesiaca* behaved similarly but, like *L. graeca* at this locality, was more scansorial. As well as occurring on stone piles, low outcrops and rocky hillsides with bushes of Kermes oak *(Quercus coccifera),* it climbed on isolated boulders, rock cuttings along roads and even on sheer cliffs. In general, lizards were commoner in such open situations than among oak scrub and vegetated hillsides without obvious rocks. Mean height above the ground when first seen was 0.26 m for *P. peloponnesiaca* and 0.24 m for *L. graeca* at Sparti and 0.63 m and 0.74 m respectively at Stymphalia.

At both localities, *P. peloponnesiaca* was replaced as the common climbing lizard by *L. graeca* in damper situations. The latter species appears morphologically better adapted to climbing on rocky surfaces and taking refuge in crevices and certainly moves on precipitous faces with more agility than *P. peloponnesiaca* which, although it climbs unhesitatingly, is quite clumsy. The greater apparent degree of physical adaptation in *L. graeca* may be related to the fact that it is more often associated with continuous rock surfaces and uses crevices more as refuges.

Podarcis erhardii

A characteristic species of the southern Balkan Peninsula and European Greek islands which is only present in the north-east of the Peloponnese.

I only saw *P. erhardii* near Stymphalia at a height of over 1100 m. Here it occurred on and around boulders and on a road bank with scree and vegetation in pine forest. Wettstein (1953) records it from nearby Mount Killene at 1400 m, but further east it is found at lowland localities (Corinth, Mycenae). Cyrén (1941) reports *P. erhardii* from the southern part of its mainland range in dense undergrowth and on flattish ground among stones and the twigs of compact bushes.

Podarcis muralis

In the Peloponnese, this species only seems to have been recorded from the Taygetos mountains, near Sparti, above 1200 m (Werner, 1938) and on Mount Killene at 1400 m (Wettstein, 1953).

Podarcis muralis and *P. erhardii* may replace other small lacertid species at high altitudes in southern Greece. How they differ ecologically where they occur together, for instance on Mount Killene, is unknown, but further north in its range *P. erhardii* apparently occupies warmer, drier situations than *P. muralis* (Cyrén, 1933, 1941).

Podarcis taurica

At Stymphalia, as on Corfu, *P. taurica* was a ground-dwelling lizard hunting among herbage and taking refuge in holes under stones and in vegetation. It foraged in open areas with a low, fairly sparse growth of papillionaceous herbs and grass, and in shallow grassy ditches. Basking took place on piles of stones and on low banks between fields. Here lizards were very conspicuous but hunting animals were usually much more difficult to see. In southern Greece at least, this species is bright green in the spring, matching the fresh vegetation, but later in the year when the herbage dries and becomes browner, so does the lizard.

Lacerta trilineata

As in western Yugoslavia and on Corfu, *L. trilineata* is mainly associated with dense vegetation in southern Greece. In the absence of *Lacerta viridis,* however, it occurs in relatively moist habitats and highland areas as well as in dry lowland regions similar to those the lizard occupies further north. General environments where it was encountered ranged from meadows and road edges to olive groves and open woodland. Adults were often seen in and around brambles but occurred in bushes and piles of brushwood as well and sometimes foraged in the more open surroundings. Young animals, up to about 7 cm from snout to vent, tended to occupy rather different places from their parents, being found in denser, lower and often more herbaceous vegetation including long grass, rushes and small shrubs. These situations were more thickly provided with plants than those in which *Podarcis taurica* usually lives.

Near Sparti, *L. trilineata* was common around bushes and brushwood piles in open deciduous woodland, interspersed with small streams. Adults were occasionally seen to swim across these, a habit also recorded for this species in the Danube delta by Fuhn & Mertens (1959).

Algyroides moreoticus

A species that is confined to the Peloponnese and the southern Ionian islands.

Near Sparti, *A. moreoticus* was seen mainly in piles of old, dry brushwood and twigs from pruned olive trees that were overgrown with creepers and herbaceous plants. In most cases, these were situated on north and north-easterly slopes that received restricted sun at an oblique angle. The lizards tended to bask in semi-shaded places and not expose themselves to full sun very much, disappearing as soon as the brush piles were strongly illuminated. They avoided newer heaps of brushwood and their colouring and rough scaling blended well with the bark of the old twigs among which they lived, making them very inconspicuous. Individuals moved jerkily around within the piles and did not come to their outer surfaces much.

Near Stymphalia, *A. moreoticus* was in similar situations, among dead brambles, in areas of herby vegetation and deciduous leaf litter, especially on sloping banks, and on low tree stumps. Again, the lizards were usually close to shade and, during overcast conditions, they were more active than other species of lizards in the area. In general, *A. moreoticus* was more often heard than seen, as it rustled against dry leaves and twigs.

Clark & Clark (1970) encountered this lizard in habitats of the same type: 'leaf covered banks and piles of brushwood, often near water and in rather shady situations'. Buchholz (1964) found one individual in leaf litter in an oak wood, another on stones by a stream and a third 2.5 m up on the bole of a tree. Other authors have noted this species in open situations, such as stony, rocky places with some vegetation (Cyrén, 1909; Schreiber, 1912; Werner, 1938) and Cyrén (1941) and Werner (1938) state that it is found close to areas of human activity. All these observers regard *A. moreoticus* as rare. It is likely that they were seeing only animals that occasionally occur in untypical habitats, for in the environments described earlier in this paper, the species, though often secretive, is quite common.

Greece—Milos Island

Podarcis milensis

Confined to Milos and nearby islands where it is the only small lacertid present.

Podarcis milensis is found in a very wide range of habitats. It is most abundant in gardens and cultivated areas, especially if irrigated, where small fields of citrus trees, cereals and vegetables are separated by dry-stone walls and banks that often have a good growth of vegetation. Away from such places it occurs at lower densities in rocky areas of degraded woodland, scrub and abandoned cultivation, along road-side banks and among rushes and halophytes on damp ground near the sea.

In cultivated places, lizards were conspicuous on walls and stony banks where they basked, but they hunted substantially on the ground and then were harder to see. Foraging took place on paths, ploughed ground and among grass and other herby vegetation, from where lizards sometimes ran quite long distances to refuges in walls etc. when disturbed, although most did not travel very far (see p. 776).

Podarcis milensis has a broader spatial niche than most mainland forms, being observed in a range of microhabitats that are occupied by two or three species elsewhere. For instance it occurs in environments where, in western Yugoslavia, *P. melisellensis* and *P. sicula* would be expected and, in the Peloponnese, *P. peloponnesiaca, P. taurica* and, to a lesser extent, *Lacerta graeca.*

Cyrtodactylus kotschyi *(Gekkonidae)*

In Europe, this gecko is found in the southern Balkan Peninsula and the Aegean Islands.

Although not a lacertid, it is at least partly active by day and consequently potentially likely to interact with the similarly sized *Podarcis milensis,* and is therefore discussed here. On Milos, *C. kotschyi* was quite commonly observed, occurring with *P. milensis* on drystone walls and banks and also on rocks and boulders in pasture, degraded scrub and woodland. Unlike *P. milensis,* nearly all its time during the day was spent perched on rocky surfaces and very few individuals were seen on the ground. The average height at first sighting was 0.54 m compared with 0.24 m in the lacertid. The gecko spent more time than *P. milensis* on vertical surfaces and was a much more adept climber, being able to run upside-down on the lower surfaces of boulders. Fleeing animals took refuge almost exclusively in crevices and holes, and flight distances were much shorter than in the wall lizard.

Cyrtodactylus kotschyi also differed from *P. milensis* in its thermal regime. Although the geckoes exposed themselves to the sun early and late in the day during the spring, they spent much more time in shade and semi-shade than *P. milensis* and the frequency of sightings was more markedly bimodal, few animals being seen in the middle of the day, suggesting that they retreated into refuges at this time. Body temperatures of diurnally active individuals were also relatively low (Table XI). It is not certain that *C. kotschyi* actually feeds in the day and its exposure at this time could be largely for thermoregulatory reasons. The gecko may be more crepuscular and nocturnal in the warmer part of the year, in which case any direct competitive interaction with *P. milensis* is likely to be reduced.

Lacerta trilineata

As elsewhere, *L. trilineata* was sometimes seen in dense vegetation, such as in bushes and *Aloe* plants on grassy banks. But it was also observed on dry-stone walls with isolated shrubs and sometimes foraged on open, bare ground.

Iberian Peninsula

Lacerta monticola

A species that is confined to mountain regions of the north, west and central Iberian peninsula: Pyrenees above 2000 m, the Cantabrian area usually above 400 m but as low as 50 m near Coruña (Elvira & Vigal, 1982); Serra de Estrella, Sierra de Gredos etc. and Sierra de Guadarrama above 1500 m.

This mainly high-altitude lizard is confined to cool areas with copious rainfall and often long, snowy winters as well, although this is not always so. It usually replaces *Podarcis* species altitudinally with little overlap, the transition often taking place close to the tree line. In the Cantabrian mountains near Puerto de Panderrueda at 1450 m, *L. monticola* was found at and above the upper edge of open oak woodland. Here it lived on low rocks along small streams descending from pasture land, on scree with heather, and on slopes with steep rock outcrops and boulders of a rough conglomerate interspersed with usually low (1 m high) bushes of broom *(Cytisus),* heath (*Erica)* and juniper *(Juniperus).*

Lacerta monticola was largely confined to rocky substrates on which it climbed with relative ease, even on vertical surfaces. Refuge was taken in crevices, holes and vegetation. Use of crevices was relatively low for an archaeolacerta but this was at least partly due to the nature of the rock at this locality which provided relatively few of them. *Podarcis muralis* was also present but did not extend far beyond the tree line, although it was abundant in open oak woodland and on banks and screes along paths and roads at lower altitudes. Where it contacted *L. monticola,* it climbed less and was usually seen on earth, stones and leaf litter rather than on rock; refuge was most frequently taken in vegetation. Body temperatures of active *P. muralis* averaged 1.4°C higher than those of *L. monticola* taken over the same period *(P. muralis:* x = 34.36°C, n = 40. *L. monticola:* x = 32.98°C, n = 25). This may reflect the cooler, more exposed situations occupied by the latter species.

