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ANNOUNCEMENTS

OPINIONS FROM THE INTERNATIONAL COMMISSION ON ZOO-LOGICAL NOMENCLATURE.

(i) *Synapturanus* Carvalho, 1954 (Amphibia, Anura): *Synapturanus mirandaribeiroi* Nelson & Lescure, 1975 designated as the type species

(ii) *Liasis* Gray, 1842 (Reptilia, Serpentes): *Liasis mackloti* Duméril & Bibron, 1844 designated as the type species

FRONT COVER: European smooth snake *Coronella austriaca*

REVIEW:

STATUS AND CONSERVATION OF TORTOISES IN GREECE

RONALD E. WILLEMSEN[1] AND ADRIAN HAILEY[2]*

[1] *MonteCassinostraat 35, 7002 ER Doetinchem. Netherlands;* [2] *Department of Zoology, University of Thessaloniki, Greece 540 06.*

* *Present address: Department of Physiology. The Medical College of St. Bartholomew's Hospital. Charterhouse Square, London EC1M 6BQ. UK.*

ABSTRACT

The present status of tortoises (*Testudo* spp.) in Greece is described, based on studies from 1975 to 1986. The survey includes 79 single species populations at 42 sites throughout the country, at which about 9,600 individuals have been marked and released. Tortoises were still common in Greece in 1986. However, 28 per cent of populations are immediately threatened by catastrophic decline, and 39 per cent have declined in the recent past or are liable to long-term decline. The remaining 33 per cent are not apparently threatened at present. There was no significant difference in these proportions between dense and sparse populations, or between the three species. Most of the highly threatened sites were near the coast; many of the sites under no apparent threat were in mountainous areas. Threats included habitat loss to cultivation or building, fires started for pasture improvement or by accident, herbicide spraying, agricultural machinery, and direct predation of tortoises or nests by rats near rubbish dumps. Most (61 per cent) of the threats to sites were associated with agriculture.

Testudo hermanni is the most widespread and common species, found in woods, scrub, heath, grassland, and farmland. There was substantial variation of body size between populations, which was apparently at least partly genetic; a range of sites would need to be protected to preserve this variability. Populations in the south are in danger, but overall this species is not threatened in Greece. *Testudo marginata* is widespread in Greece, where it is endemic; its typical habitat is thorny scrub. Only one out of 23 populations of this species was found at high density; we recommend protection for this site (at Gytheion). *Testudo marginata* is the largest and latest-maturing species, with the lowest proportion of juveniles in the total marked sample. It is particularly vulnerable to slow decline from occasional loss of adults, such as those killed by machinery while foraging in cultivated areas, or casual collection. *Testudo graeca* is restricted to north eastern Greece, where it usually occupies coastal habitats which are most likely to be disturbed. It is the most threatened species in Greece, but is widely distributed elsewhere.

The reptile faunas associated with tortoises are described, to evaluate the 'biogenetic reserve' concept for reptiles in Greece. Three quarters of the 33 native species of lizards and snakes in mainland Greece have been found with tortoises. In addition, tortoises may be found in very disturbed areas, and they may be affected by factors which affect them but not other reptiles. The presence of tortoises therefore cannot be used as an indication of a particular reptile community, or of an area of high reptile species richness. The herpetofauna of the Alyki coastal heathland is described in detail. We suggest that Alyki merits protection as an unexploited coastal heathland containing almost all the reptile species likely to be found in that habitat. Larger reserves may contain more species, but will not be as effective in conservation if they simply contain the most common species inhabiting many different habitats.

INTRODUCTION

The conservation of tortoises must be based on knowledge of their ecology which can only come from detailed work concentrated at a few sites. Conservation also requires, however, information on the current status of populations and the problems they face (e.g. Honegger, 1982; Andren, Nilson and Podloucky, 1986; Dolmen, 1986). Lambert (1969, 1979, 1981) provided this information for *Testudo graeca* in North Africa, where the major problem was (until 1984) large scale collection for the pet trade. Felix (1983) and Cheylan (1984) have discussed the status of *T. hermanni* in western Europe, where it is threatened by habitat loss.

The main object of this review is to summarise data about the current status of populations, resulting from our field studies of tortoise ecology in Greece. We do not discuss the techniques suitable for management of tortoise populations (see Devaux, Pouvreau and Stubbs, 1986). It should be noted that our field work was not designed as a conservation survey of Greek tortoises, but provides the most comprehensive data available at present.

Although studies of status and ecology are essential background to conservation, they will only be effective when applied within a rational strategy. Modern conservation theory and practice has moved away from protecting individual threatened species, towards

preserving areas of habitat and the species which live there. The idea for such 'biogenetic reserves' for reptiles and amphibians has been discussed by Corbett (1986). In this review we also consider other species of reptiles found at our sites, and evaluate one well-studied site, the Alyki heath, as a biogenetic reserve for reptiles. Four questions were used as a framework for this analysis:

1) Community. Does the presence of tortoises define a particular assemblage of reptile species?

2) Richness. Does the presence of tortoises define an area with many other species of reptiles?

3) Habitat. Does Alyki provide optimal habitat for a species, or dose the species occur in greater numbers in other natural habitats?

4) Disturbance. Which species are limited to natural habitats, and which may be found in altered or disturbed areas?

We do not analyse the many published works on the distribution of tortoises and other reptiles in Greece and its islands (e.g. the series of papers by Clark, 1967, 1969, 1970, 1972), unless these provide recent information on status, for three reasons. First, such reports are already being collated by full-time conservationists, for a projected atlas of chelonians throughout the Mediterranean area (D. Ballasina, personal communication). Further records of this type should be sent to the addresses in the Appendix. Second, records based on short visits may give an unreliable estimate of the status of populations (see the Discussion). Third, the sites of which we have first-hand experience give an even coverage of the whole of Greece, and are sufficiently numerous for statistical analysis.

It should be stressed that tortoises (and other reptiles) are protected in Greece by national and European Community regulations. They may only be collected under permit from the Ministry of Forestry, Athens.

METHODS

Observations at most sites in north-eastern Greece were made by A.H. between 1980 and 1986. Work at most sites in central and southern Greece was by R.W. on annual visits from 1975 to 1986. The sites were selected as areas having habitat suitable for tortoises; their location is shown in Fig. 1. Some of the sites were selected for marking studies (see Table 2), because of high population density, ease of access and ecological interest. Tortoises were marked in areas of a few tens of hectares, though at most sites the suitable habitat covered a much larger area. Other sites were visited for short periods, and few or no tortoises were marked. We had no preference for studying any particular species of tortoises.

Tortoises were marked by notching the marginal scutes with a file or hacksaw (the coding scheme differed between workers). The number of individuals recorded at marking sites is shown in Table 2; the
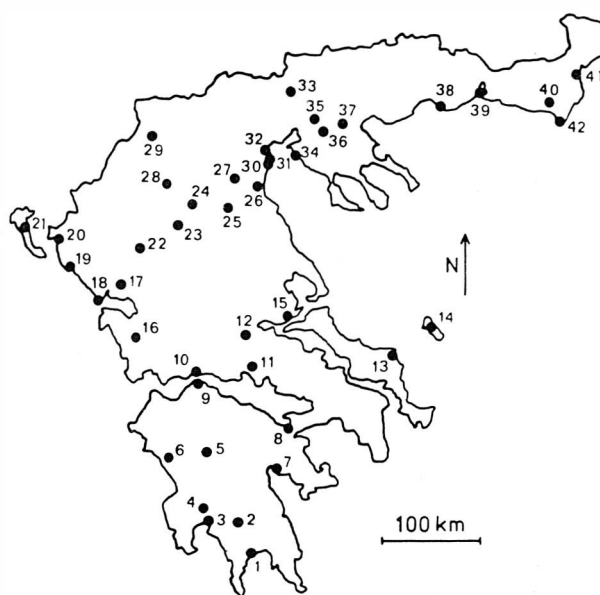

Fig. 1   Location of the study sites, numbered as in Table 1 and in the text.

number of these which were juveniles when first found is shown as an indication of population structure. Juveniles were defined as individuals which could not be sexed by external characters. The size at which tortoises could be sexed varied between the species, (smallest in *T. hermanni* and largest in *T. marginata*) and between populations of *T. hermanni* (because of variation in adult body size). Full details of population size and dynamics at the sites studied in detail will be given elsewhere.

Vegetation at most sites was described in general terms, not as a result of botanical surveys. The following natural types were recognised:

Coastal Heath. Very open vegetation of herbs, grasses and maritime plants on loose sand. Infrequent cover from *Tamarix* bushes and marram grass (*Ammophilla arenaria*), especially on dunes.

Dry Heath. A few bushes such as *Crataegus* (hawthorn), broom and brambles, and low shrubs (e.g. *Artemisia maritima, Ruscus aculeatus*), with sparse ground cover of grasses and herbs.

Grassland. Dense cover of grasses, height depending on grazing intensity. Asphodels (*Asphodelus microcarpus*) common in overgrazed areas.

Thorny scrub. Dense scrub about 2m high with little ground flora, the dominant species often holly oak. Access usually difficult except along goat tracks.

Woodland. Broadleafed or coniferous woods of various dominant species. Some small single-species woods were apparently plantations for timber or shade cover.

The other species of reptiles seen were noted, but no attempt was made to provide a complete survey at each site. Amphibians and terrapins are not discussed here, as their habitat requirements differ from those of tortoises. In the interests of standardization, the species are considered in the order used by Arnold, Burton and Ovenden (1978).

RESULTS

STATUS OF TORTOISES AT SPECIFIC SITES

The results of the survey take the form of a brief description of each site, its vegetation, tortoise populations, and conservation problems. Sites are numbered as in Fig. 1 and Tables 1 and 2, the name of the nearest village or town is shown, together with a code summarising the status of the tortoise populations present. These codes are:

Species (Hermanni, Marginata, Graeca),

Density (Dense, Sparse),

Status (0 = no apparent threat, 1 = past decline or long-term threat, 2 = immediately threatened).

	Site	*T. hermanni*	*T. marginata*	*T. graeca*	
1	Gytheion	S 1	D 1	—	RW
2	Sparta A	D 1	S 1	—	RW
2	Sparta B	—	S 0	—	RW
3	Kalamata A	D 2	S 1	—	RW
3	Kalamata B	—	S 0	—	RW
4	Arfai	S 2	S 2	—	RW
5	Langadia	D 0	—	—	RW
6	Olympia A	D 2	S 2	—	RW
6	Olympia B	S 1	S 1	—	RW
7	Nauplion	—	S 2	—	RW
8	Korinthos	—	S 0	—	RW
9	Rion	D 2	S 2	—	RW
10	Antirrion	S 2	S 2	—	RW
11	Delphi	—	S 0	—	RW
12	Bralos	S 1	S 1	—	RW
13	Kymi	S 1	—	—	RW
14	Skyros	—	S 0	—	RW
15	Pelasgia A	D 1	S 1	—	AH
15	Pelasgia B	—	S 0	—	AH
16	Fitiae	D 0	—	—	RW
17	Arta	D 1	—	—	RW
18	Preveza	S 2	—	—	RW
19	Parga	D 2	S 1	—	RW
20	Igoumenitsa	D 1	S 1	—	RW
21	Kerkyra	S 1	—	—	RW
22	Mesochoron	S 0	—	—	RW
23	Meteora A	D 1	S 1	—	RW
23	Meteora B	S 0	S 0	—	RW
24	Deskati A	D 0	—	—	RW
24	Deskati B	D 0	—	—	RW
25	Agios Dimitrios	D 0	S 0	—	RW
26	Litochoron	D 1	S 1	—	RW
27	Elassona	S 0	—	—	AH
28	Grevena	S 0	—	—	RW
29	Kastoria	D 0	—	—	RW
30	Korinos	S 2	—	—	AH
31	Alyki A	D 2	—	S 1	AH
31	Alyki B	D 2	—	—	AH
31	Alyki C	S 1	—	—	AH
32	Agathoupolis	S 1	—	—	AH
33	Kilkis	D 1	—	S 1	RW
34	Epanomi	D 0	—	D 0	AH
35	Kolhiko	S 0	—	S 0	AH
36	Langadiki	S 2	—	S 2	AH
37	Mikra Volvi	D 1	—	D 1	RW
38	Keramoti A	D 1	—	D 1	AH
38	Keramoti B	S 0	—	D 0	AH
39	Lagos A	D 2	—	D 2	AH
39	Lagos B	S 1	—	—	AH
40	Avas	S 0	—	S 0	AH
41	Souphli	—	—	S 2	AH
42	Evros	D 2	—	D 2	VG

TABLE 1: Summary of the density and status of *Testudo hermanni, T. marginata* and *T. graeca* populations at all sites. Population density coded as D (dense) or S (sparse). Status coded as 0 (no threat), 1 (long term decline) or 2 (immediately threatened). The author responsible for work at each site is also shown.

1 GYTHEION (HS1, MD1)

The vegetation was dense thorny scrub, with patches of grassland and dry heath which were sometimes grazed. This site was unique in that *T. marginata* was the dominant species, and was present at high density. Three *T. hermanni* were also found, all in a wet area near a freshwater canal. Several tortoises were found killed by farmers, but this would have a small effect on the population. A more serious loss was the clearance of large areas of scrub to make new olive groves, during which many tortoises were killed. However, the area used by tortoises was large, so that the site as a whole was not immediately threatened.

2 SPARTA A (HD1, MS1)

The plain of Sparta was mostly used for intensive citrus orchards, a habitat which is unsuitable for tortoises. However, a dense population of *T. hermanni* was found in an abandoned orchard near Sparta, together with two juvenile *T. marginata*. No tortoises were found in the surrounding citrus groves or dense scrub of *Sarcopoterium spinosa. Testudo hermanni* from the plain of Sparta are characterised by small body size. A high proportion of junveniles was found, despite the presence of many nests destroyed by predators. This population was found over a small area, and would be threatened if the area was reclaimed for cultivation, which seemed likely. However, it would also be threatened by further encroachment of the dense *Sarcopoterium* scrub.

2 SPARTA B (MSO)

The hills surrounding the plain of Sparta were covered with thorny scrub. A few *T. marginata* have been found at low density in these areas, which were not threatened.