Above the Puerto de Cotos (1830 m) in the Sierra de Guadarrama, central Spain, *L. monticola* was observed on treeless slopes with granite boulders and outcrops interspersed by juniper bushes. It also occurred in open areas just below the tree line, on road cuttings that exposed a mixture of earth, scree and rocks on which there was a very sparse growth of stunted pines. Animals behaved here similarly to the Cantabrian ones described above, although they were more frequently found on earth and stones. Again, the use of crevices as refuges was not especially frequent. *Podarcis muralis* and *P. hispanica* occurred at altitudes just below those of the lowest *L. monticola* populations.

Martinez-Rica (1977) reported *L. monticola* from regions in the Pyrenees above 2000 m and beyond the altitudinal range of *P. muralis.* Here they occur in rocky areas close to places where snow lies throughout the year, and take refuge in holes beneath stones.

Podarcis hispanica

This wall lizard occurs in the Iberian peninsula, in the adjoining west Mediterranean coastal region of France and in north-west Africa.

At all localities where it was encountered, this lizard was associated with rock-faces, outcrops, boulders and their man-made analogues. It was also sometimes found in less precipitous micro-habitats as well, but was usually replaced in these by other lacertids, when these were present. *P. hispánica* climbed frequently and well and, in a high proportion of instances, utilized crevices as refuges. It was much more closely associated with rocks and similar structures than other *Podareis,* and in general occupied quite dry, sunny habitats. However, in south-west Spain this species appears to be less obviously scansorial and may occur on tree boles where rocks are absent (Mellado *et al.* 1975).

Podareis muralis

In Spain, *P. muralis* is widespread only in the extreme north, but occurs further south in a few mountain areas including the Sierra de Guadarrama.

In moist areas of the Pyrenees and Cantabrian mountains and the north Atlantic seaboard of Spain, *P. muralis* is widespread and frequently the only *Podarcis* species present. It occurs in a variety of broken and precipitous habitats on substrates that often include a considerable proportion of rock and stone and may habitually climb quite high, for instance at Cangas de Onis. At high altitudes in the Pyrenees, Cantabrians and the Sierra de Guadarrama, it is sometimes found close to, or in contact with, populations of *Lacerta monticola,* but areas of actual sympatry are very restricted. Where the two exist together at Puerto de Panderrueda in the Cantabrians, *P. muralis* was observed to occupy less precipitous habitats, climb less high and use crevices as refuges less than at Cangas de Onis where it occurs on its own. This may represent a habitat displacement (see p. 767).

In the Lozoya valley in the Sierra de Guadarrama between about 1500 m and 1800 m, *Podarcis hispanica* and *P. muralis* overlap quite broadly but, at lower altitudes, for instance around Rascafria, the latter becomes restricted to the proximity of rivers and to villages before disappearing altogether. It is also confined to such habitats on the south face of the Cantabrians at the lowest altitudes where it occurs, such as below Aleje. In areas of broad overlap the two species show differences in structural habitat, *P. muralis* climbing less high, occurring less frequently on rocky surfaces and using crevices as refuges less. It tends to be a species of mixed earth and stone road-banks, overgrown scree, low dry-stone walls and gravelly areas near rivers, often with willow scrub.

Podarcis bocagei

Confined to north-west Spain and northern Portugal.

This Iberian species was not observed but its ecology has been discussed by Peréz Mellado (1981). Although largely allopatric from *P. muralis,* it resembles this species in occupying parts of the Iberian Peninsula where the climate is influenced by the Atlantic Ocean and rainfall is comparatively high. It is also alike in being quite extensively sympatric with *P. hispanica* and its structural niche differs in a similar way. Unlike *P. hispanica, P. bocagei* is not closely associated with rocky habitats and occurs in stony places at the edge of roads and woods, in woods among leaf litter and on fallen tree trunks and in scrub situations; nor does it use crevices as refuges very much. In the Sierra Cabrera at 1500 m *P. bocagei* contacts *L. monticola* which is found here in rocky places with scarcely any vegetation.

Lacerta vivipara

In the Iberian Peninsula confined to the Cantabrian and Pyrenean regions.

Lacerta vivipara was found near Cangas de Onis basking on a low dry-stone wall and in a humid meadow adjoining it. At Puerto de Panderrueda it occurred on moist grassy slopes and took refuge in vegetation. This lizard was also seen in similar situations near Lac Bleu de Bigorre (2000 m) in the French Pyrenees.

Lacerta viridis

In Spain, confined to the extreme north.

This green lizard was only encountered near Puerto de Panderrueda at 1200 m and at Cangas de Onis. In these quite moist areas, it occurred in situations typical of the species, being found in and around brambles and bushes in meadowland and retreating into such vegetation when disturbed.

Lacerta schreiberi

North-west, west and central Iberian Peninsula.

Lacerta schreiberi was seen on the southern slope of the Cantabrian mountains between Riaño and Cistiernas and in the Lozoya valley in the Sierra de Guadarrama between about 1200 m and 1700 m. Its general habitat and behaviour were very like those of *L. viridis* with the same predilection for bushy vegetation (bramble, oak bushes and broom). In the Cantabrians it occurred at lower altitudes than *L. viridis* where the climate was drier and warmer. Here it favoured rather lush habitats, often near water, being replaced by *L. lepida* in more arid places. Similar separation from this species occurred in the Lozoya valley and in both areas *L. lepida* became the only green lizard at lower altitudes.

Lacerta lepida

Iberian peninsula, Mediterranean France etc.

This large species is the common green lizard over most of Iberia, entirely replacing *L. viridis* and *L. schreiberi* in drier, warmer areas. At many places where these lizards were observed, they behaved similarly to *L. viridis* in living in and around bushy vegetation. For instance, near Cistiernas they were present on open banks and other areas with dense shrubs into which they retreated when disturbed. However, *L. lepida* occurs more widely and may be encountered in more open habitats where it forages on the ground and takes refuge in holes, rock crevices or the interstices of dry-stone walls. It also occasionally climbs high in trees.

Algyroides marchi

This *Algyroides* is known only from the Sierra de Cazorla, Sierra de Segura and Sierra de Agua in south-eastern Spain, where it is found from about 1000 m to 1500 m.

In the Sierra de Cazorla, I found this species near Piedra de Aguamula. Here it was always close to streams in generally moist situations and commonest in wooded gullies where, in May, water was exposed only as small pools between often mossy boulders and occasional tumbled, fallen tree trunks. The dominant trees were *Quercus pubescens* and various pines. *Algyroides marchi* climbed on the boulders, especially near pools, and often ran along the fallen tree trunks as well. It also occurred on the sloping forest floor at the stream edges, on stones and leaf litter and among bushy vegetation. When disturbed, refuge was taken in holes between rocks, under the bark of old tree trunks and in crevices in their wood. Apart from in these generally shady habitats, *A. marchi* was seen more rarely on low boulders in small meadows by streams and among rocks in the actual stream beds where there was not much surface water.

Klemmer (1960) also saw *A. marchi* in pine forest in situations very similar to those described above and Valverde (1958) and Eikhorst, Eikhorst, Nettmann & Rykena (1979) report them from stony stream beds in forested country. Palacios *et al.* (1974), in a wider survey, are in agreement with other sources about the general habitat requirements of the species, but indicate that it occurs in a wide range of woodland types, being commonest in very humid ravines with *Quercus pubescens* as the dominant tree species. Again, they emphasize its association with stream beds and rocky, shady habitats and mention that it also occurs on the stumps of felled pines. In drier situations within its range, *A. marchi* is replaced by *Podarcis hispanica* as the common small climbing lacertid.

Psammodromus algirus

Iberian Peninsula up to about 1400 m; also adjoining Mediterranean France and north-west Africa.

This species, which is very abundant in many areas, is typically an inhabitant of quite dry bushy situations. It was encountered in open and degraded woodland, both deciduous and coniferous, with a well-developed understorey of shrubs, and also occurred in lower maquis habitats. Lizards were usually seen in and around bushes and shrubs that were usually over 0.5 m high, often considerably so. They included *Quercus coccifera* and *Q. ilex,* gorse *(Ulex), Pistacea lentiscus,* heather *(Erica), Arbutus unedo, Genista scorpio,* rosemary *(Rosmaria officinalis)* and *Cistus* spp. Around Alicante *P. algirus* also inhabits hedges of prickly pear *(Opuntia),* a habitat noted for this species in Tunisia (Mosauer, 1934). It frequently hunts in the deep litter of fallen leaves and twigs at the base of such bushes and may climb in them to a height of 1.5 m or more. Camouflage is good in such situations and the lizard can move swiftly even in very dense and spiny shrubs, which it enters more frequently and readily than other European bush-associated lacertids, such as members of *Lacerta* part I. Animals may bask on sand, earth or rock surfaces some distance from vegetation, and young individuals spend more time in such habitats. Observations by Mellado Camacho (1980) on this species are similar.

Psammodromus hispanicus

Iberian Peninsula and adjoining areas of Mediterranean France.

A small lacertid that is strictly ground-dwelling in dry places, being encountered in flat areas and on hillsides. In central Spain and southern Portugal it is found on sandy or stony surfaces with a garigue type of vegetation, consisting of small, dense, bushy plants, often widely separated, that are frequently twiggy or spiny and normally do not exceed about 0.3 m in height. In southern Portugal, plants present included *Thymus* spp., *Coridothymus capitatus, Genista* spp., *Lavandula stoechas* and dwarfed specimens of *Cistus* spp., *Pistacea lentiscus, Quercus coccifera* and *Chamaerops humilis. P. hispanicus* was often seen basking in the open spaces between such shrublets, but retreated into them when disturbed, pushing its way deeply into the interstices at their bases. On the Mediterranean coast at Alicante, this lizard occurred in similar habitats but was also seen in more open areas, such as fields and gravelly plains with very sparse vegetation. Here it often ran rapidly for long distances when pursued. Small dense shrubs were again used as refuges but the lizard hid under stones as well. Other lizards like *Lacerta lepida* and *Acanthodactylus erythrurus* may occur in the same environments as *P. hispanicus* but are much larger and take bigger prey (Mellado *et al,* 1975; Busack & Jaksić, 1982).

Acanthodactylus erythrurus

Widespread in the Iberian peninsula except the northern parts; related populations occur in north-west Africa.

In central Spain, *Acanthodactylus erythrurus* behaves similarly to populations from the south-west of the country reported by Mellado *et al.* (1975). It is a strictly terrestrial species usually found on sandy ground and in more open habitats than the similarly sized *Psammodromus algirus.* It may occur at some distance from vegetation, although most animals were seen within a metre of a bush or small shrub. However, while *A. erythrurus* may hunt under these if they are relatively open at the base, it does not usually enter very dense vegetation as *Psammodromus algirus* does. When disturbed, it often flees into short burrows. Busack (1976) and Busack & Jaksić (1982) also discuss aspects of its ecology.

The features differentiating microhabitats

The microhabitat features in which European lacertids differ can be divided into two main classes: structural and climatic. Structural features include such factors as whether the microhabitat is flat or raised, whether its surfaces are more or less continuous or broken, the nature of the substrate-rock, stones, earth, vegetation etc., whether plant cover is present or at least close by, and the kind of refuges used. These are responsible for the species differences discernible in the data constituting Appendix 1. The structural microhabitat parameters summarized there show a tendency to correlate with each other. In western Yugoslavia, for instance, species that climb high have elevated scores for occurring on rock or its functional equivalents and for using crevices as refuges. In contrast, forms that climb relatively little have low scores for both these features. Such a relationship is not unexpected in as much as all climbing lizards in western Yugoslavia make considerable use of natural rock surfaces and their analogues, such as dry-stone walls. Such structures are well supplied with narrow openings that can be used as refuges. The same trend is apparent in Greece, although the use of crevices by *Podarcis peloponnesiaca* and *P. milensis* is low in relation to their scores for height above ground when first seen and occurrence on rock. Instead they frequently flee into vegetation, but this does not appear to be due to a lack of crevices in their habitat. Spain exhibits a similar correlation, but in the north-west *L. monticola* shows an unexpectedly low crevice score that appears to be due to the nature of the rocks on which it lives at the one locality examined. Here they are a conglomerate with occasional surface hollows but few real crevices.

Climatic features include the humidity, temperature and shadiness of the micro-habitat. In fact these three parameters are often inter-related. Environments which are moist or shaded, or both, are typically relatively cool as well, and shaded ones also tend to retain humidity. Difference in humidity between microhabitats can be recognized either directly by obvious variations in water content or indirectly by the kind of vegetation present. Species from generally similar structural niches can be arranged in a series on the basis of the relative humidity of their

TABLE II

Relative humidity of microhabitat, altitudinal range and general distribution of lacertids with similar structural niches in different parts of Europe. For each area, species are arranged in order of decreasing humidity of microhabitat: brackets join forms known to be syntopic. Information on altitude comes from various sources, including Castroviejo, Castroviejo & Salvador (1970), *Elvira & Vigal (1982), Radovanović (1951) and Werner (1938)*

	Approximate altitudinal Range (m)	Main distribution	Maximum latitude north (°)
Species common in well-vegetated habitats			
North-west Spain			
Lacerta vivípara	**150- 2500**	**N. and central Europe and climatically similar areas**	**70 +**
Lacerta viridis	**0- 1800**	**Central Europe and climatically similar areas**	**50**
Lacerta schreiberi	**0- 1270**	**W. and central Iberia: areas affected by Atlantic**	**43**
Lacerta lepida	**0- 1000**	**Drier areas of Iberia etc.**	**46**
West Yugoslavia			
Lacerta vivípara	**-3000**	**N. and central Europe and climatically similar areas**	**70 +**
Lacerta agilis	**400- -2000**	**N. and central Europe and climatically similar areas**	**61**
Lacerta viridis	**200- 1000**	**Central Europe and climatically similar areas**	**50**
Lacerta trilineata	**0- 200**	**Mediterranean regions of Balkans**	**46**
Species common in rocky and stony habitats			
North-west Spain			
Lacerta monticola	**(0)650 -1700**	**Mountains of N., W. and central Iberia**	**43.5**
Podarcis muralis	**0- 1500**	**Central Europe and climatically similar areas**	**51**
Podarcis bocagei	**0- 1230**	**W. Iberia: areas affected by Atlantic**	**43.5**
Podarcis hispanica	**0- 1400**	**Iberia and Mediterranean France**	**44**
North-west Yugoslavia			
Lacerta horvathi	**600- 1200**	**Mountains of north-western Yugoslavia**	**46.5**
Podarcis muralis	**0- 1200**	**Central Europe and climatically similar areas**	**51**
Podarcis melisellensis	**0- 800**	**East Adriatic littoral**	**45.5**
Podarcis sicula	**0- 100**	**Italy, north-east Adriatic coast etc.**	**47**
South-west Yugoslavia			
Lacerta mosorensis	**600- 1500 +**	**Mountains of south-west Yugoslavia**	**43.5**
Podarcis muralis	**200- 1300**	**Central Europe and climatically similar areas**	**51**
Lacerta oxycephala	**0- 1500 +**	**South-west Yugoslavia**	**44**
Podarcis melisellensis	**0- 1000**	**East Adriatic littoral**	**45.5**
Podarcis sicula	**0- 100**	**Italy, north-east Adriatic coast etc.**	**47**
Greece-Peloponnese			
Podarcis muralis	**1200- 2000**	**Central Europe and climatically similar areas**	**51**
Podarcis erhardii	**1000- 1400**	**Southern Balkan Peninsula and Aegean Islands**	**42.5**
Lacerta graeca	**0- 1500**	**Peloponnese**	**38.3**
Podarcis peloponnesiaca	**0- 1200**	**Peloponnese**	**38.3**

microhabitats where they occur at the same locality. This has been done in Table II for a number of assemblages of *Podarcis* and *Lacerta* from various areas. It will be clear from this that the relative humidity of microhabitats occupied usually correlates with broader distributional differences. Thus a species that occupies comparatively moist microhabitats typically has a more elevated altitudinal range in the area concerned and a cooler and wetter total geographical distribution. In widespread forms the total range also often extends further north. These broader correlations suggest that forms occupying the more humid microhabitats at a particular locality are also likely to be tolerant of cooler conditions, shorter summers, lower insolation and higher rainfall than the species they occur with. Such species may actually need a humid microhabitat to survive, or at least to compete successfully with other species. Casual observation of captive animals suggests that *Lacerta mosorensis* and *Podarcis muralis* are more rapidly affected by desiccation than, respectively, *L. oxycephala* and *P. melisellensis* which are found in drier micro-habitats. Semi-shaded habitats are typical of *Algyroides* species and in most forms these habitats are also moist. On Milos, the gecko *Cyrtodactylus kotschyi* occupies shadier positions than the resident small lacertid, *Podarcis milensis.*

European lacertids show niche complementarity (Schoener, 1974). That is, forms similar in structural microhabitat tend to differ in climatic requirements and vice versa. For instance, *Lacerta* group I species occupy very similar structural environments but sympatric forms differ in the humidity of the microhabitats they occupy. Again, at Gacko there are three pairs of species each with a different range of structural environment. In each pair, one species often occupies a more humid microhabitat than the other. Thus, there are two rock-dwellers, *L. oxycephala* and *L. mosorensis,* two species strictly confined to the ground and low vegetation, *L. agilis* and *L. vivipara,* and two species from intermediate habitats, *P. melisellensis* and *P. muralis;* in each pair the second species occurs in more humid conditions.

Correlations between taxonomic groups and microhabitats

It is apparent that there is considerable correlation between the systematic group to which a species is assigned and the kind of microhabitats it occupies. This relationship is discussed more fully below and, where possible, extended to include members of particular groups not previously discussed here.

Lacerta part I, green lizards

The five species already discussed were all observed to be frequently associated with quite dense, bushy vegetation. This is especially true of *Lacerta viridis. L. schreiberi* and *L. trilineata* which are often found in and around bramble patches, although other bushy plants are also occupied. Foraging takes place in the vicinity of such vegetation in which the lizards climb and frequently take refuge. *L. agilis* is at first sight rather different, often living in open areas of herbaceous vegetation and in heather and not climbing so high as the other species sometimes do. However, it too may occur about small bushes and the structural nature of its other habitats is frequently rather similar, consisting largely of matrices of stalks or twigs. *L. lepida* is usually more catholic than the other species and may occur in fairly open places but it too is often encountered around bushy vegetation. The remaining two species in the group are *L. strigata* of the Caucasus which is generally similar to other green lizards in its ecology (Bischoff, 1970) and *L. princeps* of south-east Turkey, north Iraq and western Iran. In Turkey the latter is associated with scrubby vegetation (Eiselt, 1968) in particular with bushes of *Quercus brandti* (Rykena, Nettmann & Bings, 1977).

Green lizards occur in a wide range of microclimates. Young animals may inhabit rather different environments from adults (see p. 753), but again these tend to involve quite dense vegetation.

***Lacerta** part II—archaeolacertas*

All five species observed are typically associated with rock surfaces and climb on them extensively. Most use crevices as their most frequent refuges. Archaeolacertas usually occupy quite humid microhabitats, typically moister than those of syntopic *Podarcis.* However, *Lacerta oxycephala* also occurs in rather drier environments than the other species. Where they have been adequately checked, body temperatures of active archaeolacertas are lower than those of *Podarcis* species at the same localities (p. 777).

A similar association with rock habitats is reported for other species that were assigned to the subgenus *Archaeolacerta* when this used to be recognized. These include *L. bedriagae* of Corsica and Sardinia (Lambert, 1967; Schneider, 1971), *L. danfordi* of Turkey (Wettstein-Westersheimb, 1967) and the *L. saxicola* complex in the Caucasus (Darevskii, 1967). This trend is also present in other *Lacerta* part II species that are morphologically similar to archaeolacertas, like *L. perspicillata* in north-west Africa (Doumergue, 1901), *L. cappadocica* of east Turkey and north Iraq (Bird, 1936; Reed & Marx, 1959) and *L. cyanura* of Oman (Arnold, 1972).