3 KALAMATA A (HD2, MS1)

The site extended from sea level up the slopes of the Taygetas hills, which were terraced, mostly for olive groves, but with some vegetable plots. The scrub vegetation of the low terrace walls was important cover for tortoises. A rotation system was followed up to 1985, in which fields were left fallow for one year. Weeds in these areas provided food for tortoises, which was increased by irrigation in summer. The result was a flourishing population of *T. hermanni*, with many young adults and a very high proportion of juveniles. Most tortoises were found near the terrace walls, and only older animals used the open areas.

No signs of nest predation were seen in the cultivated area, but opened nests were seen in the scrub. Farm machinery killed several tortoises each year, and some were deliberately killed by farmers who believed them to be pests of vegetables, although crop damage must be negligible. In recent years farmers have increasingly sprayed the wall vegetation with the herbicides 2, 4 D and 2, 4, 5 T. Almost no tortoises were subsequently seen in these areas. Citrus trees were planted under the olive trees after 1985; this will cause the population to decline as citrus plantations are unsuitable for

	Site	T. hermanni		T. marginata		T. graeca	
1	Gytheion	3	(1)	227	(8)		
2	Sparta A	385	(48)	2	(2)		
3	Kalamata A	319	(107)	7			
4	Arfai	36	(3)	2			
5	Langadia	54	(1)				
6	Olympia A	879	(117)	7	(3)	1	
9	Rion	38	(2)	2			
10	Antirrion	26	(5)	6			
12	Bralos	30		4			
13	Kymi	24	(1)				
19	Parga	176	(5)	2			
20	Igoumenitsa	329	(44)	5	(2)		
23	Meteora A	1560	(228)	2			
24	Deskati A	181	(2)				
25	Agios Dimitrios	115	(5)	11	(3)		
26	Litochoron	98		9			
29	Kastoria	304	(24)				
30	Korinos	27	(1)				
31	Alyki A,B	3597	(678)			51	(22)
33	Kilkis	91	(3)			13	
34	Epanomi	50	(11)			143	(83)
37	Mikra Volvi	278	(1)			87	(2)
38	Keramoti A,B	92	(9)			152	(34)
39	Lagos A	88	(3)			97	(3)
	Total	8780	(1299)	286	(18)	544	(144)
	Per cent juveniles		14.8		6.3		26.5

TABLE 2: Details of work at sites where more than 10 tortoises were marked. The total number of each species marked at each site is shown (with number of juveniles), and the total for all sites. The percentage of juveniles differs significantly between the three species ($X^2 = 72$, 2 d.f., $P < 0.001$).

tortoises. Many parts of the site have also been lost to building in recent years.

The cultivated area was surrounded by dry heath and thorny scrub. Only *T. marginata* were found in this scrub, at lower density than the *T. hermanni* nearby in the cultivated area. There was a sharp distinction between the habitats occupied by the two species.

3 KALAMATA B (MS0)

The mountain slopes around Kalamata were covered in thorny scrub, in which only *T. marginata* was seen at low density. These populations were in no apparent danger.

4 ARFAI (HS2, MS2)

This was an area of grassland with hedges and olive groves, bordered to the east by thorny scrub-covered hills. The grassland was used intensively for agriculture, and the soil under the olive trees was rotavated regularly to clear weeds. The population density of tortoises was low, probably because of this disturbance; high mortality was suggested by many pieces of carapace. Local people indicated that tortoises were very much more common in the past, and blamed modern agricultural practices for the decline.

5 LANGADIA (HD0)

This was the highest site where we have studied tortoises, at 1100-1300 m, close to the altitudinal limit of *T. hermanni* in southern Greece. The vegetation was mainly coniferous wood (*Abies cephalonica*) and patches of grassland. The carapace of a very old female *T. marginata* was found, but local people did not know this species. Several female *T. hermanni* were found in sandy fields in June 1982, and the whole area was littered with pieces of eggshell in August; nest predation was apparently was apparently very high. This population suffered from a high degree of scute irregularities. The area was protected from hunting and there were no human settlements nearby, and the population was apparently not threatened.

6 OLYMPIA A (HD2, MS2)

The site was in a large area of open, park-like vegetation with olive groves, hedges, cypress and pine woods, and patches of thorny scrub. This was one of the first of our sites, and nearby 900 *T. hermanni* have been marked near the village of Flokas since 1975. *Testudo marginata* was much less common, and a single *T. graeca* was also found (Willemsen, 1987), probably moved there by man. Traditional agricultural methods prevailed during the first years of the study, when the tortoise density was about 30 ha⁻¹. Ground vegetation in the olive groves was cleared by scythe and then burnt, activities which caused few tortoise casualties.

Manual clearance of ground vegetation has been replaced by spraying with herbicides in recent years. Very large areas were sprayed with Grammoxone (paraquat) and atrazine in spring, so that many of the hills around Olympia became yellow and brown before summer. There was no obvious effect on tortoises,

although these have been seen eating recently sprayed plants and basking on dead vegetation. More seriously, areas of woody vegetation and *Asphodelus microcarpus* were sprayed with 2, 4 D and 2, 4, 5 T. These herbicides apparently affect tortoises directly, rather than indirectly through their food and shelter plants. Tortoises with swollen eyes and fluid discharge from the nose were commonly found in these areas. From 1980, the site was mapped into sectors to study the movements of tortoises; some of these sectors were sprayed, others not. The number of tortoises decreased rapidly in the sprayed sectors (Fig. 2), while remaining constant in unsprayed areas. The widespread use of herbicides also resulted in the start of serious soil erosion.
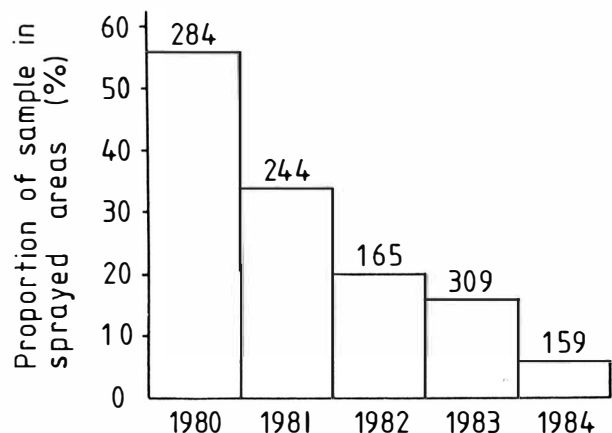

Fig. 2   The effect of spraying with 2, 4 D and 2, 4, 5 T on the relative number of tortoises in sprayed and unsprayed areas of the Olympia A site. Sample sizes shown. Spraying began in 1980, when about half of the tortoises found were in areas which were sprayed. The decline in subsequent years was due to mortality in sprayed areas, and was not caused by migration to unsprayed areas.

Physical disturbance was also a problem. Some hedges and trees were removed for firewood, and the remainder were burnt, killing many tortoises. The area has been increasingly used as a rubbish dump in recent years. The population of rats (*Rattus norvegicus*) increased greatly, and these were seen more frequently every year after 1978. Rats gnaw the forelegs of even adult tortoises to the bone, resulting in loss of limbs or death. These characteristic injuries have been seen at several sites, but nothing like on the scale at Olympia in recent years. This site became so disturbed that research was impossible, and was abandoned after 1984.

6 OLYMPIA B (HS1, MS1)

An area of open pine wood was also investigated near Olympia. This suffered from large forest fires in 1972, 1975 and 1981. Vegetation recovered quickly in burnt areas, but the pine wood was replaced by dense thorny scrub, which was apparently unsuitable for tortoises. A large area of scrub resulting from the fire of 1972 was examined in 1983, and no tortoises, or traces of them, were found. In contrast, five *T. hermanni* and three *T. marginata* were found in a small area of pine wood untouched by the fire.

7 NAUPLION (MS2)

The great plain of Argolis was intensively used for citrus orchards. Citrus trees give dense shade so that the ground flora is usually restricted, and many pesticides are used on this crop. Citrus orchards are therefore unsuitable for tortoises, and only two *T. marginata* were found; tortoises in the plain were scarce and threatened. The plain is surrounded by mountains with thorny scrub. This is typical habitat for *T. marginata*, but none have been found during several visits to an area near Nemea, although a few traces of tortoises were seen.

8 KORINTHOS (MS0)

This area was known years ago for a population of *T. marginata* (Klingelhofer, 1931). Stemmler (1957) could not find any tortoises during a visit in 1957, and suggested that they had been a victim of the pet trade. However, nine *T. marginata* were marked on the east slope of Acrocorinth in 1982. The area was protected, and the population was not threatened.

9 RION (HD2, MS2)

The vegetation was grassland and cultivated ground, with patches of thorny scrub. Tortoise density was apparently normal for this type of habitat. The area was under threat from agriculture and building. *T. hermanni* was limited to the small cultivated areas, and so was especially vulnerable.

10 ANTIRRION (HS2, MS2)

The vegetation was grassland with hedges intensively used by farmers, and patches of dry heath. Both *T. hermanni* and *T. marginata* were present at low density. Many tortoises were killed each year by mowing machines. This population appeared to be one of the most susceptible to increased agriculture.

11 DELPHI (MS0)

The Parnassos mountains contain large areas of thorny scrub. Six *T. marginata* have been seen, including one juvenile. Local people knew of only this species. Although population density was low, the area is important because of its large extent. The areas immediately around Delphi are well-protected as this is a national monument.

12 BRALOS (HS1, MS1)

The vegetation was a patchwork of open oak wood, grassland, cultivated fields and thorny scrub. Both *T. hermanni* and, less often, *T. marginata* have been found. Two visits to the area have both been at periods when tortoise activity was low at other sites, so that the population may be more dense than the numbers marked indicate. Local people reported that tortoises were much more common in the past, and that large forest fires during the civil war (1948) had reduced populations. There seemed to be no other threats to this population.

13 KYMI (HS1)

The habitat was olive groves and patches of pine woods, dry heath and abandoned fields. Only *T. hermanni* was found, at a rather low density for this type of habitat. No tortoises were found at other places on Euboea, including a variety of habitats, although a few traces were seen. The only danger to tortoises was apparently forest fires, which have occurred in recent years.

14 SKYROS (MS0)

Watson (1962) recorded *T. marginata* from this island, and five were marked at a site with dry heath and patches of pine wood. Several other traces of tortoises were seen, but the density was apparently low. However, local people recognise *T. marginata*, and know where they can be found. Skyros is a remote island with a small human population and little tourism, and the tortoises seemed in little danger.

15 PELASGIA A (HD1, MS1)

Testudo hermanni and *T. marginata* were found in an area close to National Highway 1, where there were orchards and fields just below a thorny scrub-covered hillside. It is likely that many tortoises in these cultivated areas were making foraging trips from the scrub. The orchards were rotavated to clear weeds, and some carapace bones were seen at the edges of these fields. Several dug-out nets were seen at the edge of the scrub.

15 PELASGIA B (MS0)

Two *T. marginata* were found in small overgrown olive groves among dense thorny scrub in a very rocky area near the village. Several dug out nests were also seen. Access was difficult to this area, and direct human disturbance was not likely.

16 FITIAE (HD0)

This was an area of olive groves and hedges, supporting a dense population of *T. hermanni* typical of this type of habitat. There was no apparent threat to this population.

17 ARTA (HD1)

Eight *T. hermanni* were marked in an area of hazel nut orchards, and traces of tortoises were common so that the density was not low. Farmers used many herbicides in this area, and although these had apparently not affected tortoises to date, they would be vulnerable to use of more toxic sprays.

18 PREVEZA (HS2)

This was an area of grassland and hedges used rather intensively by farmers. The habitat was apparently very suitable for tortoises. However, only a few tortoises were seen, although the site was sampled at a time (May 1982) when high activity was found at other sites. Tortoises were threatened by agricultural machinery.

19 PARGA (HD2, MS1)

The vegetation was olive groves and hedges, in which many *T. hermanni* were marked. Two *T. marginata* were found in the theory scrub surrounding the olive groves. Some areas of this scrub

were too dense to search for tortoises. Reynolds (1984) has also reported *T. marginata* around Parga. Farmers have destroyed hedges in recent years, resulting in the death of several tortoises and in loss of cover. Killing of tortoises for fun was more common here than elsewhere. The population of *T. hermanni* was vulnerable to cultivation.

20 IGOUMENITSA (HD1, MS1)

This was an area of grassland with rushes (*Juncus*) surrounded by olive groves and mountain slopes with thorny scrub. Both *T. hermanni* and, infrequently, *T. marginata* were found in the grassland, where population density was over 100 animals ha⁻¹. Population density was lower in the olive groves, and only a few *T. hermanni* were found in the thorny scrub. Hoogmoed (personal communication) reports finding *T. graeca* in an olive grove in this area. The presence of all three species of Greek tortoises would be unusual and requires further investigation; possibly the *T. graeca* are a result of translocation by man. The grassland was grazed by cattle, which may benefit tortoises by preventing encroachment by trees. This area is rather small, and so vulnerable to disturbance. About 25 per cent of the area was lost some years ago when a graveyard was constructed.

21 KERKYRA (HS1)

A few *T. hermanni* were seen in olive groves at three locations in 1976. There was a small threat from agricultural machinery. Durrell (1956) observed large numbers of tortoises in the late 1930s, but this island has since been subjected to considerable development for tourism.

22 MESOCHORON (HS0)

This was an area of deciduous woodland with large patches of grassland. Three *T. hermanni* were marked, and there seems to be a low population density. It was amazing to hear that a dealer had been active in this remote part of the central mountains, offering 50 drachmas for tortoises in 1984. Human activities were very limited, and the tortoises were not in danger.

23 METEORA A (HD1, MS1)

This site has been visited many times between 1976 and 1986. There were many habitats in the area: vineyards (some abandoned), grassland with hedges, and patches of thorny scrub and open oak wood. Agriculture has up to now been of traditional forms. Population density of *T. hermanni* was highest near human settlements, and was more than 100 ha⁻¹. Lower population density was found in thorny scrub. Most juveniles were found near settlements, where there were few dug-out nests. Fewer juveniles and more destroyed nests were found further away.

This is one of the few populations where there were predators of adult tortoises. A large colony of Egyptian vultures (*Neophron percnopterus*) live near Meteora. These birds are important predators of tortoises, which may be smashed by dropping them from height, or taken to the nest and eaten there (Obst

and Meusel, 1978). Tortoises may sometimes be left alive in unusual places, and have been found by climbers high up in the rocks. Vultures forage through an area more than 20 km from Meteora, but do not come near human settlements, so that tortoises will suffer less predation in these areas. Several species of corvid birds are important predators of juveniles, and again these avoid the area around human settlements. Many carapaces of juveniles were found beneath solitary trees in open areas.