***Lacerta** part II—zootocas*

Lacerta vivipara is a ground-dweller, usually in quite humid situations with herbaceous vegetation in which it often takes refuge. Other species originally assigned to *Zootoca* are also typically ground-dwelling, often in rather moist places: *L. praticola* of south-east Europe and the Caucasus (Lantz & Cyrén, 1947; Fuhn & Vancea, 1961; Street, 1979); *L. derjugini* of the Caucasus (Lantz & Cyrén, 1947; Bischoff, 1974).

***Podarcis,** wall lizards*

The members of this genus cover a very wide range of structural microhabitats. *P. hispanica* is frequently like archaeolacertas in climbing on rock faces and their functional equivalents and in using crevices extensively as refuges. In contrast, *P. taurica* is a strict ground-dweller that flees into vegetation and holes in the ground. Other species are intermediate between these extremes. *P. muralis* may resemble *P. hispanica* ecologically in some areas and *P. melisellensis* approaches *P. taurica* in its general life mode, but the remaining species often make use of a relatively broad section of their structural environment, climbing to a marked extent but also often hunting on the ground. In many areas of mainland Europe and on large islands like Corsica and Sardinia and Sicily the microhabitat occupied by a particular *Podarcis* species is often apparently restricted by the presence of other kinds of small to medium-sized lacertid, but in other places, especially the smaller Mediterranean islands, a single *Podarcis* is the only species in this size range present and may have a very broad structural niche, as *P. milensis* does on Milos.

Podarcis covers a similar, albeit somewhat smaller, total range of structural niches to *Lacerta* part II (when both archaeolacertas and zootocas are considered). However, as already noted, microhabitats tend to be less humid and body temperatures may be rather higher. This difference is reflected in total distributions. *Lacerta* part II is widespread in north and central Europe, where it is represented by a single species, but restricted in the south to a few small enclaves that are typically montane and moist. *Podarcis*, on the other hand, has a continuous range through the Mediterranean region with a single species extending into parts of central Europe. It seems likely that *Podarcis* has expanded at the expense of *Lacerta* part II (Arnold, 1973, 1981).

Algyroides

The three species observed in the field are often associated with woodland and woodland-edge situations, although this is not so apparent in *A. nigropunctatus* in the north of its range. In environments that have not been radically disturbed by man, they are frequently encountered among forest detritus such as fallen trunks, branches, brushwood and litter. All of them bask but are often found close to shade and in places where insolation is restricted. It is also possible that the body temperature of active animals is relatively low (p. 751). *A. marchi* and *A. moreoticus* seem to favour humid places, although this trend is less marked in *A. nigropunctatus.* The fourth member of the genus, *A. fitzingeri* of Corsica and Sardinia, has not been directly assessed but remarks by Gene (1838) and Southoff (1914) suggest it may sometimes be associated with woodland habitats, taking refuge under bark and occurring on the lower boles of large trees. Schneider (1972, 1981) records it from maquis situations and more open grassy places and notes that it usually occurs near water.

Psammodromus

Both European *Psammodromus* species occur in Mediterranean plant communities with dense, tough, sometimes spiny shrubs. *P. algirus* and, in many areas, *P. hispanicus* hunt in and around these, although they may also forage and bask in more open habitats, especially the latter form. *P. hispanicus* occupies low, garigue-type vegetation and more open ground, instead of the higher shrubs in woodland and maquis habitats favoured by the large *P. algirus. P. blanci* of Algeria, which is very like *P. hispanicus,* occurs in similar environments to this species (Doumergue, 1901) and the same is probably true of *P. microdactylus* in Morocco.

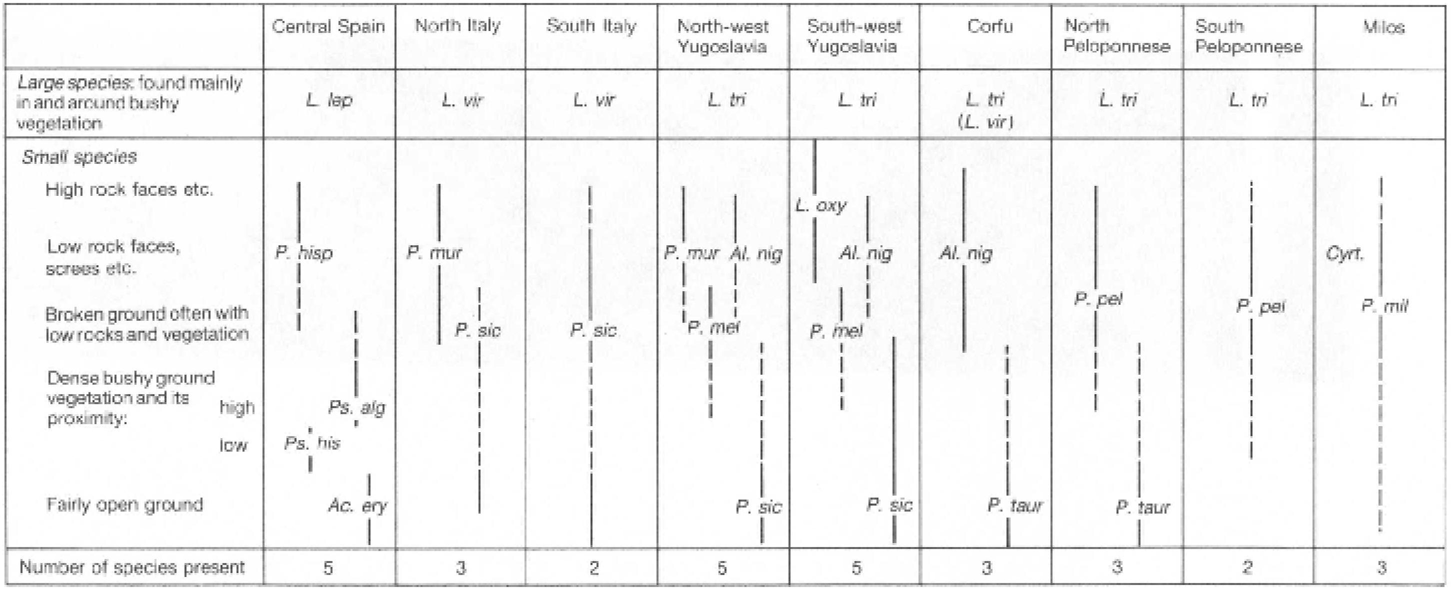
Acanthodactylus

Acanthodactylus erythrurus is typical of its genus (Arnold, 1983) in being ground-dwelling, usually in open sandy places where it forages around vegetation but does not usually enter very dense shrubs and often takes refuge in burrows.

Structure of lacertid communities in different parts of southern Europe

Europe has three southern peninsulas: Iberia, Italy and the Balkan Peninsula. All cover similar ranges of latitude and extend southwards to around 36 °N or 37 °N. They each include regions with typical Mediterranean climate and vegetation and possess often elevated areas bordering these which have greater resemblance in weather and plant cover to central Europe. In spite of these similarities, the peninsulas have very different lacertid faunas, both in size and composition. Iberia has 12 species, Italy only three and the Balkan Peninsula 18. If attention is limited to the western parts of the latter area, three forms with very restricted distributions in the east are excluded (namely *Lacerta praticola, Eremias arguta* and *Ophisops elegans),* reducing the number present to 15. Few species occur in more than one of the three areas and nearly all that do are widely distributed in central Europe, so that they have continuous ranges north of the peninsulas.

FIG. 1. Simplified representation of the structural microhabitats of lacertids at various Mediterranean localities in Europe. Solid lines: habitats where species frequently occurs; broken lines: habitats where species occasionally occurs. Species listed (abbreviations used are bold): ***Ac**anthodactylus **ery**thrurus, **Al**gyroides*



***nig**ropunctatus, **Cyrt**odactylus kotschyi, **L**acerta **lep**ida, **L. oxy**cephala, **L. tri**lineata, **L. vir**idis, **P**odarcis **hisp**anica, **P. mel**isellensis, **P. mil**ensis, **P. mur**alis. **P. pel**oponnesiaca, **P. sic**ula, **P. taur**ica, **Ps**ammodromus **alg**irus, **Ps. his**panicus.*

These are *Podarcis muralis, Lacerta vivipara, L. agilis* and *L. viridis*. The only other shared species is *Podarcis sicula* which is widespread in Italy and also extends on to the north-western coast of the Balkan Peninsula. Considerable variation also exists in the main groups present. In Italy there are only *Podarcis* and *Lacerta* part I; the Balkan Peninsula has in addition *Lacerta* part II (both archaeolacertas and zootocas) and *Algyroides;* while in Iberia all these occur, together with *Psammodromus* and *Acanthodactylus.*

The ways the range of structural habitats present in the three areas is filled are also different. Figure 1 gives a simplified summary of what lacertids are present at various localities in the Mediterranean regions and their approximate structural niches. The distribution of large lizards mainly living in bushy places is quite uniform. They are all members of *Lacerta* part I and a single species is present at nearly all localities. No such regularity exists among the smaller species. In all three peninsulas, they tend to be distributed along a spatial niche continuum ranging from high rock faces to relatively open ground, but the number of species present at a locality varies from one to four, with corresponding variation in niche breadth. Even where the number is the same, the species may divide the available habitat differently. For instance, among the two-species situations, North Italy has a habitual climber and a relatively more terrestrial species which nevertheless climbs to a significant extent. In the northern Peloponnese, the terrestrial form scarcely climbs at all and this is also true of Corfu where, however, the climbing species is distinctive in preferring at least partly shaded habitats. Iberia is singular in having a specialized, open sandy ground species, *Acanthodactylus erythrurus,* and two species of *Psammodromus* which are both associated with dense bushy ground vegetation. Elsewhere, *Podarcis* occurs in these environments but they do not seem to be filled so efficiently or so intensively. Thus, while *P. sicula* hunts on the ground in western Yugoslavia, it also climbs to a significant extent, as does *P. milensis* on Milos, and *P. taurica,* although strictly ground-dwelling, enters dense vegetation more than *Acanthodactylus* but less than the similarly sized *Psammodromus algirus. P. melisellensis, P. peloponnesiaca, P. sicula* and sometimes the young of *Lacerta* part I also occur at times in the sorts of habitat occupied by *Psammodromus* but they do not seem to exploit them to the same degree. These species do not exist at such high densities as members of that genus in the harsh dense shrubs that they favour, nor do they seem to spend so much time in them. Indeed some habitats in Greece that look very similar to those occupied by *Psammodromus* in Iberia are often largely devoid of lizards.