Farmers previously used pesticides which had no obvious effect on tortoise populations in the vineyards. However, hedges have been sprayed with 2, 4 D and 2, 4, 5 T in recent years. Only small areas had been sprayed up to 1986, but their further use is a major cause for concern. Access to the site was restricted to donkey transport up to the summer of 1984, when road construction opened it to cars and tractors. Many hedges were destroyed, causing the death of many tortoises which were sheltering there, out of proportion to the area involved. Improved access also resulted in road deaths, and the use of the area as a rubbish dump (with the risk of rats). Thus although the site was large and losses were still small, there is every indication that losses will increase in future.

23 METEORA B (HS0, MS0)

Another population was studied in a mountainous area about 7 km north of the town, with dense oak wood and some grassland. Both *T. hermanni* and *T. marginata* were found; the former were much less dense than in the cultivated site near the town. The area was protected, and grazing was forbidden, so that the populations were not threatened.

24 DESKATI A (HD0)

This site had an almost complete cover of open oak wood, with some arable fields in lower areas. Only *T. hermanni* were found, with an age distribution dominated by old animals; only 20 tortoises had less than 20 scute annuli. These animals were of large body size compared to other populations in Greece. The herbicides isoproturon and dinoterb were used extensively in spring, but are unlikely to affect tortoises which remain in the woods at this time. Increasing use of the wood by local people for firewood may open up the habitat and make it more suitable for tortoises. There seem to be no threats to this population.

24 DESKATI B (HD0)

Three other places were also examined in the large area of oak wood between Deskati and Meteora. A high density of *T. hermanni* was found in each area, and none of the populations were threatened.

25 AGIOS DIMITRIOS (HD0, MS0)

The vegetation was sparse thorny scrub on rocky soil, and part of the area was grazed grassland. The population density of *T. hermanni* appeared to be rather high for this type of habitat; a few *T. marginata* were also found. The area was protected from hunting, and although several used cartridges have been found, the tortoises do not seem to be under any threat.

26 LITOCHORON (HD1, MS1)

This was an area of thorny scrub on the lower slopes of Mount Olympus, in which there were several cultivated fields, patches of grazed grassland, and orchards. About a hundred *T. hermanni* and several *T. marginata* were marked, and similar numbers were seen during a study of reproduction (Hailey and Loumbourdis, 1988). The habitat in this area was not threatened. The only threat to tortoises was their habit of entering cultivated areas and meadows to feed, as little food was available within the scrub. Agricultural machines killed many tortoises in these areas. One field was visited in May 1986 shortly after the lucerne crop had been cut by tractor, and 10 dead tortoises were found, including three *T. marginata*, in an area of about 1 ha. Annual losses on this scale would be a severe drain on tortoise populations in the surrounding scrub.

27 ELASSONA (HS0)

A low density of *T. hermanni* was seen in deciduous woodland and rocky areas near a small river. The population was apparently not threatened.

28 GREVENA (HS0)

This was an area of open oak woodland. A single tortoise sighting (although the site was not visited at the best time for tortoise activity) and a few traces suggested a low population density. There were no apparent threats to this area.

29 KASTORIA (HD0)

The vegetation was open oak wood and grassland with hedges. Many *T. hermanni* were marked, but no other species was found. Hunting was forbidden, and the tortoises were not threatened at present.

30 KORINOS (HS2)

This area is a continuation of the southern heath at Alyki (below), but was more intensively used. The sand dunes were undisturbed, but behind them the grassland (with *Juncus*) was heavily grazed by cattle. A survey in 1982 found *T. hermanni* at a lower density than on the Alyki main heath. Much of the area was burnt in 1986 for pasture improvement, but few dead tortoises were found. Many more dead tortoises were seen after similar fires in the southern heath and the main heath. The tortoise density at Korinos was thus lower than at Alyki, and declining. The main threat is further fires for pasture improvement.

31 ALYKI A (HD2, GS1)

The areas known as the main heath and the southern heath (Stubbs, Swingland, Hailey and Pulford, 1985) included coastal and dry heath and grassland. These areas held a large population of *T. hermanni*, but were burnt and then rotavated in 1980 (Stubbs, Hailey, Tyler and Pulford, 1981; Stubbs, 1981a, 1981b). This was a deliberate attempt by local people to destroy the wildlife value of the heath, and so to overcome objections to building holiday homes. The tortoise population was reduced by about half (Stubbs *et al.*, 1985). The vegetation regenerated by 1982, apart from large bushes. Recovery of the tortoise population will take much longer, even if the area remains undisturbed.

Many plots for holiday homes, and the path of a new road, were marked out with stakes and concrete posts in 1983, but there was no further development to June 1988. Each year a few tortoises were run over, and one or two were killed by sportsmen with shotguns. Although unsightly, these deaths have negligible effects on the population. Much more serious were deaths from small fires started for pasture improvement. About five per cent of the heath was burnt each year. Most of the area was grazed by sheep between October and May, but this had little if any direct effect on tortoises. The small population of *T. graeca* in coastal heath (Hailey, 1988) would be vulnerable if the beach was improved for bathing by bulldozer; part of the southern heath was destroyed in this way in 1987 (Goutner, personal communication).

31 ALYKI B (HD2)

A high density of *T. hermanni* was found on the isolated salt-works heath (Stubbs *et al.*, 1985). This area was disturbed several times in recent years, by construction of a road to the salt works, small fires, and by improvement of the beach for bathers. This disturbance is expected to increase with modernisation of the salt works.

31 ALYKI C (HS1)

A low density of *T. hermanni* were present in mixed arable farmland, orchards, poplar wood and waste ground around Alyki. These were threatened by mechanised farming, fires to clear fields, and by cutting down woods.

32 AGATHOUPOLIS (HS1)

The Aliakmon river estuary north of Agathoupolis is surrounded by a large area of flat land, most of which must have originally been marsh and heath similar to Alyki. Almost all of the drier parts of this land were intensively cultivated, or used as a rubbish dump. A few *T. hermanni* were found in abandoned fields and waste ground, which were threatened by further slow deterioration of their habitat.

33 KILKIS (HD1, GS1)

Most of the plains of northern Greece were under arable cultivation, and the natural vegetation was only retained on hills. These vegetation islands were the last strongholds of tortoise populations inland in this region. The fields were rendered unsuitable for tortoises by annual fires started to clear up after the harvest; these large fires sometimes spread to the hills.

An isolated tortoise population (mostly *T. hermanni*) was found on a thorny scrub-covered hill near Kilkis. Isoprobuteron and Dinoterbe were used in the surrounding fields, but most tortoises were unlikely to come into contact with these. The main threat was fires spreading from the fields; one part of the hill was burnt years ago, and several carapaces were found in that area. Local people noted that tortoises were much more common in the past, and that changed agriculture had caused the decline.

34 EPANOMI (HD0, GD0)

This was an area of coastal and dry heath and grassland surrounding a lagoon, with both *T. hermanni* and *T. graeca*. These populations had a high proportion of juveniles, and seemed to be flourishing (Hailey *et al.*, 1988). The area was protected, and hunting was banned. There may be some interference with the tortoise population, as two of the *T. graeca* found had been painted white; these were probably pets which had been released.

35 KOLHIKO (HS0, GS0)

This was a large area of thorny scrub-covered hills intersected by small rivers, with areas of close-cropped grassland and bare rocks. It was intensively grazed. A few *T. hermanni* and *T. graeca* were seen in the grassy areas. The population density was low, but the tortoises are not threatened as farming did not involve machinery or spraying.

36 LANGADIKI (HS2, GS2)

The scrub-covered hills typified by sites 35 and 37 gave way to a patchwork of arable fields and grassland with hedges in the low fertile areas around the large lakes. *Testudo hermanni* and *T. graeca* were present at low density in these areas, where they were highly threatened by road traffic and agricultural machinery; only dead animals were found (Stubbs *et al.*, 1981).

37 MIKRA VOLVI (HD1, GD1)

The site was part of a large area of thorny scrub covering the hills to the north of Lake Volvi. Some parts of the scrub were cleared by farmers in recent years, although this affected a small proportion of the total habitat. Both *T. hermanni* and *T. graeca* were common. Tortoises suffered from a high degree of egg predation, judging by the large number of destroyed nests found. The main threat to this population was large fires, of which there have been several in surrounding areas in recent years.

38 KERAMOTI A (HD1, GD1)

The land around the mouth of the Nestos river included damp grassland and cultivated fields, lagoons and marshes, coastal heath and strips of deciduous wood. A dense population of *T. hermanni* and *T. graeca* was found in an area of woods, coastal heath and grassland near the town (Hailey *et al.*, 1988). This population was in a vulnerable position if the town or camping site were further developed. This is a major tourist area, with the ferry port to the popular island of Thasos.

38 KERAMOTI B (HS0, GD0)

Both *T. graeca* and *T. hermanni* were found on a small island west of the town, connected to the land by a small bridge (Hailey *et al.*, 1988). These were apparently under no threat.

39 LAGOS A (HD2, GD2)

A high density of *T. hermanni* and *T. graeca* were found near the town in a coniferous plantation on coastal heath. There were very few juveniles, however, probably because of disturbance from human commensals (Hailey *et al.*, 1988). The population appeared to be declining.

39 LAGOS B (HS1)

A few *T. hermanni* were found in intensively used grassland separated from the Lagos A site by a main road (Area 3 of Wright, Steer and Hailey, 1988). These were apparently threatened by increasing use of the area to dump rubbish.

40 AVAS (HS0, GS0)

The Avas Gorge included steep rocky sides covered in dense thorny scrub, some olive groves, and arable fields in flat areas near the river. A low density of tortoises were found; two *T. hermanni* and five *T. graeca* in several man-days sampling (Stubbs *et al.*, 1981). Tortoises were not apparently threatened.

41 SOUPHLI (GS2)

This site was a patchwork of coniferous woodland, thorny scrub, and grassland and cultivated fields. There was a low density of *T. graeca*, only two being found, one of which had been killed by a tractor. Tortoises in the fields were threatened by mechanised farming.

42 EVROS DELTA (HD2, GD2)

The region with highest tortoise density was the western coastal part of the delta. This was an area of coastal heath, where both *T. graeca* and *T. hermanni* were common. A large part of this area was threatened by the scheduled development of a fish farm (Goutner, personal communication).

HERPETOFAUNA OF TORTOISE SITES

The tortoise populations thus suffered from very varied degrees of disturbance. Many populations in isolated areas were completely undisturbed, and were unlikely to be disturbed in the future (such as Delphi, Skyros, Mesochoron). Other populations had been devastated during our studies, and were in further danger (such as Olympia A, Alyki A). The types of threat were also varied, including fires, building, pesticide spraying and dumping of rubbish. No simple trends are shown by the results, apart from the observation that large numbers of all three species have not been found together (Table 1); *T. marginata* and *T. graeca* have exclusive distributions.

Before presenting a quantitative evaluation of these results (in the Discussion), we consider the other species of reptiles found at the sites, and especially at the Alyki A site. These observations are summarised in Table 3, which excludes sites where few other reptiles were seen. Lizards and snakes were in the same habitat as the tortoises, unless indicated otherwise. The abundance of reptiles at Alyki is shown as the total number of sightings; values above 10 are approximate.

Status of reptiles at Alyki

These notes describe the status of each of the reptiles seen at Alyki A (the main heath) up to June 1988,

Species	31	1	2	3	5	6	13	19	20	23	24	25	26	27	29	32	33	34	35	37	38	40	41	42
Cyrtodactylus kotschyi	+	0									0														0
Agama stellio																				0					
Algyroides moreoticus				0		0																			
Ophisops elegans																								0	
Lacerta trilineata*	500		0			0	0				0	0		0		0	0			0	0	0	0		0
Lacerta graeca		0																							
Podarcis taurica	2000		0	0		0		0			0	0	0	0			0	0	0		0	0	0		
Podarcus erhardii	+														0										
Podarcis muralis											0				+	0									
Podarcis pelopponesiaca		0	0			0																			
Ophisaurus apodus	100	0		0			0	0	0	0				0						0					
Anguis fragilis				0										0											
Ablepharus kitaibelii	20		0	0								0													
Eryx jaculus	5																		0						0
Malpolon monspessulanus	20		0																		0				0
Coluber jugularis	100																		0						
Coluber gemonensis														0											
Elaphe situla											0							0							0
Elaphe quatuorlineata	5													0											
Elaphe longissima					0																				0
Natrix natrix	20													0			0		0	0			0		0
Natrix tessellata	+														0	0					0		+		
Vipera ammodytes	20	0		0							0	0													

TABLE 3: Other reptile species found at tortoise sites. Details of tortoises are given in Tables 1 and 2. Approximate numbers of sightings are given for Alyki (site 31). Presence at the other sites is indicated by: 0 in same habitat as tortoises; + in other habitat. * Not distinguished from *L. viridis* at most sites.

including noteworthy records at other sites. They should be used in conjunction with the maps of the Alyki site given by Stubbs *et al.* (1985).

Emys orbicularis and *Mauremys caspica*

One *Emys* and four *Mauremys* were found in damp areas of the main heath. These had probably dispersed from freshwater dykes in the southern heath and the saltworks heath, where terrapins were common. A few dry carapaces have also been found in the dry pools in sector 12. Terrapins are unlikely to breed on the main heath, but are common in freshwater dykes, pools and streams in the Alyki area and throughout Greece.

Lacerta trilineata

Those green lizards which have been captured at Alyki and at other sites have all proved to be *L. trilineata*. The presence of *L. viridis* at some sites cannot be discounted, as these species are impossible to distinguish unless striped juveniles are seen, or specimens can be examined in the hand. *L. viridis* was identified in orchards at Edessa in Macedonia. Green lizards were quite common at Alyki in dry heath and grassy heath/*Juncus* marsh, foraging in open areas and climbing bushes to escape. Also found in farmland, and often run over as they basked on roads in the evening. The highest density was seen in thorny scrub at Kolhiko, Mikra Volvi and Avas.

Podarcis taurica

Very common in coastal heath and grassland, typically running between low shrubs (*Artemisia*) or patches of grass. High densities also seen in coastal

heath at Epanomi and Keramoti. Widely distributed in northern Greece, present in meadows and fields at low density. Another wall lizard, *P. erhardii*, was also present at Alyki and elsewhere in northern Greece. This inhabits rocks and buildings (see Hailey, Gaitanaki and Loumbourdis, 1987), and was not found on the main heath.