When the more mesic areas adjacent to the Mediterranean region are considered, a similar situation is found. Again there is substantial variation in the number of species present, in the way the niche continuum is divided among these and in apparent niche breadth (see Fig. 2).

The great variation between the climatically similar south European peninsulas is at first sight surprising, especially as they are quite close geographically and the majority of their inhabitants are fairly near relatives, all belonging to one section of the Lacertidae. It contrasts strongly with what Fuentes (1976) found in the Mediterranean areas of California and Chile. The lizard faunas of these two regions are widely separated geographically and phylogenetically, yet community structure and species number are similar, having apparently converged over a long period.

The situation in southern Europe may arise from a combination of its recent climatic history and its dissected topography. During the Pleistocene period, there were cold interludes during which the peninsulas would have been completely isolated from each other, so far as reptile migration was concerned. At such times, areas with Mediterranean and near-Mediterranean climate and vegetation would have been severely curtailed. Because of the surrounding sea, the degree to which the ranges of species could shift southwards in response to these changes is likely

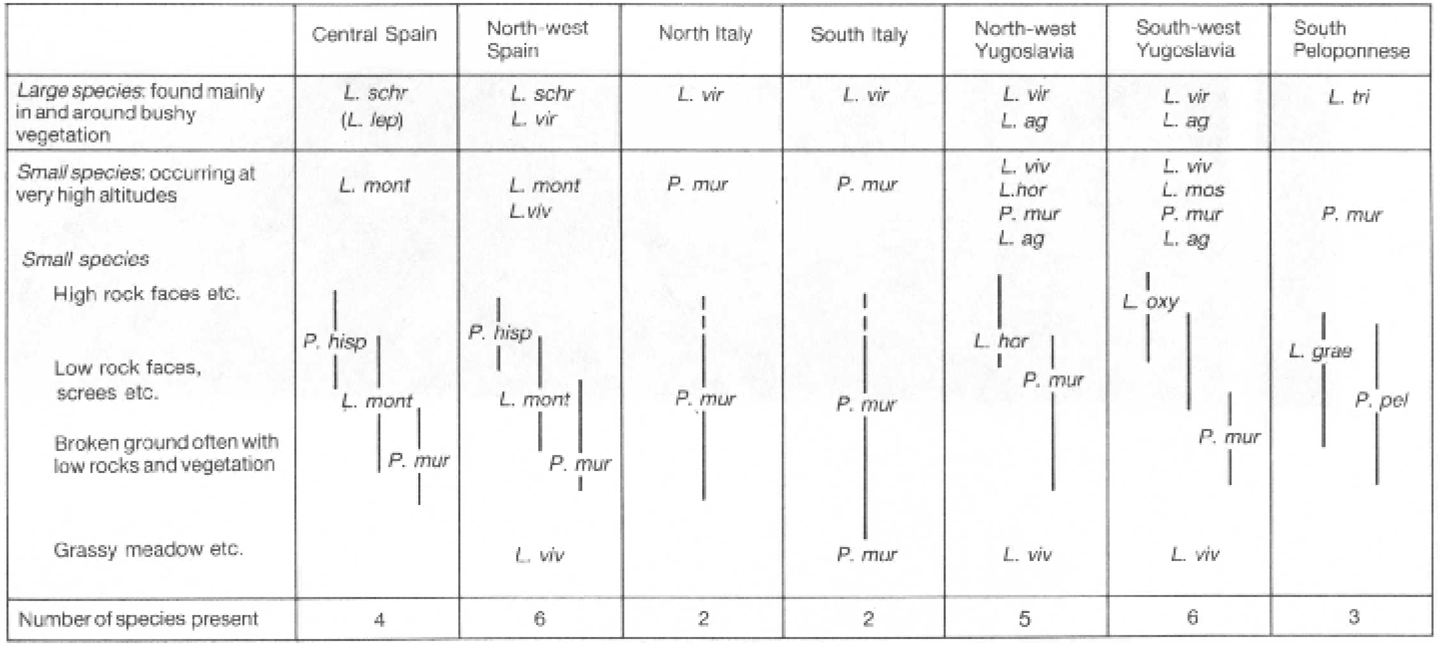


FIG. 2. Simplified representation of the structural microhabitats of lacertids in various mesic montane areas adjacent to the Mediterranean region of Europe. Solid lines: habitats where species frequently occurs; broken lines: habitats where species occasionally occurs. Species listed (abbreviations used are **bold**): ***Lacerta agilis*, *L. graeca*, *L. horvathi*, *L. lepida*, *L. monticola*, *L. mosorensis*, *L. oxycephala*, *L. schreiberi*, *L. trilineata*, *L. viridis*, *L. vivipara*, *Podarcis hispanica*, *P. muralis*, *P. peloponnesiaca*.**

to have been limited and substantial extinction may have occurred. This would apply especially to Italy which has a smaller total area and a more restricted Mediterranean region than the other peninsulas.

With climatic amelioration, it might be thought areas with few species, like Italy, would have been able to receive many from neighbouring peninsulas but, as we have seen, even at the present time their faunas are still largely isolated. The distributions of many species do not extend far enough north to enable them to spread outside their own peninsulas and, even when they do so, geological and climatic barriers may prevent them reaching another one. Thus *Podarcis hispanica*, two *Psammodromus* species and *Lacerta lepida* all extend beyond the Iberian peninsula into southern France but have not invaded peninsular Italy. *Lacerta lepida* actually reaches the Ligurian coast but does not cross the cooler surrounding mountains into the rest of Italy.

Possible habitat displacement

There is evidence that the microhabitat occupied by a particular lizard species may be restricted by the presence of other forms. Heatwole (1977) discusses a number of cases among iguanids in which species have broader spatial niches where they exist alone than in areas where a second form is present in part of this ecological space. In such instances, experimental removal of the second species may allow the spatial niche of the first to expand to the dimensions usual in areas where it is solitary, indicating that it was actually displaced from part of its possible niche by the other form.

Although no such experimental evidence is available for European lacertids, there are a number of cases where regional differences in niche breadth, correlated with the presence or absence of particular syntopic species, suggest that habitat displacement may occur (see Table III). Thus, in Yugoslavia, *Podarcis muralis* climbs higher at Opatija, where it is the only widespread scansorial form, than at localities where archaeolacertas coexist with it and occupy the higher parts of rock faces and similar structures. This species shows a similar upward shift in structural niche at localities in north-western Spain where both *Podarcis hispanica* and *Lacerta monticola* are absent. Finally, the mainly ground-dwelling *Podarcis melisellensis* climbs higher at two localities in Yugoslavia where *P. muralis* is not present than at two places where these lizards occur together.

Summary

Communities of lacertid lizards were examined in western Yugoslavia, Greece and Iberia in order to determine patterns of resource partition, see whether different taxonomic groups have characteristic niche types, and compare community structure in different areas.

1. No marked interspecific differences in times of activity during the day, such as occur in some other communities (see e.g. Arnold, 1984), were encountered.

2. Incidental observations suggest that there are no gross interspecific differences in hunting method, all forms being substantially active foragers.

3. Diet consists primarily of arthropods and differences in prey type probably reflect relative availability in different environments. However, adults of large species take significantly bigger prey than small ones.

4. By far the most important factor differentiating species is spatial separation, syntopic forms usually occupying different microhabitats. Differences were detected in both physical structure

TABLE III

Possible cases of habitat displacement

1. In western Yugoslavia, *Podarcis muralis* climbs higher in the absence of archaeolaccrtas. Difference between Opatija and Soča—*P* = <0.01; between Opatija and other localities -*P* = <0.001.

Locality	Opatija	Soča	Gacko	Boračko Jezero
Archaeolacertas present		+	+	+
% of *P. muralis* seen more than 0-3 m from ground	78	42	18	16
Total number of *P. muralis* observed	81	66	213	145

2. In south-western Yugoslavia, *Podarcis melisellensis* climbs higher in the absence of *P. muralis.* Differences between localities with *P. muralis* (Gacko and Boracko Jezero) and those without (Korcula and Mostar)-P= <0.05.

Locality	Korčula	Mostar	Gacko	Boračko Jezero
Podarcis muralis present	—	—	+	+
% of *P. melisellensis* seen more than 005 m off ground	41	40	22	18
Total number of *P. melisellensis* observed	32	72	92	90

3. In north-western Spain, *P. muralis* climbs higher in the absence of other scansorial species. Differences between Cangas de Onis and other localities —*P* =< 0.001.

Locality	Cangas de Onis	Puerto de Panderrueda	Aleja
Other climbing species present	—	*L. montícola*	*P. hispanica*
% of *P. muralis* seen more than 0 3 m from ground	76	13	24
Total number of *P. muralis* observed	93	88	50

and microclimate of these microhabitats, the parameters examined including height from the ground at first sighting, substrate type, kind of refuge used and humidity of microhabitat.

5. Forms occupying similar structural niches at a particular locality tend to have different microclimate requirements and vice versa.

6. Microclimate differences between species often correlate with climatic differences in their total distributions.

7. The main systematic groups of lacertids in southern Europe have characteristic ranges of microhabitats: green lizards *(Lacerta* part I) are largely associated with bushy vegetation and, within *Lacerta* part II, archaeolacertas are climbers in rocky places that are relatively moist while zootocas occur in usually humid herbaceous situations. The wall lizards *(Podarcis)* cover a wide spectrum of habitats and range from climbers on rock surfaces to strictly terrestrial forms. They occupy drier environments than *Lacerta* part II species. The members of *Algyroides* were probably mainly associated with often moist, partly shaded, woodland habitats, although some of them now exist in degraded environments as well. *Psammodromus* species live in and around dense vegetation in maquis and garigue habitats, while *Acanthodactylus erythrurus* is a specialized ground-dweller in relatively open, often sandy places.

8. The three peninsulas of southern Europe have very different lacertid faunas with few species in common. Numbers of species and taxonomic groups present are very variable, as is community structure. This may result from the comparative isolation of the three peninsulas from each other and from their recent climatic history.

9. There is some evidence of habitat displacement where certain small lacertids coexist.

10. All the species for which temperature data were gathered appear to be shuttling heliotherms with small ranges of voluntary body temperatures. There may, however, be specific differences in preferred temperature.

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Appendix 1. Data on spatial microhabitats

Observations of height above ground when first seen, substrate, refuge and distance fled to cover are summarized in Tables IV VII. These parameters were recorded in the way described on p. 742-743. For each of them, and for every species, the number of individuals observed is given (*n*) and the proportion in each category expressed as a percentage. For substrate and refuge, the percentages do not always add up to 100 because the category 'other' is not included in the Tables. Instances where only a few individuals of a species were observed at a particular locality are omitted.

Appendix 2. Localities where observations were made

The localities where observations were made are listed in Tables VIII-X together with their geographical co-ordinates, altitude, dates when visited and the species of lizard encountered at each.

The area of western Yugoslavia where investigations were conducted consists largely of Mesozoic karst limestone. The region is mountainous with the ranges running parallel to the coast and can be divided into two main biogeographic parts: the Adriatic seaboard and the western Dinaric mountains. The former includes all the offshore islands but is relatively narrow on the mainland, except where it penetrates the Neretva Valley to beyond Mostar. The Adriatic seaboard is characterized by a Mediterranean climate with a wet, not especially cold winter and a hot, sunny summer with little rainfall. Vegetation probably originally included much oak and pine forest, but this has been destroyed in most regions, often being replaced by a sparse maquis, and some areas, such as the seaward slope of the Velebit mountains, are now virtually barren. The western Dinaric montane area begins quite abruptly behind the coast and rises in places to over 2000 m. Winters are cold and summers generally cool. Rainfall is heavier than on the coast and more evenly distributed through the year, exceeding 2500 mm in some places. At high altitudes insolation only exceeds 50% of the possible maximum for two months of the year, whereas it exceeds 75% for four months on the coast. Vegetation is generally like that of central Europe. There are considerable forests of oak, ash, hornbeam and pine, and at higher altitudes beech is common.

All Greek localities visited are in the Mediterranean climatic region. They include Corfu, a large, well-wooded island close to the mainland of north-west Greece, and localities in the Peloponnese. Of these, the Stymphalia area is relatively high with a quite cold winter. The island of Milos in the Aegean Sea is of volcanic origin and has a more obviously maritime climate than the other Greek localities.

The north-west Spanish localities are all in the Cantabrian region. Cangas de Onis lies just to the north of the mountains and, like Puerto de Panderrueda near their watershed, is influenced by the nearby Atlantic Ocean, having a high rainfall and a cool summer. Aleje, on the southern slope of the mountains, is hotter and drier at this time of year. Similar variation occurs in central Spain, summer being cool and wet at Puerto de Cotos in the Sierra de Guadarrama but hot and dry in the lower parts of the nearby Lozoya Valley and at Aranjuez. This is also true of the two south-eastern localities, although here rainfall is generally higher.

Appendix 3. Cloacal temperatures of active lizards

Where possible, cloacal temperatures of lacertids were taken in the way described on p. 743. The summary of observations given in Table XI is confined to temperatures obtained when the weather was fine and

TABLE IV

Data on spatial microhabitats: Yugoslavia

Locality	Species	*n*	Height above ground when first seen (m) 0-005	005-0-3	0-3-0-6	0-6-0-9	0-9-1-2	1-2 +	Mean	*n*	Rock	Stone	Earth	Vegeta-tion	Timber	Refuge *n*	Crevice	Hole	Vegeta-tion
Mount Učka	*L. horvathi*	81	2	1	10	4	35	48	1.91	81	96	4	—	—	—	81	94	6	—
Soča Valley	*L. horvathi*	20	—	—	20	10	15	55	2.08	24	83	17	—	—	—	18	100	—	—
	P. muralis	66	26	32	18	6	9	9	0.57	66	68	17	12	3	—	46	39	48	13
Plitvice	*L. horvathi*	9	11		11	11	11	56	1.42	9	89	11		—		9	78	22	
	P. muralis	20	35	30	5	15	15	—	0.52	20	65	20	10	5	—	20	45	40	15
Jablanica	*P. muralis*	55	38	38	4	7	4	9	0.37	60	35	23	33	8	—	48	15	10	75
	P. melisellensis	22	73	27	—	—	—	—	0.06	17	—	59	24	18	—	18	—	17	83
	L. viridis	18	66	11	11	—	6	6	0.47	20	10	—	20	70	—	18	—	—	100
Boračko																			
Jezero	*L. oxycephala*	347	20	32	18	7	8	14	0.70	332	77	13	8	—	2	284	42	52	2
	P. muralis	155	60	24	6	4	4	2	0.26	146	38	34	20	5	3	166	18	55	22
	P. melisellensis	90	82	16	—	2	—	—	0.06	92	9	15	48	28	—	75	—	24	76
	L. viridis	78	63	20	9	8	—	—	0.17	79	25	25	6	14	55	65	—	6	94
Nevesinje	*L. oxycephala*	14	14	14	21	7	29	14	0.84	14	86	14		—		12	75	17	8
	L. mosorensis	8		25	25	37	13	—	0.71	8	100	—	—	—	—	8	63	37	—
Gacko	*L. oxycephala*	213	13	19	18	13	15	26	1.26	211	91	7	2			195	91	8	1
	L. mosorensis	131	18	35	25	11	7	4	0.55	127	85	5	2	6	2	130	77	20	3
	P. muralis	197	48	34	9	6	3	—	0.37	182	44	24	24	6	2	192	20	56	24
	P. melisellensis	92	78	19	3	—	—	—	0.08	66	11	13	35	41	—	74	4	16	80
	L. vivipara	17	94	6	—	—	—	—	0.05	17	—	12	12	76	—	17	—	18	82
	L. agilis	98	95	5	—	—	-	—	0.05	95	—	2	6	92	-	96	-	35	65
Opatija	*P. muralis*	71	11	11	27	14	25	11	0.94	64	78	8	6	8	—	66	50	35	15
	P. melisellensis	26	84	12	4	—	—	—	0.05	24	8	54	29	8	—	25	8	36	56
	A. nigropunctatus	26	12	23	15	23	23	4	1.05	60	75	—	8	16	—	22	55	32	13
Krk	*P. melisellensis*	67	51	38	12	—	—	—	0.16	66	29	44	24	3		62	14	14	72
	P. sicula	46	59	26	9	6	—	—	0.16	36	8	12	50	22	—	36	15	54	31
	A. nigropunctatus	60	6	18	33	12	14	16	0.78	60	73	7	3	12	4	53	66	20	14
Trogir	*P. melisellensis*	30	57	33	10	—	—	—	0.13	30	27	36	20	17	—	—	—	—	—
	P. sicula	142	47	16	11	7	11	8	0.44	142	30	7	29	30	4	142	27	22	51
Korčula	*L. oxycephala*	74	5	11	14	23	34	14	1.13	71	90	10				71	90	7	
	P. melisellensis	32	59	31	10	—	—	—	0.13	35	34	29	11	26	—	27	11	70	19
Ston	*L. oxycephala*	20	—	—	10	5	—	85	3.14	20	90	—	—	—	10	17	94	6	—
Mostar	*L. oxycephala*	133	11	10	18	11	16	34	1.55	125	68	22	6	4		133	71	27	2
	P. melisellensis	72	60	34	6	—	—	—	0.12	65	20	32	33	15	—	65	11	32	57
	L. trilineata	14	—	—	43	14	29	14	0.99	14	43	—	14	43	—	13	31	31	38

TABLE V

Data on spatial microhabitats: Greece

Locality	Species	Height above ground when first seen (m)								Substrate						Refuge			
		n	0–0·05	0·05–0·3	0·3–0·6	0·6–0·9	0·9–1·2	1·2+	Mean	*n*	Rock	Stone	Earth	Vegetation	Timber	*n*	Crevice	Hole	Vegetation
Corfu	*P. taurica*	39	77	13	—	—	—	—	0·05	40	10	8	54	28	—	35	—	40	60
	A. nigropunctatus	166	9	30	37	7	8	9	0·73	172	46	3	6	3	40	113	18	21	61
Sparti	*L. graeca*	87	41	38	10	9	2	—	0·24	88	59	19	11	4	7	86	58	26	10
	P. peloponnesiaca	44	41	32	27	—	—	—	0·26	44	48	20	23	5	5	41	7	49	44
	L. trilineata	53	83	11	6	—	—	—	0·10	53	4	4	22	68	2	39	—	—	100
	A. moreoticus	57	77	18	5	—	—	—	0·06	21	—	10	—	90	—	21	—	—	100
Stymphalia	*L. graeca*	40	5	13	35	—	20	27	0·74	38	89	11	—	—	—	34	85	15	—
	P. peloponnesiaca	246	22	22	25	7	12	12	0·63	232	68	16	15	1	—	189	29	32	39
	P. taurica	58	66	34	—	—	—	—	0·06	62	11	26	47	16	—	58	—	72	28
	L. trilineata	32	50	25	19	6	—	—	0·26	32	12	19	25	44	—	28	7	7	86
	A. moreoticus	57	77	18	5	—	—	—	0·06	57	77	18	5	—	—	54	—	11	89
Milos	*P. milensis*	399	48	31	12	5	2	2	0·24	412	41	16	32	11	—	337	15	26	59
	*C. kotschyi**	124	2	39	37	12	10	—	0·54	136	89	11	—	—	—	95	72	22	6
	L. trilineata	16	56	6	19	19	—	—	0·30	16	56	6	19	19	—	16	—	63	37