Ophisaurus apodus

Most sightings at Alyki were in spring, in dry heath and grassland. Almost all individuals were adults of about 1m total length; only two juveniles have been seen. Some aspects of their biology have been described by Hailey (1984) and Hailey and Theophilidis (1987). A much higher density was found in meadows at Litochoron and Olympia, where several were sometimes seen per day. Glass lizards were often seen dead on roads after rain in spring, in farmland with thick hedgerows.

Ablepharus kitaibelii

Early sightings of this skink at Alyki were of juveniles in drift-line debris in summer (Stubbs *et al.*, 1981). Subsequent sightings have been in the grassy heath of sectors 11 and 12 in spring and autumn. Also seen in farmland at Olympia and more frequently in woods at Deskati. This species is resistant to disturbance; several were seen in roadside verges in the industrial estate at Sindos (near Thessaloniki).

Eryx jaculus

Five seen in dry heath and coastal heath at Alyki, and present in similar habitat at Epanomi (Goutner,

personal communication). Two sand boas have been found dead on roads through arable farmland and orchards at Alyki.

Malpolon monspessulanus

This snake was restricted to grassland and *Juncus* marsh in sectors 2, 11 and 12 on the main heath. An adult was seen ingesting a green lizard, and a juvenile was found choked on an adult *P. taurica*. Also seen in dense vegetation around the salt works, and dead on roads in arable farmland and orchards.

Coluber jugularis

The most abundant snake, common in dry heath, and occasionally seen in coastal heath. Also found in similar habitat at Epanomi, and seen dead on roads passing through arable farmland. The only prey recorded was a sand boa.

Elaphe quatuorlineata

Three individuals were sighted from 1980-1986. These were in sectors 9 and 13, and had probably dispersed from the far end of the southern heath where there were permanent livestock shelters (with rats), and tall tamarisk scrub leading to woods. It is unlikely that there was a breeding population on the main heath, as there were few small animals.

Large numbers of small mammals were seen all over the heath in May and June 1988. This population explosion occurred elsewhere in Greece at the same time, following an exceptionally mild winter (Th. Sofianidou, personal communication). Five voles were trapped in dry heath (sectors 1 and 2), grassy heath (sectors 3 and 17) and the coastal dunes (sector 9), all apparently *Microtus guentheri* (van den Brink, 1973; Vohralik and Sofianidou, 1987). Two adult *E. quatuorlineata* were seen in sector 2 in May 1988; these had probably entered the main heath from the southern heath, in response to the vole population explosion.

Natrix natrix

Seen in coastal heath, grassland and *Juncus* marsh, mostly in sectors 2 and 3, usually in the evening. Two melanistic adults with reduced dorso-lateral stripes were found in May 1988. Recorded prey were the toads *Bufo viridis* and *Pelobates syriacus*. A similar heathland population occurred at Epanomi. Grass snakes were more often seen around streams and pools in farmland and natural habitats at several sites, feeding on green frogs.

Natrix tessellata

One seen in sector 2 had probably dispersed from the deep freshwater dykes on the far side of the salt works, and this snake was not thought to breed on the main heath. A few seen in dykes and streams at the other sites: this species is common in Lake Volvi.

Vipera ammodytes

Most vipers were found when basking in spring, in dry heath and coastal heath in sectors 7 and 10. Several juveniles were found in the evening on tracks through arable farmland at Alyki, mostly in October. An adult was seen ingesting *L. trilineata* at Litochoron.

Other species

Four amphibians were found on the main heath. The most abundant was *Bufo viridis*, in dry heath and coastal heath. *Pelobates syriacus* had a similar distribution but was much less common. These toads bred in shallow pools in sector 12 in wet years; these pools dried before tadpoles had developed in the dry year 1985. Four *Hyla arborea* were seen between 1980 and 1986, in dry heath vegetation. Many were heard calling in May and June 1988. Two *Bufo bufo* were found in *Juncus* marsh in 1980, but the common toad has not been seen since at Alyki.

Four other species were seen in the Alyki area, but not on the main heath. These are:

Triturus vulgaris; a single male from a stream,
Rana ridibunda; common in dykes, pools and streams,
Cyrtodactylus kotschyi; on buildings and trees,
Podarcis erhardii; on buildings.

DISCUSSION

STATUS OF TORTOISE POPULATIONS

The unit of analysis used here is the species-population, that is a population of a single species of tortoise at a single site. This was used because the species sometimes differed in density or status at a single site. The survey included 79 species populations at 42 sites. Overall, 22 populations (28 per cent) were immediately threatened, and 26 (33 per cent) were not apparently threatened at present. The other 31 populations (39 per cent) had declined in the past, or were liable to long-term decline.

The three species differed significantly in the relative numbers of sparse and dense populations. The percentages were:

	Sparse	Dense	(N)
T. hermanni	45	55	44
T. graeca	50	50	12
T. marginata	96	4	23

($X^2 = 16.6$, 2 d.f., P = 0.00024). The only dense population of *T. marginata* was found at Gytheion, the other 22 populations of this species being sparse. In contrast, about half of the populations of *T. hermanni* and *T. graeca* were dense; there was no significant difference between these two species ($X^2 = 0.0022$, 1 d.f., P = 0.96).

There was no significant difference between the three species in the proportion of populations in each threat status category. The percentages were:

	Status 0	Status 1	Status 2
T. hermanni	32	39	29
T. graeca	33	33	33
T. marginata	35	43	22

($X^2 = 0.74$, 4 d.f., P = 0.95). The species were therefore pooled, and the status of the 48 sparse and 31 dense

populations were compared. There was no significant difference, the percentage in each status category was:

	Status 0	Status 1	Status 2
Sparse	35	40	25
Dense	29	39	32

($X^2 = 0.59$, 2 d.f., $P = 0.74$). This result was contrary to our expectation that the sparse populations would be less threatened. It is explained as the sparse category includes threatened populations in agricultural land, as well as populations in the large areas of thorny scrub in mountainous regions which are under no threat.

There was a noticeable trend in the location of populations of different threat status. Many of the populations in no apparent danger were in the central mountainous regions (Fig. 3a), or in places where steep hills approached the coast (Pelasgia, Delphi, Korinthos). In contrast, most of the immediately threatened populations were in flat areas at or near the coast (Fig. 3b).

THREATS TO TORTOISE SITES

In total, the 42 sites suffered from 51 identified threats (some sites were subject to several types of threat), which may be grouped into categories. The percentage of the total number of threats made up by the different categories was:

Agricultural development	22
Agricultural machinery	20
General development	10
Agricultural spraying	10
Agricultural burning	8
Forest fires	8
Tourism development	8
Direct slaughter	8
Human commensals	6

Numerically, the most important threats at tortoise sites were agricultural, making up 61 per cent of the total. Threats from urbanisation (general and tourism development, human commensals) made up only 23 per cent of the total. Note that threats from tourism were numerically rather small compared to agriculture, and even compared to other forms of urbanisation. The remaining 16 per cent of threats were more casual; from forest fires and the direct slaughter of tortoises.

Despite these threats to sites, it must be concluded that tortoises are still rather common animals in Greece, where their conservation is a much less serious problem than that of sea turtles, large mammals, or birds of prey. However, about two thirds of Greek tortoise populations are currently threatened by long-term decline or sudden catastrophe. The situation should be monitored, preferably by surveys specifically for this purpose. Such surveys should improve on this review in three respects:

1) Quantitative estimates of population density should be made using short term census techniques such as that described by Hailey (1988).

2) The number of tortoise sites should be found by intensive survey of a few large regions (say 1000 km²), for use as a calibration. The total number of sites
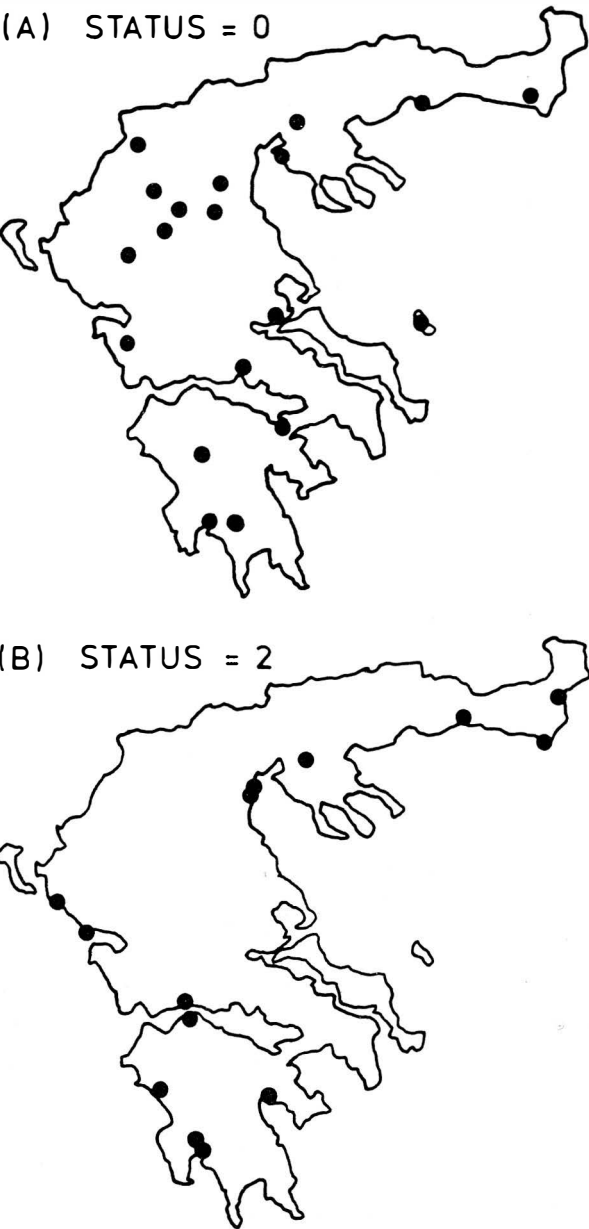

Fig. 3 Location of sites at which populations which were (a) not apparently threatened, and (b) immediately threatened, were found. Note that many of the safe sites are in the central mountainous region, and the majority of the most-threatened sites are near the coast.

occupied by tortoises in Greece, and the total number of animals, can then be estimated.

3) As much attention should be given to investigating the threats to a site, as to the details of the tortoise population. In our survey, the 46 populations at sites where tortoises were marked were apparently more threatened than the 33 populations at sites visited for shorter periods. The percentages were:

	Status 0	Status 1	Status 2
Marked sites	19	48	33
Short visits	52	27	21

($X^2 = 8.92$, 2 d.f., $P = 0.012$). One possible reason for this difference is simply that more threats become apparent during a longer study.

Casual collecting is another threat to Greek tortoises, which is hard to quantify but probably widespread (Sofianidou, personal communication). This affects all species (it has been observed twice at Alyki), and is likely to be responsible for translocation of tortoises found well outside the natural range of the species (for example *T. gracea* in western Greece or the Peloponnese). It typically involves Central Europeans touring by car, who see 'the alert, vigorous, herb-scented beasts that plough through the undergrowth' (Arnold *et al.*, 1978) and collect one or two on impulse. The beasts are considerably less attractive after a few days, when they have covered themselves and the boot of the car with their faeces, and are likely to be liberated, perhaps hundreds of kilometres from where they were captured. Translocated animals might persist in the wild for 10 or 20 years, but still represent a loss to the original population.

STATUS OF THE THREE SPECIES

Testudo hermanni was the most widespread and common species, found throughout Greece, at high density in a variety of natural habitats and at the edge of cultivation, and at low density in thorn scrub and agricultural land. It was unusual in showing wide regional variation of body size (Table 4). The variation is partly explained by climatic and ecological factors; tortoises are larger to the north and in woodland habitat. This is not, however, a simple relationship, because mean adult size may change abruptly between adjacent populations in similar habitat (Willemsen, in preparation). This will be considered in more detail elsewhere; it implies some regional genetic variation, which will be lost if only a few populations remain. *T. hermanni* in southern Greece and the Peloponnese, which are of characteristic small body size, are the most threatened. These populations occupy small areas, usually of cultivated ground liable to disturbance. In general, *T. hermanni* as a species seems to be in no danger at present in Greece.

Type	Site	SCL (mm)	Range
1	Deskati	198 ± 17	NC Greece
2	Volvi	168 ± 10	NE Greece
3	Meteora	159 ± 8	C Greece and coastal sites
4	Olympia	151 ± 7	N & C Peloponnese
5	Sparta	138 ± 9	S Peloponnese and Euboea

TABLE 4: Size variation of *T. hermanni* in different parts of Greece. Measurements are mean straight carapace length (± 1 S.D.) of adult males of five recognisable types. The data are for a typical site for each type, and the geographic range of the type is shown (C = central). Unpublished data of Brinkerink and Willemsen. The range of mean length shown corresponds to a three-fold variation of weight, from about 500 to 1500g.

Testudo marginata was almost as widespread, but absent from north-east Greece. It was much less abundant as most populations were sparse, whether in natural habitats or in cultivated areas. The site at

Gytheion would merit protection as this dense population of *T. marginata* is unique in our experience. Elsewhere, this species was not threatened in the thorn scrub which seems to be its natural habitat; this vegetation is typical of rocky areas which have little value for other uses. The main danger was from a slow loss of animals at the edge of cultivated land. Thorn scrub contains little food, and tortoises often enter fields to feed on herbs and weeds, where they are killed by machinery and pesticides. *Testudo marginata* is especially vulnerable to this slow drain on populations because it is large (adult females weigh about 2 kg) and slow maturing. Only 6 per cent of the animals marked were juveniles, compared to 15 and 26 per cent in *T. hermanni* and *T. graeca*, respectively (Table 2). The slow population turnover also makes *T. marginata* vulnerable to loss of a few adults by casual collecting; this species seems to be more sought after than the other two (Sofianidou, personal communication). In general, we regard the future of this species with more optimism than Keymar and Weissinger (1987), though it is endangered in some regions (around Athens, for example).

Testudo graeca was restricted to north-east Greece, mostly in coastal habitats (see Wright *et al.*, 1988). The populations in Greece were in danger because coastal areas are the most likely to be disturbed. However, the main distribution of this species is in Asia Minor (the subspecies *T. g. ibera*) and North Africa (*T. g. graeca*), so that the Greek populations are of little importance for the future of the species. In contrast, *T. marginata* is endemic to Greece, and *T. hermanni* is largely a Balkan species. Therefore although *T. graeca* is the most threatened tortoise in Greece in national terms, its fate in Greece is of lesser importance in world terms.