* — Gekkonidae

TABLE VI

Data on spatial microhabitats: Iberia

Locality	Species	Height above ground when first seen (m) n	0-005	005-0-3	0-3-0-6	0-6-0-9	0-9-1-2	[-2 +	Mean	n	Rock	Stone	Earth	Vegeta-tion	Timber	Refuge n	Crevice	Hole	Vegeta-tion
Cangas de Onis	*P. muralis*	93	15	9	19	6	31	19	0.89	92	55	10	6	29	—	64	39	10	51
	L. vivípara	18	15	2	1	—	—	—	0.07	18	16	6	11	67	—	18	11	39	50
Puerto de															—				
Panderrueda	*L. montícola*	101	21	28	15	9	9	18	0.63	102	80	7	8	1	—	74	30	36	34
	P. muralis	89	60	27	11	—	2	—	0.15	86	14	27	42	17	—	76	10	28	62
	L. vivípara	12	75	25	—	—	—	—	0.08	12	—	17	17	66	—				
	L. viridis	21	71	19	10	—	—	—	0.12	21	5	14	33	48	—	21	—	14	86
Aleje	*P. muralis*	50	46	26	8	16	—		0.28	50	30	48	14	8	—	38	37	42	21
	P. hispánica	83	25	7	33	2	1 1	22	0.79	83	70	25	5	—	—	71	66	6	28
	L. lepida	20	55	20	20	5		—	0.23	20	20	25	40	15	—	20	20	20	60

TABLE VII

Distances fled to refuge by lizards

Species	Locality	*n*	Mean distance fled to refuge (m)	% of animals fleeing more than 1 m
Yugoslavia				
Lacerta horvathi	Učka	50	0.45	12
	Soča	8	0.93	25
Lacerta oxycephala	Boračko Jezero	95	0.55	11
	Gacko	51	0.58	8
	Korčula	9	0.57	0
Lacerta mosorensis	Gacko	49	0.54	8
Podarcis melisellensis	Boračko Jezero	23	0.90	35
	Gacko	22	1.03	19
	Krk	14	0.59	14
Podarcis muralis	Soča	17	0.40	27
	Boračko Jezero	51	0.80	18
	Gacko	85	0.58	14
	Opatija	11	0.81	
Podarcis sicula	Trogir	138	1.81	36
Lacerta agilis	Gacko	32	1.62	50
Lacerta viridis	Boračko Jezero	21	0.97	33
Algyroides nigropunctatus	Opatija	8	0.42	0
	Krk	17	0.27	0
Greece				
Lacerta graeca	Peloponnese	40	0.50	8
Podarcis peloponnesiaca	Peloponnese	69	0.9	17
Podarcis táurica	Corfú	13	0.5	15
Podarcis milensis	Milos	237	0.9	11
Lacerta trilineata	Peloponnese	21	1.8	48
Algyroides moreoticus	Peloponnese	33	0.1	0
Algyroides nigropunctatus	Corfú	49	0.7	0
Cyrtodactylus kotschyi	Milos	83	0.5	0
Spain				
Podarcis hispanica	Aleje	30	0.6	20
Podarcis muralis	Aleje	24	0.9	4

See p. 743 for details. Distances run to the nearest refuge are usually short and in most cases less than 1 m. In general, differences seem to be related to the kind of habitat occupied. Lizards living in rocky or stony places with many holes and crevices flee only short distances, while species like *Podarcis sicula* at Trogir and *Lacerta agilis* at Gacko which forage in open areas often travel much further. Such differences can often be detected in a single species. For instance, the average distance fled by *P. milensis* was 0-59 m (n = 237), but for animals living in a grassy area with few refuges it was 0-94 m (*n* = 40). The very short distances covered by *Cyrtodactylus kotschyi* probably arise because it emerges in the day largely for thermal reasons rather than to hunt and consequently does not need to move far from its refuges. *Algyroides moreoticus* and *A. nigropunctatus* also appear to stop especially close to cover but it is not obvious why this should be.

warm with direct sunshine and many lizards were active. Data collected in poor weather, early or late in the day, and when most visible animals were only basking have been excluded. The Table consequently gives some idea of the temperatures voluntarily adopted by the lizards concerned since, in the climatic conditions specified, it would be possible for them to have body temperatures substantially higher or lower than the majority of those actually observed, either by increasing their exposure to the sun or by selecting heavily shaded microhabitats. At other times, for instance when the sun was largely obscured, lizards being ectotherms might not be capable of reaching the temperatures they preferred. Table XII shows temperatures of wild European lacertids recorded by other workers.

It will be seen that the range of means for the 22 samples and 14 lacertid species in Table XI is quite small: 32.5-36.3 °C, a spread of only 3.8 °C. Published observations listed in Table XII only increase the range to 4.5 °C. When samples in Table XI of 12 or more are considered, over 70% of individuals in each had temperatures within 2 °C of the mean. Relatively high body temperatures that are usually well above the ambient, the small spread of means and the close conformity of most observations to those means confirms the initial impression gained when watching European lacertids: that they are indeed shuttling heliotherms adjusting their temperatures closely by behavioural means. This is done by selection of sites within the environment that suit the immediate temperature requirements of the lizards and, when basking, by adopting postures that increase or decrease net heat intake from insolation. In cool conditions, lizards of all the species encountered rotate the ribs forwards, so that the lateral spread of the body and consequently its total dorsal area is increased. The body may also be angled, so that the maximum surface is presented as perpendicularly as possible to the rays of the sun.

Temperatures reported by different investigators may differ because techniques for taking temperatures and criteria of activity used are not identical (see, for example, Avery, 1982). However, apart from such artifacts, a number of other kinds of variation exist.

1. Between observations made on the same population on different days during a comparatively short period.

2. Between observations made on populations from different localities of the same species at similar times of year. For instance, between *Podarcis muralis* from Boracko Jezero, Yugoslavia, and from Puerto de Panderrueda, Spain, during August.

3. Between observations of the same species at different times of year. Thus *Podarcis pityusensis, Lacerta vivipara* and *L. agilis* appear to have lower temperatures in spring than in summer (Sveegaard & Hansen, 1976). Similarly, the cloacal temperatures of *Podarcis muralis* and *P. sicula* from northern Italy in March are lower than those of the same species in Yugoslavia during August (see Tables XI and XII).

4. Between different species in the same general environment. For example, the low temperatures of *Lacerta oxycephala* and *L. mosorensis* compared with *Podarcis muralis* and *P. melisellensis* at the same localities and of *L. monticola* compared with syntopic *P. muralis.*

Such variations could result either from environmental differences or from differences in preferred temperature of the lizards concerned, or a combination of the two. It would be necessary to assess preferred temperatures under controlled conditions to be sure which factors were the more important. In 1, environmental change is very probably the main cause, for differences in mean cloacal temperatures often correlate with changed weather conditions. The same may apply in the case of 2 (thus Puerto de Panderrueda is generally cooler than Boracko Jezero in summer) and possibly 3 as well. Even in the instance of different species monitored over the same period in the same general environment (4), microclimatic factors may be significant. Avery (1978) considers the possibility that *P. muralis* may have lower temperatures than ***P. sicula*** because it forages more in shady places. A similar argument could be applied to the examples given in 4 above, for all three *Lacerta* species involved climb more than the syntopic *Podarcis* and spend more time on vertical surfaces which tend to be less sunny than horizontal ones. *L. monticola* also tends to occur in places more exposed to wind. However, microclimate may not be the principal factor, at least in the Yugoslav lizards. The temperatures of *L. oxycephala* at Boracko Jezero were taken in very warm, sunny conditions when many animals were spending a substantial portion of their time in the shade, suggesting that higher voluntary temperatures could easily have been achieved. Conversely, this species and *L. mosorensis* appear to have very similar mean body temperatures even though they occupy climatically different microhabitats, which suggests they must differ in thermoregulatory behaviour. In the case of *P. muralis* and *P. sicula,* Patzl (1932) notes that the muscle of the former species loses excitability at a lower

TABLE VIII

Western Yugoslavia: localities visited and species observed

Locality		Altitude (m)	Dates visited	Species observed										
				Lacerta horvathi	*Lacerta oxycephala*	*Lacerta mosorensis*	*Podarcis muralis*	*Podarcis melisellensis*	*Podarcis sicula*	*Lacerta vivipara*	*Lacerta agilis*	*Lacerta viridis*	*Lacerta trilineata*	*Algyroides nigropunctatus*
Dinaric localities														
Mount Učka	45°17′ N 14°12′ E	1100–1300	26–28.VII.67, 30. VII–1.VIII.70	+							+			
Soča Valley	46°15′ N 13°35′ E	700	11–14.VIII.71	+			+			+		+		
Plitvice	44°54′ N 15°36′ E	600	29.VIII.65	+			+							
Jablanica	43°39′ N 17°45′ E	270	21.VIII.67, 15.VIII.70				+	+				+		+
Boračko Jezero	43°53′ N 18°02′ E	400	20–23.VIII.67, 12–14.VIII.70		+		+	+				+		
Nevesinje	43°16′ N 18°07′ E	1000	30.VII.67		+	+								
Gacko	43°10′ N 18°32′ E	960	31.VII–9.VIII.67, 6–10, 16–18.VIII.70		+	+	+	+		+	+	+		
Mediterranean localities														
Opatija	45°20′ N 14°19′ E	0–1000	25–28.VII.67, 30.VII–1.VIII.70				+	+					+	+
Krk	45°02′ N 14°35′ E	0–50	2–3.VIII.70					+	+				+	+
Zadar	44°07′ N 15°15′ E	0	4.VIII.70						+				+	
Trogir	43°32′ N 16°15′ E	0	24.VIII.67, 21–22.VIII.70					+	+				+	
Korčula	42°58′ N 17°08′ E	0–50	14–15.VIII.67		+			+					+	
Ston	42°50′ N 17°42′ E	0–30	16.VIII.67, 5.VIII.70		+			+					+	
Mostar	43°21′ N 17°49′ E	50	17–19.VIII.67, 19–20.VIII.70		+			+					+	
Dubrovnik	42°39′ N 18°07′ E	0–30	10.VII.67		+			+	+				+	
Kotor	42°25′ N 18°46′ E	0–50	11–12.VIII.67		+								+	