BIOGENETIC RESERVES FOR REPTILES

Most reptiles are difficult to find and will be missed in short surveys. Tortoises, however, are conspicuous, and it would be useful if their presence could be used as an indicator of a particular assemblage of reptile species. There are 33 native species of lizard and snakes in mainland Greece (Arnold *et al.*, 1978), and 23 of these (70 per cent) were found with tortoises. *Testudo hermanni* was associated with 22 species. Many of the remaining species are secretive (*Chalcides ocellatus, Ophiomorus punctatissimus, Typhlops vermicularis, Coronella austriaca*) or nocturnal/crepuscular (*Tarentola mauretanica, Hemidactylus turcicus, Telescopus fallax*), and are likely to be identified by more detailed surveys. Reynolds (1984) has noted two additional species found at tortoise sites in western Greece; *Algyroides nigropunctatus* and *Coluber najadum*. Thus about three quarters of the reptile species of mainland Greece have been found with tortoises. It must be concluded that the presence of tortoises provides little or no information about other species of reptiles likely to be found in an area.

The presence of tortoises might still be a useful indicator of the herpetological potential of a site, by showing an area of high species richness, rather than identifying a particular community. Unfortunately, this also seems to be invalid. Tortoises were found at very disturbed sites such as Lagos, and indeed may be

one of the most resistant of reptiles to disturbance over a few years. Ultimately, of course, tortoise populations must die out where recruitment is interrupted (Lambert, 1984).

Another possibility is using the population structure of tortoises to show whether a site is disturbed and has a low richness of other reptiles. The population structure at disturbed sites is often adult-dominated, with few juveniles (Hailey *et al.*, 1988). However, population structure may be affected by factors specific to tortoises, such as predation on nest aggregations (Stubbs and Swingland, 1985). For example, the declining tortoise population in the Massif des Maures in southern France is in an area with many other reptile species (Stubbs, personal communication).

The herpetofauna of the main heath at Alyki is substantially less rich than the 39 species which have been identified in the proposed biogenetic reserve in Thrace, north-eastern Greece (Anonymous, 1987). However, simple numbers of species, or numbers of threatened species, should not be used as the main criterion for selecting a reserve. It is important to distinguish the contributions of within-habitat and between-habitat richness to the number of species present. Reptiles are often rather habitat-specific (Heatwole, 1976), so that an area containing many types of habitat will have a large number of species. For example Kitchener, Chapman, Dell, Muir and Palmer (1980) examined the lizard faunas of 23 reserves in the wheatbelt of Australia, to see the effects of area, isolation and habitat diversity. Their main conclusion was that:

'Multiple regression analysis shows that 75 per cent of the variation observed in lizard species richness between reserves is accounted for by the logarithm of the number of vegetation associations in these reserves; addition of other reserve variables examined (including area) does not significantly increase this explained variation.'

It is suggested below that Alyki merits protection as an undisturbed coastal heathland containing most or all of the reptile species likely to be found in that habitat. Larger areas may hold a greater number of species, but will not be as effective for conservation if they simply contain the most common species from many different habitats.

ALYKI AS A RESERVE FOR REPTILES

The reptile most deserving of attention at Alyki is *T. hermanni*, of which there is a large population in an apparently optimum habitat for the species. Conservation of the site would also benefit the other species of reptile which breed there. After *T. hermanni*, the snakes *E. jaculus* and *V. ammodytes* are of most interest. These are not abundant anywhere, and coastal and dry heath seem to be their typical habitat. These snakes also occur in traditionally farmed land, but would be vulnerable to intensive land use; *Eryx* to mechanised farming, and *Vipera* to direct persecution.

Three further groups of reptile species present at Alyki may be recognised.

a) Those for which the main heath provides typical natural habitat, but which are abundant in disturbed areas and of low priority for conservation: *P. taurica, M. monspessulanus, C. jugularis.*

b) Those which are abundant at Alyki, but are even more abundant in other natural habitats: *L. trilineata* (scrub), *O. apodus* (meadow), *A. kitaibelii* (woods), *N. natrix* (marsh).

c) Those present in small numbers for which Alyki is at the edge of the geographic range (*T. graeca*) or which do not breed on the heath (*E. orbicularis, M. caspica, E. quatuorlineata, N. tessellata*).

Alyki contains almost all the reptiles which occur in coastal heathland in northern Greece. We have not seen any other reptiles in coastal heathland in this area which are not present at Alyki. Three other species might occur (Arnold *et al.*, 1978), but their habitat preferences are not known in detail. *Chalcides ocellatus* and *Typhlops vermicularis* may require ground cover of rocks, which is not present at Alyki. These two species are otherwise common; *Chalcides* has a wide geographic range in the Middle East, and *Typhlops* also inhabits disturbed areas such as the suburbs of Thessaloniki. Another possibility is *Telescopus fallax*, although the typical habitat of this snake seems to be fields with dry stone walls and rocky areas; it has been found in Chalkidiki around farms.

In conclusion, it must be admitted that there are no reptiles at Alyki which do not occur elsewhere at similar or greater densities. The site is worth conserving, however, as an example of a little disturbed coastal heathland; it is also important for bird and plant life (D. Stubbs, V. Goutner, personal communications). The survey of tortoise sites showed that coastal areas were the most threatened. There are rather few good coastal sites in Greece, as steep hills come down to the sea in most places; coastal heathlands are restricted to the areas around lagoons and estuaries. The Alyki heath is at present one of the best remaining examples of this habitat in Greece, and should be protected.

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APPENDIX

Further records of the distribution and status of tortoises and other reptiles in Europe are always useful. These should be sent direct to:

DR BRIAN GROOMBRIDGE: IUCN Monitoring Centre, 219c Huntingdon Road. Cambridge CB3 0DL, UK.

and

DONATO BALLASINA: R.A.N.A. – Belgium vzw' Populierenlaan 17'B – 1980 Tervuren. Belgium.

IMMUNOCYTOCHEMICAL AND QUANTITATIVE STUDY OF INTERSTITIAL CELLS IN THE HIGH MOUNTAIN TOAD *BUFO BUFO GREDOSICOLA* DURING THE SPERMATOGENETIC CYCLE

BENITO FRAILE*, RICARDO PANIAGUA,* FRANCISCO J. SAEZ*, & MARINA C. RODRIGUEZ‡ AND MIGUEL LIZANA‡

* Department of Cell Biology and Genetics. University of Alcatá de Henares. E-28871 Alcatá de Henares. Madrid, Spain.

‡Department of Cytology and Histology. Faculty of Biology. University of Salamanca. E-37008 Salamanca. Spain.

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ABSTRACT

The interstitial cells of the toad *Bufo Bufo gredosicola* were studied throughout the seasonal period of spermatogenesis (from April to October) by means of immunocytochemical detection of testosterone and quantitative histological studies. The total number of interstitial cells per testis did not vary during the spermatogenetic period. However, in April, May and October, there were many interstitial cells showing an abundant testosterone content, whereas from June to September poorly-differentiated interstitial cells with a scanty testosterone content are the most abundant interstitial cell type. Since the interstitial cells with abundant testosterone content are larger than the interstitial cells with scanty testosterone content, the volume occupied by interstitial cells decreased in June-September. The development of thumb pads coincides with that of testosterone-containing interstitial cells.

INTRODUCTION

It is generally accepted that, as in other vertebrates, the interstitial cells or Leydig cells represent the major source of testicular steroid hormones in anuran amphibia. This ideas has been supported by direct evidence from cytochemical (presence of cholesterol-rich cytoplasmic droplets and $\Delta^5 3\text{ß}$-hydroxysteroid dehydrogenase activity), and ultrastructural studies (Lofts, 1974; Unsicker, 1975; Rastogi and Iela, 1980). However, unlike in higher vertebrates, no tissue cultures and incubation experiments with dissociated cell populations of the anuran testes have been performed and it cannot be excluded that other cells such as the Sertoli cells, which also show $\Delta^5\text{-}3\text{ß}$-hydroxysteroid dehydrogenase activity, might be involved in steroid biosynthesis (Lofts and Bern, 1972).

A variety of studies have shown that the interstitial cells of the anuran testes show seasonal changes in their content in lipid droplets, Δ^5-3ß-hydroxysteroid dehydrogenase activity, and their ultrastructural steriod-synthesising characteristics (Van Oordt and de Kort, 1969; Lofts and Bern, 1972; Schulze, 1972, Chanda, 1982). These changes have been related with those observed in the development of thumb pads which have been considered as androgen-dependent structures (Miller, Obert and Schneider, 1977).

The aim of the present report was to investigate the evolution of interstitial cells in the hibernating toad of the 'Gredos' high mountains during the seasonal period of spermatogenesis by means of quantitative studies on histologic sections stained for immunocyto-chemical localisation of testosterone and to correlate these findings with the degree of thumb pad development. The results of this study provide new data concerning qualitative and quantitative circannual changes in the interstitial cells of this species of toad, data which can probably be extended to other anuran amphibia.

MATERIALS AND METHODS

Six adults male toads (*Bufo bufo gredosicola*) were collected during each of the months corresponding to the seasonal period of spermatogonesis (from April to October) in 'Laguna Grande', located at 2000 metres in the 'Gredos' mountains (Spain). During the period of testicular quiescence (from November to March) the toads were hidden under the snow and they could not be collected. In order to eliminate the influence of 'body weight' in the quantitative studies only toads weighing between 60 and 65 g were collected. The animals were anaesthetised with methane sulphonate (MS-222, Sandoz) and perfused throughout the aorta with 3 per cent phosphate-buffered glutaraldehyde-paraformaldehyde (30 minutes). Following this, both testes were removed and weighed; testicular volumes were calculated by water displacement. The right testes were sliced into small fragments which were processed for electron microscopy.

The left testes were fixed for an additional 6 hours in the same fixative, dehydrated and embedded in paraffin. Five sagittal sections (7μm in thickness) of each testis at points 1/6, 1/3, 1/2, 2/3, and 5/6 of the transverse testicular diameter were performed and stained with hematoxylin and eosin and the peroxidase-anti-peroxidase (PAP) method for cellular detection of testosterone (Chemes, Gottlieb, Pasqualini, Demenichini, Rivarola and Bergadá, 1985). Rabbit antitestosterone γ-globulin (Biogenex Laboratories, Dublin, Ireland) was used as first antibody at a dilution of 1/100. Goat anti-rabbit γ-globulin at a dilution of 1/300 was used as the second antibody. After the PAP incubation and washing, peroxidase activity was detected by diaminobenzidine and hydrogen peroxide. This stain seems to be specific for testosterone.

The interstitial cells were classified according to their testosterone content as measured with a cytophotometer (Wicker Instruments, York, England) in the PAP-stained sections. A scoring range from 0 (interstitial cells without testosterone) to 4 (cells with the highest testosterone content) was established. According to this range the interstitial cells were designated as T$^-$ (from 0 to 1), T$^+$ (1-2), T^{++} (2-3), and T^{+++} (3-4).

In each PAP-stained section the following parameters were calculated:

1) Volume density of seminiferous tubules, testicular interstitium and each Leydig cell type (surface occupied by these structures divided by total surface of the section) by use of a semiautomatic image analyser.

2) Numerical density (number of cells per unit volume of the testis) of each interstitial cell type, by use of the Floderus (1944) equation: $N_v = N_a/(T+D-2h)$, where N_a is the number of cell nuclei per unit area, D is the average nuclear diameter (measured with a vernier ocular in at least 50 nuclei of each interstitial cell type), T is the average thickness of the section (6.9μm), and h is the height of the smallest recognisable cap section of the nucleus (about 10 per cent of the nuclear diameter), according to Wing and Christensen (1982).

3) Total number (per testis) of interstitial cells from each type by multiplying their numerical density by the testicular volume and by a correction factor (0.76) which results from transformation of testicular volume after perfusion in testicular volume after embedding. This factor was previously calculated using 50 testes from toads.

4) Average volume of each interstitial cell type by dividing the volume density of each cell type by its numerical density.

The means and standard deviations for each group (month) were calculated from the values for each animal. Comparison of the means between the different groups was carried out by the one-way ANOVA test and Scheffe's pairwise comparison.

The degree of thumb pad development was evaluated measuring the thickness of the epidermis in histological sections of the thumb pads. According to these measurements, the progressive degrees of development were designated as + (less than 100μm), ++ (from 100 to 134μm), +++ (from 135 to 174μm), and +++ (more than 175μm).

RESULTS

The testicular volume and the volume density of seminiferous tubules increased during the period of germ cell proliferation up to round spermatids (from April to August) and decreased during the period of spermiogenesis (September and October) (Table 1).

The numbers of cells corresponding to each different interstitial cell type (Figs. 1-4) varied during the spermatogenetic cycle (Table 2). In April and May there were numerous interstitial cells that showed an abundant testosterone content. These cells decreased in number in June; were absent in July and August, and reappeared in October. The contrary occurred with the interstitial cells showing scanty testosterone content. The total number of interstitial cells (all types) did not change during the period studied.
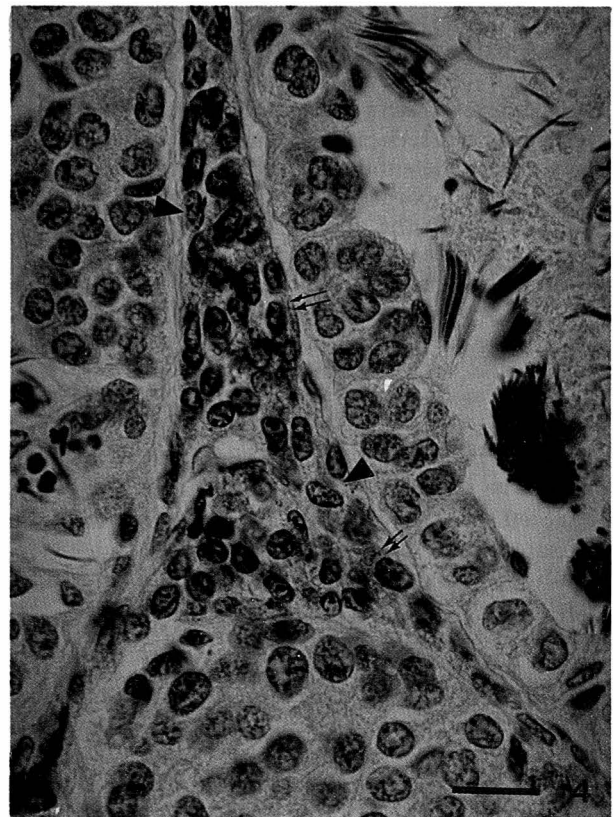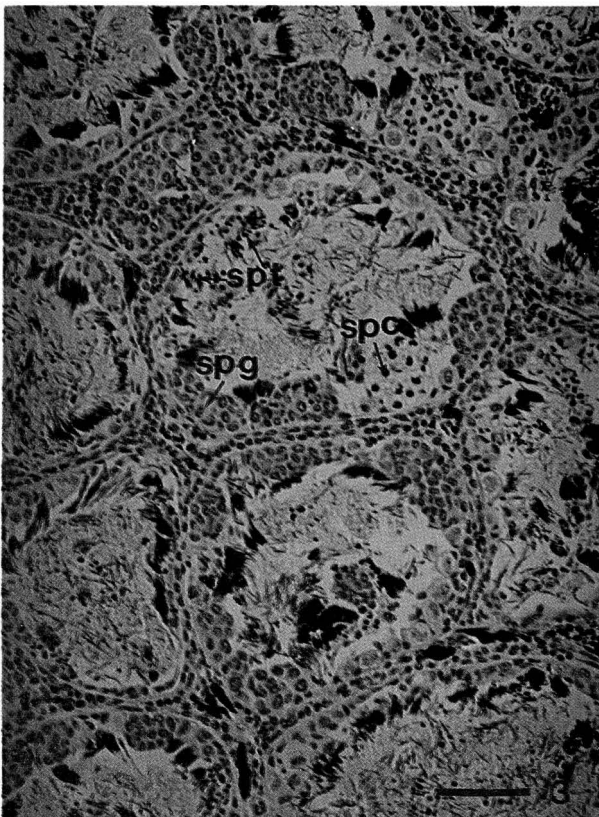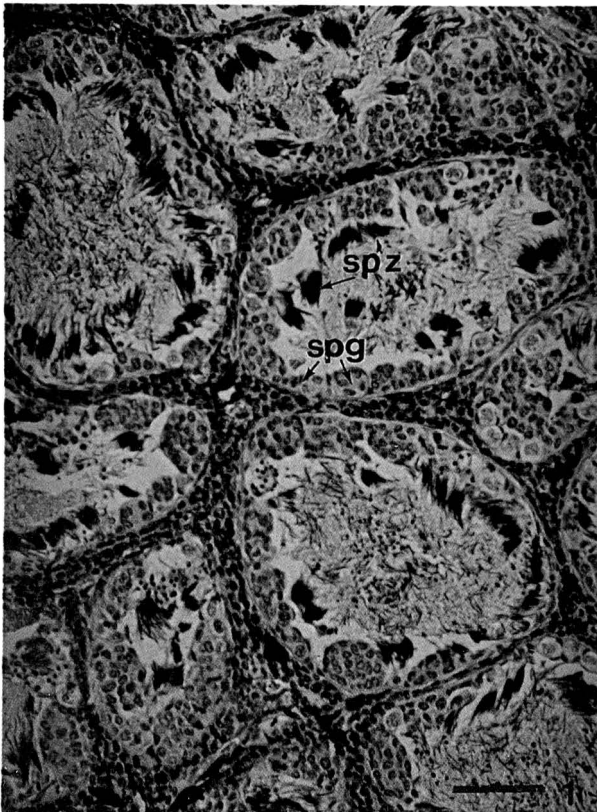
Fig. 1   Testis of *Bufo bufo gredosicola* in April. The testicular interstitium appears intensely stained with the PAP method for cellular detection of testosterone. spg: spermatogonia. The spermatozoa (spz) in the tubular lumen were formed in the preceding cycle. Bar = 80μm.

Fig. 3   Testis of *Bufo bufo gredosicola* in August. The testicular interstitium appears less stained than in April. spg: spermatogonia. spc: spermatocytes. spt: spermatids. Bar = 80μm.

Fig. 2   Detail of Figure 1 at higher magnification. Intensely stained cells of types T^{++} (small arrows) and T^{+++} (large arrows) predominate in the testicular interstitium. Bar = 20μm.

Fig. 4   Detail of Figure 3 at higher magnification. Interstitial cells with a scanty (arrowheads) or moderate (double arrows) testosterone content predominate in the testicular interstitium. Bar = 20μm.

	April	May	June	July	August	September	October
Body weight (g)	62 ± 1	63 ±1	61 ± 1	62 ± 1	60 ± 1	63 ± 1	63 ±1
Left testis volume (mm³)*	99 ± 12[a]	108 ± 22[a]	120 ± 17[a,b]	141 ± 24[b]	156 ± 24[b]	126 ± 18[a,b]	117 ± 18[a,b]
Volume density of seminiferous tubules (%)	77 ± 6	79 ± 6	85 ± 7	87 ± 8	88 ± 8	86 ± 8	84 ± 8
Volume density of testicular interstitium (%)	23 ± 2[a]	21 ± 2[a]	15 ± 2[b]	13 ± 1[b]	12 ± 1[b]	14 ± 2[b]	16 ± 2[b]
Seminiferous tubule volume per testis	76 ± 9[a]	85 ± 11[a,b]	102 ± 14[b,c]	123 ± 18[c,d]	137 ± 21[d]	108 ± 15[b,c]	98 ±14[a,b,c]
Interstitium volume per testis	23 ± 3[a]	23 ± 3[a]	18 ± 2[b]	18 ± 3[a,b]	19 ± 3[a,b]	18 ± 2[b]	19 ± 3[a,b]
Thumb pad development#	++++	++++	++	+	+	++	+++

TABLE 1: Body weight and testicular parameters in *Bufo bufo gredosicola* during the period of spermatogenesis.
Valued are expressed as means ± standard deviation. For each parameter, the results of the comparison between the averages values corresponding to each month are indicated using superscript letters. Values coinciding in some superscript letters do not differ significantly between them; and those with different superscript letters differ significantly between them (P<0.01). *This represents volume after fixation, dehydration, and embedding. # This was evaluated according to the thickness of the epidermis in histological sections of the thumb pads; + not developed; ++ semideveloped; +++ developed; ++++ very developed.

Interstitial cell type	April	May	June	July	August	September	October
T⁻	195 ± 25[a]	253 ± 38[a]	437 ± 67[b]	1181 ± 189[c]	1099 ± 168[c]	475 ± 76[b]	385 ± 56[b]
T⁺	270 ± 35[a,b]	234 ± 35[a]	650 ± 100[c]	253 ± 41[a,b]	321 ± 51[b]	781 ± 117[c]	415 ± 67[d]
T⁺⁺	692 ± 90[a]	759 ± 113[a]	306 ± 47[b]	—	—	152 ± 25[c]	394 ± 67[b]
T⁺⁺⁺	202 ± 27[a]	148 ± 22[b]	—	—	—	—	145 ± 26[b]
All cell types	1359 ± 177	1394 ± 208	1393 ± 216	1434 ± 230	1420 ± 223	1420 ± 220	1339 ± 212

TABLE 2: Number of cells (X10³) per testis of the different interstitial cell types classified according to their testosterone content in *B. b. gredosicola* during the period of spermatogenesis.
Values are expressed as means ± standard deviation. The interstitial cells are classified as T⁻, T⁺, T⁺⁺, and T⁺⁺⁺ according to their increasing testosterone content as measured with a cytophotometer in the sections stained with the PAP method for testosterone detection. For each interstitial cell type, the results of the comparison between the average values corresponding to each month are indicated using superscript letters. Values coinciding in some superscript letter do not differ significantly between them; and those with different superscript letters differ significantly between them (P<0.01).

The testicular volumes occupied by each different interstitial cell type changed from April to October in a similar way to the interstitial cell numbers (Table 3). The total testicular volume occupied by interstitial cells (all types) was greater in April, May and October than in June-September. This is due to the larger average volume of testosterone-rich cells than that of testosterone-poor interstitial cells (Table 4).

The progressive development of thumb pads (Table 1) coincided with that of testosterone-containing cells.

DISCUSSION

The spermatogenetic cycle in the high mountain toad *B. b. gredosicola* is similar to that of other anuran amphibia, with the characteristic of being shorter, due to the high altitude at which these toads live. Like in other anurans (Schulze, 1972; Unsicker, 1975; Koskela, Pasanen and Vaananen, 1979; Chanda, 1982; Jorgensen and Billeter, 1982; Jorgensen, 1984) the interstitial cells of this toad also have a seasonal cycle,

and they become prominent at the end of the spermatogenetic period.

Four types of interstitial cells have been observed in ultrastructural studies on anuran testes: (1) undifferentiated, fibroblast-like cells, which were found throughout the cycle, mainly in summer; (2) semi-differentiated cells containing numerous lysosomes, a few lipid droplets, mitochondria with tubular cristae, and a moderately developed smooth endoplasmic reticulum; these cells appeared in autumn; (3) well-differentiated cells with more abundant smooth endoplasmic reticulum, and more numerous and larger mitochondria than the semidifferentiated cells; these cells were found in winter and spring; and (4) involuting cells with scanty smooth endoplasmic reticulum, and abundant lipid droplets and secondary lysosomes; these cells were observed in summer (Schulze, 1972; Unsicker, 1975; Cavicchhia and Moviglia, 1982). These four cell types have been interpreted as successive stages of interstitial cell development, from undifferentiated to involuting interstitial cells.

Interstitial cell type	April	May	June	July	August	September	October
T^-	224 ± 30^a	300 ± 44^b	$553 \pm 85^{c,d}$	1308 ± 209^e	1364 ± 209^e	597 ± 96^d	462 ± 73^c
T^+	447 ± 60^a	404 ± 59^a	1101 ± 172^b	473 ± 77^a	544 ± 85^a	1431 ± 229^b	759 ± 119^c
T^+	1778 ± 240^a	1900 ± 287^a	776 ± 119^b	—	—	401 ± 65^c	998 ± 159^b
T^{+++}	725 ± 97^a	502 ± 74^b	—	—	—	—	501 ± 81^b
All cell types	3204 ± 433^a	3106 ± 466^a	$2430 \pm 379^{a,b}$	1781 ± 288^c	$1908 \pm 298^{b,c}$	$2429 \pm 396^{a,b}$	$2720 \pm 438^{a,b}$

TABLE 3: Volume ($mm^3 \times 10^{-3}$) per testis occupied by the different interstitial cell types classified according to their testosterone content in *B. b. gredosicola* during the period of spermatogenesis.
Values are expressed as means ± standard deviation. The interstitial cells are classified as indicated in Table 2. For each interstitial cell type, the results of the comparison between the average values corresponding to each month are indicated using superscript letters. Values coinciding in some superscript letter do not differ significantly between them; and those with different superscript letters differ significantly between them ($P < 0.01$).

Interstitial cell type	April	May	June	July	August	September	October
T^-	1149 ± 101^a	1186 ± 108^a	1264 ± 118^a	1241 ± 117^a	1241 ± 119^a	1257 ± 112^a	1206 ± 111^a
T^+	1767 ± 157^b	1726 ± 141^b	1694 ± 148^b	1695 ± 131^b	1695 ± 141^b	1832 ± 153^b	1829 ± 157^b
T^{++}	2569 ± 229^c	2503 ± 210^c	2536 ± 211^c	—	—	2638 ± 224^c	2533 ± 210^c
T^{+++}	3589 ± 291^d	3392 ± 275^d	—	—	—	—	3589 ± 294^d

TABLE 4: Average volume (volume density/numerical density, μm^3) of the different interstitial cell types classified according to their testosterone content in *B. b. gredosicola* during the period of spermatogenesis.
Values are expressed as means ± standard deviation. The interstitial cells are classified as indicated in Table 2. For each interstitial cell type, the results of the comparison between the average values corresponding to each month are indicated using superscript letters. Values coinciding in some superscript letter do not differ significantly between them; and those with different superscript letters differ significantly between them ($P < 0.01$).

A comparison of ultrastructural studies and the present immunocytochemical observations suggests a close correlation between the degree of cytological differentiation and that of active testosterone synthesis in the interstitial cells. Well-differentiated interstitial cells, similar to mammalian Leydig cells, seem to correspond to the interstitial cells with the highest testosterone content. In summer, these cells initiate their regression until they become undifferentiated interstitial cells. These involuting and undifferentiated cells probably correspond to the interstitial cells with a scanty testosterone content. In autumn, the undifferentiated cells begin to differentiate again and gradually increase their testosterone synthesis; they would correspond to the cells with an intermediate testosterone content. These results agree with those of endocrine studies in *Rana esculenta* which reveal a pronounced drop in the serum levels of testosterone in the period of germ cell proliferation and a recovery of high testosterone levels during spermatozoa formation and spermiation (Rastogi, 1976; Rastogi, Tammaro, di Meglio, Iela, di Matteo and Chieffi, 1981).

Changes in interstitial cell morphology in relation to the stage of the seminiferous epithelium have also been reported in the urodele amphibia *Necturus maculosus* (Ucci, 1982; Pudney, Canik, Mak and Callard, 1983; Pudney and Callard, 1984) and *Salamandra salamandra* (Lecouteux, Garnier, Bassez and Joby, 1985). In these animals only undifferentiated interstitial cells are found around the cysts showing spermatogenesis, whereas differentiated interstitial cells appear around tubules with mature spermatozoa and reach their greatest differentiation after spermination. This led Ucci (1982) to suggest the occurrence of a local feedback control of interstitial cell development by the seminiferous epithelium. This author has postulated that a diffusable product of the seminiferous epithelium acts locally to regulate androgen biosynthesis or to modulate the sensitivity of interstitial cells to luteinising hormone. This agent might enhance or inhibit interstitial cell development during part of the cycle. A similar idea has been put forward for the rat testis by Aoki and Fawcett (1978) and Bergh (1982) who attributed the production of this agent to the Sertoli cells. Recently, a nongonadotropic Leydig cell stimulating factor has been isolated in rat testicular interstitial fluid (Risbridger, Jenkin and De Kretser, 1986).