TABLE IX

Greece: localities visited and species observed

Locality		Altitude (m)	Dates visited	Species observed										
				Lacerta graeca	*Podarcis peloponnesiaca*	*Podarcis erhardii*	*Podarcis muralis*	*Podarcis taurica*	*Podarcis milensis*	*Lacerta viridis*	*Lacerta trilineata*	*Algyroides nigropunctatus*	*Algyroides moreoticus*	*Cyrtodactylus kotschyi*
Corfu														
North Corfu	39°45′ N 19°40′ E	0–200	17–30.V.80					+		+	+	+		
Peloponnese														
Sparti	37°05′ N 22°27′ E	200–400	2–7.IV.72	+	+		(+)				+		+	+
Stymphalia	37°53′ N 22°28′ E		8–12, 16.IV.72	+	+	+	(+)	+			+		+	+
Mycenae	37°45′ N 22°44′ E	15.IV.72			+			+			+			
Milos Island														
Adamas	36°41′ N 24°15′ E	0–100	28–31.III.72						+		+			+

TABLE X

Iberia: localities visited and species observed

Locality		Altitude (m)	Dates visited	Species observed										
				Lacerta monticola	*Podarcis muralis*	*Podarcis hispanica*	*Lacerta vivipara*	*Lacerta viridis*	*Lacerta schreiberi*	*Lacerta lepida*	*Algyroides marchi*	*Psammodromus algirus*	*Psammodromus hispanicus*	*Acanthodactylus erythrurus*
North-west Spain														
Cangas de Onis	43°21′ N 5°07′ W		15, 21.VIII.72		+		+							
Puerto de Panderrueda	43°06′ N 5°01′ W	1450	18–20.VIII.72	+	+		+	+						
Aleje	45°51′ N 5°07′ W		16–17.VIII.72		+	+			+	+				
Central Spain														
Puerto de Cotos	40°50′ N 3°57′ W	1750–1900	11–13.VI.65	+	+	+			+					
Lozoya Valley	40°57′ N 3°47′ W	1100–1700	6–10.VI.65		+	+			+	+		+	+	
Aranjuez	40°02′ N 3°36′ W	490	30.V–4.VI.65			+				+		+	+	+
South-east Spain														
Cazorla	37°55′ N 3°00′ W	885	21–22.V.65			+				+		+		
Piedra de Aguamula	38°04′ N 2°49′ W	1200	23–28.V.65			+				+	+	+		
Portugal														
Sagres	37°00′ N 8°56′ W	0–30	9–14.IV.84							+			+	
Monchique	37°19′ N 8°31′ W	200	15–17.IV.84							+			+	

TABLE

Cloacal temperatures of lizards active in sunny conditions

Species	Locality	Date	*n*	Mean (°C)	% of individuals within 2° C of mean	Range (°C)
Western Yugoslavia						
Lacerta horvathi	Soča Valley	11-14 August	3	34.5		
Lacerta oxycephala	Boračko Jezero	12-14 August	80	34.1	75	29-37.5
	Gacko	6-17 August	10	34.6	80	32-37.5
Lacerta mosorensis	Gacko	6-17 August	42	34.0	83	29.5-38
Podarcis muralis	Soča Valley	11-14 August	6	36.0		33-37
	Boračko Jezero	12-14 August	51	35.9	90	32-39
	Gacko	6-17 August	18	35.6	83	30-38
Podarcis melisellensis	Boračko Jezero	12-14 August	22	35.8	91	33.5-38.5
	Krk	1-3 August	5	35.2		
Podarcis sicula	Trogir	24-25 August	23	36.3	72	31-40
Lacerta viridis	Boračko Jezero	12-14 August	6	33.9		30-35
Corfú						
Algyroides nigropunctatus	Northern Corfú	18-30 May	12	32.3	75	27.5-34
Peloponnese						
Lacerta graeca	Sparti	4-5 April	11	32.5		29.5-36
	Stymphalia	9-11 April	4	33.4		
Podarcis peloponnesiaca	Sparti	4-5 April	8	33.4		31.5-36.5
	Stymphalia	9-11 April	40	35.3	74	32.5-38.5
Podarcis taurica	Stymphalia	9-11 April	6	34.2		33.5-35.2
Milos						
Podarcis milensis	Adamas	28-31 March	49	34.6	90	31.5-37
Cyrtodactylus kotschyi	Adamas	28-31 March	16	29.5	63	24-34.6
Spain						
Lacerta montícola	Puerto de Panderrueda	18-20 August	26	33.0	77	28.5-36.5
Podarcis muralis	Puerto de Panderrueda	18-20 August	43	34.4	79	28.5-38
	Aleje	16-17 August	5	36.1		
Podarcis hispanica	Aleje	16-17 August	7	35.8		34.5-38

temperature than that of the latter, indicating that there may well be a difference in optimal temperature between the two. On Milos, the marked temperature difference between *Podarcis milensis* and *Cyrtodactylus kotschyi* occurring on the same walls also suggests a difference in inherent preference.

Appendix 4. Diet of European lacertids

Published observations on the diets of European lacertids indicate that the majority feed predominantly on arthropods. See, for instance, Avery (1966, *Lacerta vivípara),* Busack & Jaksic (1982, *Acanthodactylus erythrurus),* Darevskii (1967, *Lacerta saxícola* group), Domínguez, Elvira & Vigal (1982, *Lacerta montícola),* Kabisch & Engelmann (1969, *Podarcis muralis;* 1970, *Podarcis taurica),* Marcuzzi (1959, 1968, *Podarcis muralis, Podarcis sicula),* Martinez-Rica (1977, *Lacerta montícola),* Mellado *et al* (1975, *Podarcis hispanica, Lacerta lepida, Psammodromus hispanicus, P. algirus),* Pérez Mellado (1982, *Lacerta montícola),* Sadek (1981, *Lacerta dugesii).* Examination of small samples (*n* = 10-34) of stomach contents or faeces of the species discussed in this paper supports this conclusion. Oligochaetes, gastropods and plant matter may also be taken in some cases, although their contribution to total intake is usually small. However, *Podarcis*

TABLE XII

Cloacal temperatures of wild European lacertid lizards reported in the literature

Species	Locality	Date	*n*	Mean (°C)	Range (°C)	Reference
Lacerta montícola	Avila, 1600-2000 m	27 August	14	31.8	25.8-34.5	Busack(1978)
	Pyrenees		31	33.8		Martinez Rica (1977)
	Portugal etc.		30	33.5		Pérez Mellado (1982)
Podarcis bocagei	W. Spain (Systema Central)		78	32.3	25-39	Pérez Mellado (1983)
Podarcis hispanica	Avila, 1400 m	21 August	16	34.0	25.4-38.4	Busack(1978)
	Systema Central, Spain		157	35.1	26.5-41.0	Pérez Mellado (1983)
Podarcis muralis	Florence	March		33.6	29.9-33.6	Avery (1978)
Podarcis pityusensis	Ibiza, on rocks	12-19 August	51	33.3	28.5-41.5	Pérez Mellado & Salvador (1981)
	Ibiza, on ground	12-19 August	51	35.4	28.5-44.5	
	Ibiza	May		32.6		Sveegaard & Hansen (1976)
	Ibiza	August		35.8		
Podarcis sicula	Florence	March		35.2	33.9-36.6	Avery (1978)
Lacerta vivipara	Denmark	May		32.3		Sveegaard & Hansen (1976)
	Denmark	July-August		34.0		
Lacerta agilis	Denmark	May		33.7		Sveegaard & Hansen (1976)
	Denmark	July		35.8		
Psammodromus algirus	Madrid, 1300 m; Avila, 1600m	August	27	35.4	30.4-40.6	Busack(1978)

TABLE XIII

Proportion of strongly flying insects (Diptera, Lepidoptera and Hymenoptera) in the diets of seven lacertid species from south-western Yugoslavia

	Locality	Number of lizards	Source	Number of prey items	Percentage of strongly flying insects
Lacerta horvathi	Mount Učka	34	Faeces	150	38
Lacerta mosorensis	Gacko	18	Faeces	122	44
	Gacko	12	Stomachs	57	28
Lacerta oxycephala	Boračko Jezero	30	Stomachs	125	33
	Hercegovina	22	Stomachs	58	40
Podarcis muralis	Boračko Jezero	15	Stomachs	110	14
Podarcis melisellensis	Hercegovina	21	Stomachs	99	12
Lacerta agilis	Gacko	31	Faeces	149	6
Lacerta viridis	Boračko Jezero	16	Stomachs	60	23

TABLE XIV

Prey length in five lacertid species from south-western Yugoslavia

	Locality	Number of prey items	Percentage of prey in each size class (mm) 0-10.0	10.1-20.0	20.1 +	Mean prey size (mm)
Lacerta oxycephala	Boračko Jezero	78	**74**	26		7-4
Lacerta mosorensis	Gacko	47	**77**	23		7-8
Podarcis muralis	Boračko Jezero	128	**80**	16	4	6-5
Podarcis melisellensis	Hercegovina	95	**71**	29		7-9
Lacerta viridis	Boračko Jezero	60	33	**57**	10	12-8

Bold figures indicate the most abundant size class *sicula* living on agricultural land in Yugoslavia frequently eat the pulp of such fruits as tomato and fig, and *Acanthodactylus erythrurus* from southern Spain take significant amounts of the flowers and leaves of *Halimium halimifolium* (Busack & Jaksic, 1982). Populations of lacertids on small islands also ingest more vegetable food than is usual elsewhere (Eisentraut, 1949; Sadek, 1981) and the big species of *Gallotia* in the western Canary Islands are largely herbivorous (Krefft, 1950).

There is considerable interspecific variation in which prey taxa are eaten and in what proportion, but this may often reflect differences in availability between particular habitats. For instance, as Lundelius (1957) showed for two species of *Sceloporus* (Iguanidae), climbing lacertids take significantly more strongly flying insects than do relatively terrestrial ones (see Table XIII). This trend is also apparent in the data of Mellado *et al.* (1975) for a lizard community in southern Spain.

As in other lizard groups (Schoener, 1967, 1968), big lacertids tend to take larger prey items than smaller ones. This applies both intraspecifically (see, for instance, Sadek, 1981 for *Lacerta dugesii)* and between species. In south-west Yugoslavia, *Lacerta viridis* eats substantially longer invertebrates than four smaller syntopic species (see Table XIV). Similarly, *Lacerta lepida* ingests prey that is on average longer than that of other lacertids in the same community in southern Spain, especially *Psammodromus hispanicus* which occurs in the same habitats (Mellado *et al.,* 1975).