Another possible explanation for the seminiferous epithelium-interstitial relationship cells is that these cells would be involved in the regulation of the spermatogenetic cycle through a direct supply of testosterone to the seminiferous epithelium (Ritzén, Boitani, Parvinen, French and Feldman, 1982). An interesting finding is that the stage of the rat seminiferous epithelium (spermatozoon formation and release) showing the maximum volume density of Leydig cells correspond to the highest concentration of intratubular testosterone (Parvinen and Ruokonen, 1982). This increased testosterone concentration at the end of spermatogenesis might be responsible for sperm formation and release or the preparation of the seminiferous epithelium for the initiation of spermatogensis in the following cycle. A series of experiments in

anurans suggests that sperm formation and release are androgen-dependent processes (Lofts, 1974; Rastogi *et al.*, 1981).

The number of interstitial cells apparently decreases from May to September if quantitations are expressed as the number of cells per unit of testicular volume. However, when these values are transformed into absolute values, it is seen that the interstitial cell number per testis remains constant throughout the cycle. This suggests that the interstitial cells do not degenerate yearly but they only undergo cyclic changes in their morphology and activity. If well-differentiated interstitial cells degenerated and died in summer, the rapid increase in the number of undifferentiated interstital cells in this short period could only be explained in terms of a proliferation of these cells or their precursors; however, no mitoses were seen in the testicular interstitium.

The close association of developed thumb pads and the presence of numerous interstitial cells with an abundant testosterone content agrees with the notion that thumb pads are androgen-dependent structures (Müller *et al.*, 1977; Jorgensen and Billeter, 1982).

ACKNOWLEDGEMENTS

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OBSERVATIONS OF GUT FUNCTION IN YOUNG GREEN TURTLES
CHELONIA MYDAS L.

J. DAVENPORT, S. ANTIPAS AND E. BLAKE

Animal Biology Group, Marine Science Laboratories, Menai Bridge, Gwynedd LL59 5EH, North Wales, UK.

ABSTRACT

Food consumption in post hatchling *Chelonia mydas* rises linearly between 18°C and 33°C. It is predicted that food intake will cease between 15°C and 16°C. The large intestine of post hatchlings is only half the length of the small intestine (c.f. 2.5 times the length of the small intestine in adults). The food of post hatchlings spend most of its transit time in the stomach and small intestine; that of yearlings (i.e. animals of 0.5-1.0 kg body wt) spends most time in the large intestine. The changes in gut proportions and in the residence time of meals in the large intestine during development are correlated with a shift from a carnivorous to a herbivorous diet. Yearling turtles are capable of digesting plant material, achieving an energy absorption efficiency of 68 per cent on a diet of *Zostera* (c.f. 87 per cent on a diet of cod flesh). Yearlings have the ability to move food to and fro in the large intestine; several meals reside in the large intestine at once and become mixed. Posthatchling and yearling *Chelonia mydas* can store food for short periods in the oesophagus.

INTRODUCTION

Over the past few years there have been several studies devoted to the nutrition and energetics of the sea turtle *Chelonia mydas* L. (e.g. Bjorndal, 1979, 1980, 1985; Wood and Wood, 1981; Mortimer, 1981; Davenport *et al.*, 1982; Hadjichristophorou and Grove, 1983; Davenport and Oxford, 1984). A major reason for the interest in *Chelonia mydas* is that adult green turtles, unlike other living sea turtles species, are predominantly herbivorous with a definite preference for seagrass (*Thalassia* supp.) and eelgrass (*Zostera* supp.), although they subsist on benthic algae in some areas (e.g. Ferreira, 1968). Bjorndal (1979) showed that adult animals possessed a cellulose-degrading gut microflora in the large intestine. Thompson (1980) has demonstrated that the large intestine of adult green turtles is more than twice as long as that of the carnivorous loggerhead turtle *Caretta caretta* (compared with the small intestine) and has related this to the green turtles' herbivorous diet.

Hatchling green turtles have rarely been seen in the wild after leaving their hatching beach, and the period between hatching and arriving on seagrass beds as fairly large animals (c. 2-5 kg) is obscure (the 'lost year' — Carr, 1967). In the Caribbean, where most studies have been carried out, it seems probable that young green turtles are associated with sargassum rafts (Carr and Meylan, 1980) during this period, and are opportunistic carnivorous that feed upon ctenophores, tunicates and sea anemones (Hirth, 1971; Booth and Peters, 1972). Sargassum rafts are unavailable to some populations of *Chelonia mydas*; Davenport and Oxford (1984) reported that hatchling green turtles from Cyprus were omnivorous and would readily consume algae, sponges, invertebrates and fish (being capable of chasing and catching the mobile species). Davenport and Oxford also reported that faeces of the young turtles contained gram negative rod bacteria capable of digesting cellulose, suggesting that they too are adapted to deal with plant material in their diet.

Hadjichristophorou and Grove (1983) and Davenport and Oxford (1984) studied gut clearance times in young green turtles, and found that these were prolonged. However, the latter authors suggested that the long recorded gut clearance times might be to some extent erroneous because of the large intestine acting as a fermentation reservoir, mixing material from 'old' meals, with 'new' meals, to spread label to material with which it was not originally associated. Although experiments with radio-opaque barium sulphate labelled food tended to support this hypothesis, their qualitative nature made firm conclusions impossible.

The study reported upon here was designed to yield quantitative data about residence times of meals in various parts of the gut of young *Chelonia mydas*; to determine whether the turtles sorted material in the gut, or moved material to and fro in the large intestine; to investigate the effect of temperature on food consumption; to measure the length of the large intestine in post hatchlings; and to measure absorption efficiency in animals fed plant and flesh diets.

MATERIALS AND METHODS

COLLECTION AND MAINTENANCE

Recently hatched specimens of *Chelonia mydas* were acquired from the Lara Reserve Turtle Project, Department of Fisheries, Cyprus. Initially they weighed between 31 g and 58 g. They were studied immediately and subsequently for about 3 months during which they grew to 80-150 g. Study was then interrupted until the turtles were about 8 months old (520-645 g). Work upon them continued until they

were 13 months old (740-980 g). At this point they were returned to Cyprus for release into the Mediterranean Sea. For the purpose of this study the animals up to 3 months old will be described as 'post hatchlings'; those 8-13 months old as 'yearlings'. Throughout, animals were held in circulating sea water (34 per cent) at 25±1°C unless otherwise stated. Routine feeding was upon floating commercial trout food (Omega trout pellets).

EFFECT OF TEMPERATURE ON ROUTINE FEEDING IN POST HATCHLINGS

Two post hatchlings were held in sea water in each of five temperature baths set at the following temperatures: 18, 21, 25, 27 and 33°C. Trout pellet meals of known weight were offered to each of them daily for 9 days. Uneaten food was filtered, dried and weighed to allow the calculation of routine meal size.

INTESTINAL PROPORTIONS OF POST HATCHLINGS

Single frozen specimens of post hatchling *Chelonia mydas* and *Caretta caretta* (loggerhead) were dissected and the lengths of the small and large intestines measured.

MOVEMENT OF MATERIAL ALONG THE GUT

Post hatchlings and yearlings were fed on a diet prepared in the following manner. Trout pellets were ground in a mortar with barium sulphate (5:1 by weight) to provide a basic barium meal to outline the gut during X-radiographic studies. Radio-opaque barium sulphate spheroids (ICI Ltd) were added and carefully mixed into the barium meal, so that a 2 per cent body weight meal would contain roughly 100 spheroids (each spheroid weighing 0.9 mg). This meal was then mixed with a hot solution of gelatin in water (40 g gelatin: 100ml water) and allowed to set in plastic dishes. When cool, the meal was cut into pieces of appropriate size to allow easy swallowing by the post hatchling or yearling being studied. The gelatin was needed to prevent spheroids falling out of the meal during feeding.

In each gut transit experiment, a turtle was fed meals of trout pellets mixed with gelatin for 2 days; it was then deprived of food for 30 h (post hatchlings) or 48 h (yearlings) before being offered a 2 per cent body weight meal of the barium sulphate/barium spheroid diet. The period of food deprivation was needed to ensure complete consumption of a rather unappetising meal. The turtle was X-rayed before the meal and at regular intervals thereafter. After the barium meal the animal was fed daily (1.5 per cent body weight meals being offered) upon trout pellets mixed with gelatin until the end of the experiment.

To confirm that the barium spheroids provided a true reflection of the rate of movement of food through the gut and were not sorted, single post hatchlings and yearlings were each fed a diet containing barium sulphate, barium spheroids and fine, varnish coated iron particles. The animals were X-rayed for several days to check that the barium shadows, spheroid images and iron particle images remained together throughout gut transit.

IRON TAG EXPERIMENT

Davenport and Oxford (1984) suggested that food might be moved to and fro in the hind gut of green turtles to aid microbial fermentation. To test this hypothesis, two yearlings were each fed a barium and spheroid labelled meal which also contained a 6mm long metal tag encased in soft, thin plastic. The barium meal was preceded by a 48 h period of food deprivation. Regular X-rays were taken after the tagged meal.

ABSORPTION EFFICIENCIES

Although adult green turtles are largely herbivorous (Bjorndal, 1980, 1985; Mortimer, 1982), they will take animals on occasion (Kooyman, 1972) and it is now clear that young green turtles, like the young of other sea turtle species, are predominantly carnivorous, though they will eat plant material if hungry (Booth and Peters, 1969; Witham, 1980; Davenport and Oxford, 1984). It was decided, therefore, to compare absorption efficiencies for energy in yearlings fed upon animal and plant diets. All six available yearlings were used, and ranged between 714 g and 981 g at the time of the experiments. The following experimental procedure was used. Fresh cod (*Gadus morhua*) was skinned and muscle tissue finely minced. Sea grass (*Zostera supp.*) was collected from small beds at Morfa Nefyn (Lleyn Peninsula, North Wales); it was finely chopped. Gelatin was used to bind the diets, and chromic oxide (2 per cent by weight) was thoroughly mixed with each. Batches of food without the chromic oxide label were also prepared. Three yearlings were fed for 7 days on label-free fish, then for 4 days on labelled cod. This feeding regime was followed by 7 days of feeding on label-free sea grass and 4 days on labelled sea grass before returning to the normal trout pellet diet for several days. During this whole procedure the turtles produced green, chromic oxide-laden faeces during two periods, each lasting several days. The faeces were all collected, but only those voided at the midpoint of each period were subsequently analysed. These latter faeces therefore correspond a) to the cod meals and b) to the meals of *Zostera*. The other three yearlings were handled in similar fashion, but were fed sea grass first and cod second.

Chromic oxide labelled food and faeces samples were oven dried at 45°C for 8 days and then stored in a desiccator until analysed. Chromic oxide content was analysed by wet oxidation to dichromate and subsequent spectrophotometric determination by the diphenylcarbazide reaction (McGinnis and Casting, 1964). Energy content of food and faeces was measured by bomb calorimetry.

RESULTS

EFFECTS OF TEMPERATURE ON FOOD CONSUMPTION IN POST HATCHLINGS

The effect of temperature on food consumption in post hatchlings is shown in Table I. It appears that food consumption and temperature are linearly related over this temperature range, and from the regression

equation derived from the data it may be calculated that food consumption will cease between 15°C and 16°C. The regression also indicates that Q_{10} for food consumption is much greater at lower temperatures:

Q_{10} 18-23°C = 9.64

Q_{10} 23-28°C = 2.82

Q_{10} 28-33°C = 1.97

INTESTINAL PROPORTIONS OF POST HATCHLINGS

The ratio of the length of the large intestine to the length of the small intestine in post hatchling turtles can be compared with that in the adults measured by Thompson (1980):

	Chelonia	*Caretta*
Post hatchling	0.45	0.97
Adult	2.52	0.89

Turtle No.	Temperature (°C)	Mean Meal Size (% body wt d^{-1})
1.	18	0.13
2.	18	0.13
3.	21	0.33
4.	21	0.46
5.	25	0.59
6.	25	0.60
7.	27	0.64
8.	27	0.69
9.	33	0.99
10.	33	1.34

TABLE 1: Effect of temperature on routine food consumption (measured over 9 days) in post hatchling *Chelonia mydas*.

Regression analysis of above data shows that mean meal size (y % d^{-1}) is linearly related to temperature (x°C) by the following equation:

$$y = 0.064x - 1 \qquad (R^2 = 0.92)$$
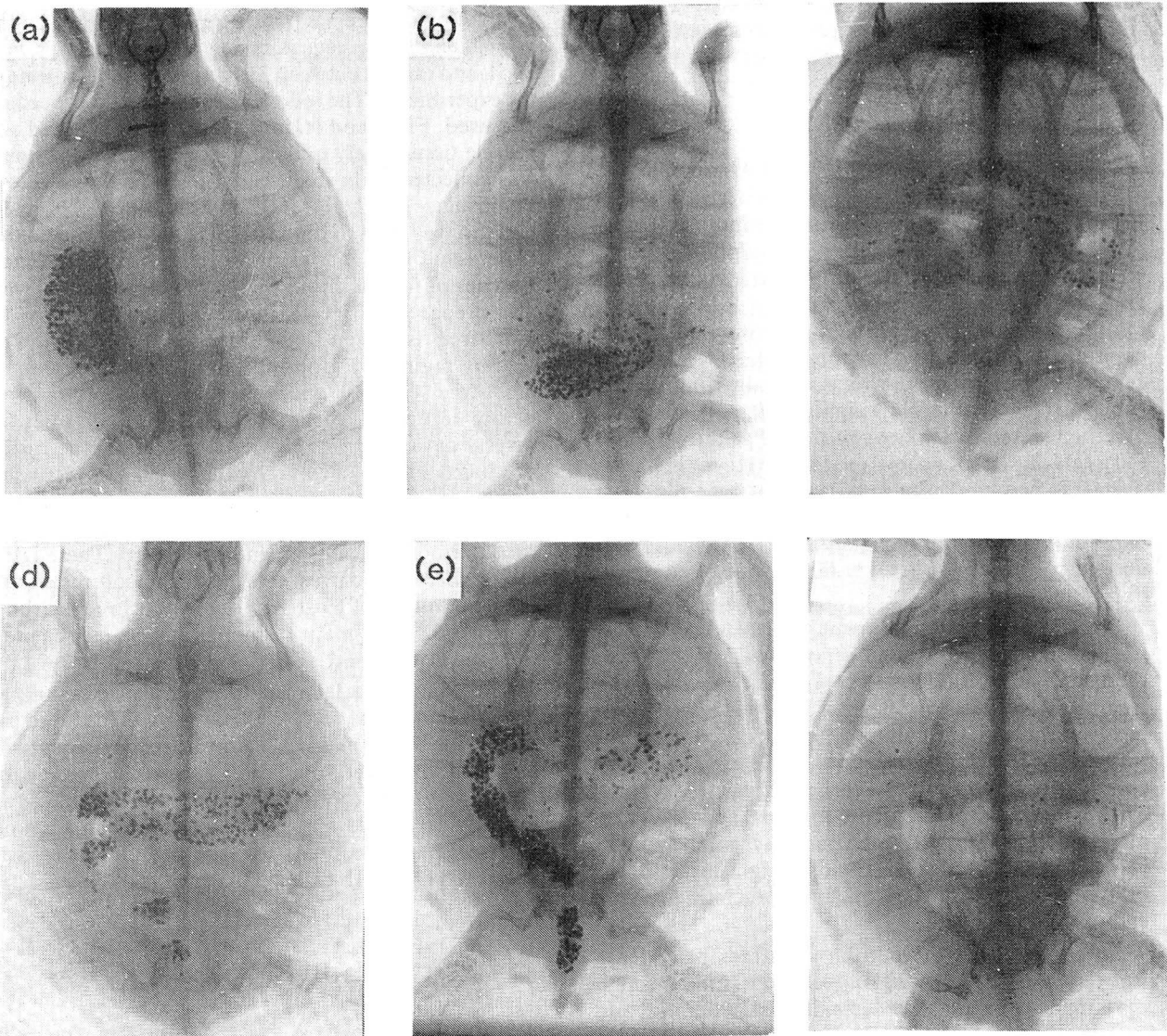
PLATE I. Progress of barium spheroid labelled meal through the gut of a post hatchling specimen of *Chelonia mydas*. (a) 15 min after meal. Note spheroids in oesophagus and stomach. A few (9) spheroids are scattered in the intestines and were apparently derived from reingested faeces. (b) 7 h after meal. Spheroids are entering duodenum. (c) 24 h after meal; spheroids mainly in small intestine. (d) 70 h after meal. Spheroids mainly in large intestine. (e) 71 h after meal. About to defaecate bulk of spheroids. (f) 97 h after meal. A few spheroids in large intestine.
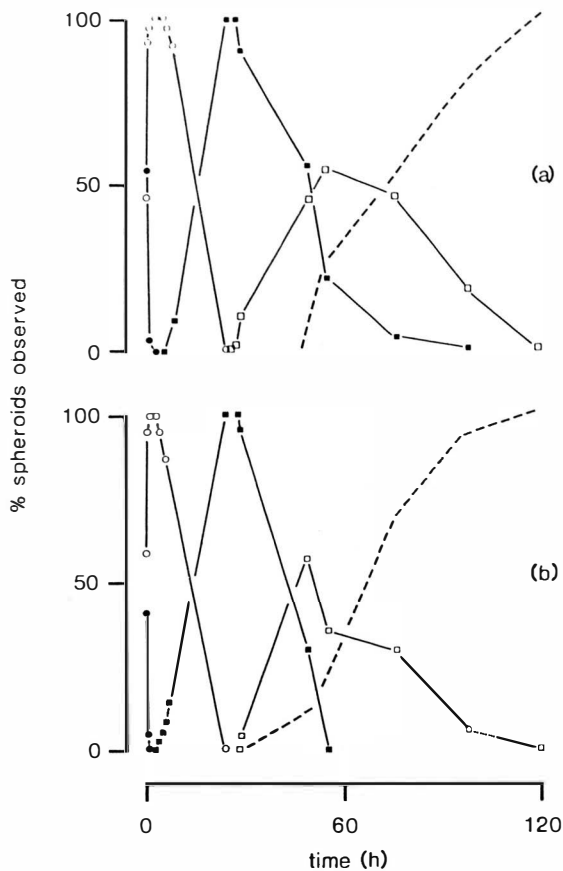
Fig. 1 Meal residence time in different parts of the gut of two posthatchling *Chelonia mydas*. Closed circles represent residence in oesophagus, open circles in stomach, closed squares in small intestine, open squares in large intestine. Dashed line represents defaecated spheroids.

Although post hatchling and adult *Caretta caretta* have similar ratios between the lengths of the large intestine and small intestine, with the large intestine being slightly the shorter, the situation for *Chelonia mydas* is different. While Thompson (1980) found that the adult green turtle has a large intestine more than twice the length of the small intestine, the post hatchling dissected in the present study possessed a large intestine less than half the length of the small intestine. Obviously more data collection would be desirable (though hardly from a conservation viewpoint !), but it seems likely that the relative size of the large intestine of *Chelonia mydas* increases substantially between hatching and maturity.

MOVEMENT OF MATERIAL ALONG THE GUT

Plate I illustrates the progress of barium sulphate spheroids through the gut of a post hatchling turtle and demonstrates their visibility. Figs. 1 and 2 show the residence times (at 25°C) of spheroid-labelled meals in different parts of the gut of post hatchlings and yearlings, respectively. These data demonstrate that gut function changes as *Chelonia mydas* grows. Firstly they indicate that total gut clearance time (TGCT) is rather longer in yearlings than in post hatchlings. Secondly, there are differences in the proportion of time that spheroids spend in different parts of the gut.

In post hatchlings there is some retention of food in the oesophagus, but within 15-30 min all of the meal is present in the stomach. The meal remains wholly within the stomach for at least 2-3 h and only after 5-7 h are significant numbers of spheroids transferred to the small intestine. By the time 24 h have elapsed all
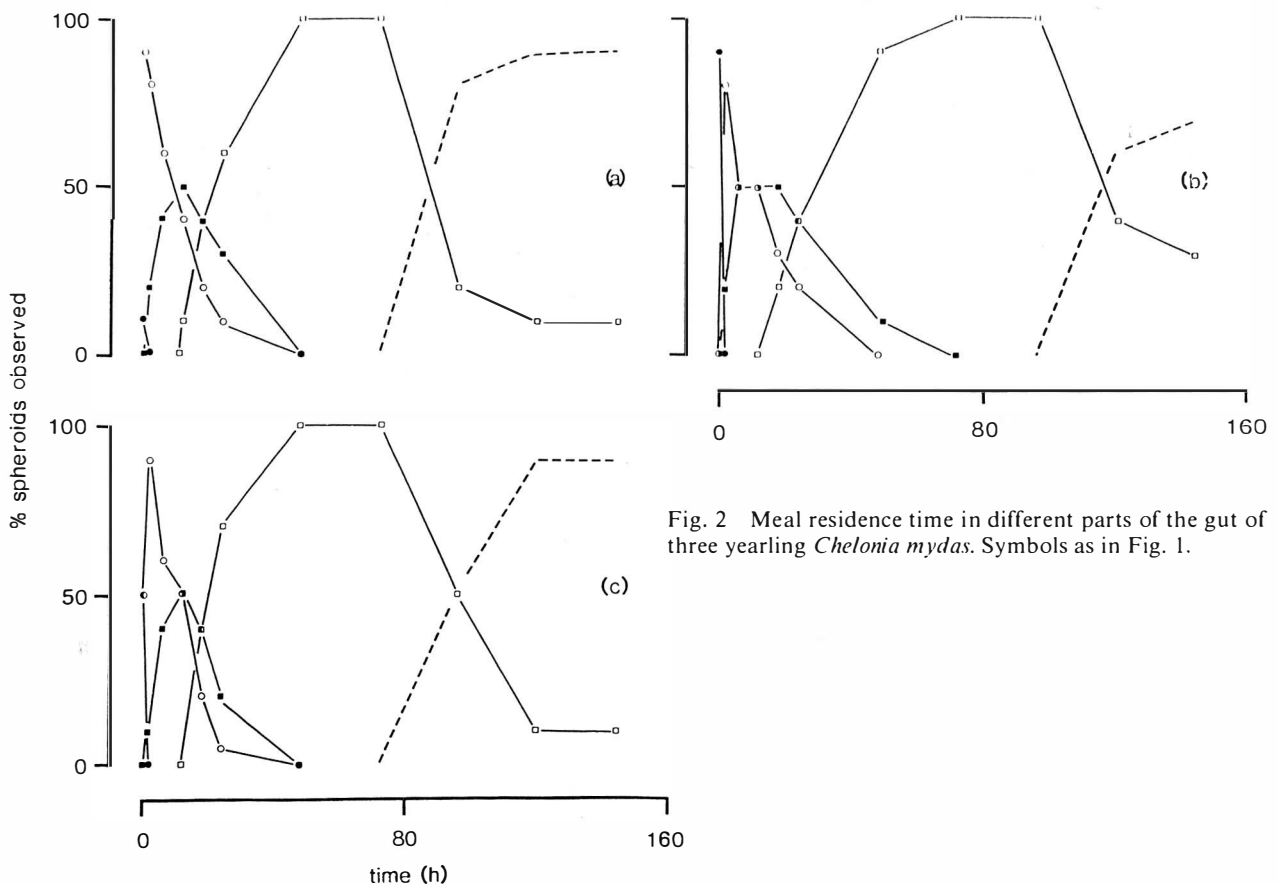
Fig. 2 Meal residence time in different parts of the gut of three yearling *Chelonia mydas*. Symbols as in Fig. 1.

of the meal is in the small intestine; small amounts start to move into the large intestine after 26-28 h. No more than 50-60 per cent of the spheroids are present in the large intestine at any one time as defaecation starts 48-72 h after ingestion of a meal. In post hatchlings it is evident that meals are accommodated in the anterior portions of the gut for most of their transit time.

In yearlings the oesophageal residence is again short (15-30 min), but by the time the last spheroids have moved from the oesophagus into the stomach, others have already entered the small intestine. In consequence, the meal is never wholly contained within the stomach. Residence time within the small intestine is relatively short and substantial quantities of spheroids reach the large intestine within 18 h. No more than 50 per cent of the spheroids are found inside the small intestine at any one time. The whole meal is held within the large intestine by the time 48-72 h have elapsed. Defaecation of the meal starts after 72-96 h, but was not complete at the end of the study period (terminated after 144 h) in any of the yearlings studied. It appears that the food of yearlings spends most of its gut residence time in the large intestine. The curves shown in Fig. 2 each represent the progress of a single meal in a sequence of daily meals. Since material from a labelled meal reaches the hind gut within 18 h, but is not fully defaecated by 144 h, the curves imply that parts of several daily meals are present in the large intestine at the same time.

The date derived from the experiments with iron tags were rather equivocal. In one yearling turtle the tag (which gave a very strong X-ray image) remained in the stomach for a while after the associated barium meal had left, but thereafter progressed steadily along the gut with no hint of to and fro movement. In the other yearling the tag moved steadily in one direction until it reached the descending colon of the large intestine, but was then left in a gas pocket before moving backwards into the loops of the large intestine. It is evidently possible for material to move to and fro in the hind gut as suggested by Davenport and Oxford (1984), but whether this happens because of two-way peristalsis or simply in association with the movement of gas bubbles is not yet clear.

During one of the iron tag experiments a yearling ate faeces containing spheroids; these spheroids 'caught up' in the large intestine with the spheroids of the previous labelled meal and mixed with them.

ABSORPTION EFFICIENCY (OF ENERGY) IN YEARLINGS

To calculate the absorption efficiency (energy) on plant and animal diets, the data shown in Table 2 were used with the following equation:

$$E = 100 \times 1 - \frac{(c^d/e^d)}{(c^f/e^f)}$$

Where E = absorption efficiency (%)
  c^d = chromic oxide content of diet
  e^d = energy content of diet
  c^f = chromic oxide content of faeces
  e^f = energy content of faeces

	Mean Chromic oxide content (mg g^{-1})	Mean Energy content (KJoules g^{-1})
(A) Foods		
1. Cod flesh	1.81	22.68
2. *Zostera* spp.	2.73	18.45
(B) Faeces		
1. Cod diet	9.09	14.73
2. *Zostera* diet	8.09	17.57

TABLE 2: Chromic oxide and energy contents of food and faeces of 6 yearling *Chelonia mydas* fed on plant and animal diets.

On a diet of cod yearlings had an absorption efficiency of 87 per cent; on a diet of *Zostera* the efficiency was 68 per cent.

DISCUSSION

The literature devoted to the thermal biology of sea turtles is extensive (see Mrosovsky, 1980 for review). Although the lower lethal temperatures of green and loggerhead hatchlings are below 10°C (Schwartz, 1978) there is abundant evidence to show that turtles do not grow at temperatures below 20°C and move away from coastal feeding grounds during winter when temperatures are low (Carr et al., 1980), Bjorndal (1980) also found that absorption efficiencies became low and variable in green turtles at low temperatures (about 20°C). At about 15°C, the temperature at which we predict feeding will cease, there is evidence that green turtles become torpid, with some populations hibernating (Felger et al., 1976). The upper lethal temperature for green turtles is not known though Bustard (1970) reported that hatchlings survived rectal temperatures of 36-40°C for 15 min. The temperature range employed in this investigation is therefore a fair reflection of the total thermal range over which feeding can take place. The steady rise in food consumption with increasing temperature is similar to that observed in young loggerhead turtles, but the maximum rate of food intake (c. 1 per cent body weight d^{-1}) is less than half that of post hatchling loggerheads (Birse and Davenport, 1987), Bjorndal (1981) suggested that adult green turtles have a low rate of food consumption rate because their sea grass diet requires a long gut residence time (thus limiting intake), but it seems that low food consumption is inherent in *Chelonia mydas* throughout life.

It is accepted that large juvenile and adult green turtles (8-66 kg) are predominantly herbivorous (e.g. Ferreira, 1968; Bjorndal, 1980), while recently hatched animals are believed to be opportunistic carnivores. The results presented in this study demonstrate that green turtles not only change their diet during development, but also alter their gut proportions and function. The large intestine of post hatchlings is less than half the length of the small intestine (this study), while that of adults is more than 2½ times the small intestine length (Thompson, 1980). We have no

measured intestinal lengths for the yearlings investigated here, but qualitative observation of X-ray plates indicates a considerable lengthening of the large intestine (and increased convolution) in comparison with the post hatchlings. The lengthening of the large intestine is associated with a change in the pattern of gut residence; meals remain longest in the foregut of post hatchlings, but in the large intestine in yearlings. The TGCT values recorded in this study with barium spheroids are much shorter than those derived from observations of coloured food label in faeces. This is particularly true of hatchlings. Davenport and Oxford (1984) recorded TGCT values as high as 394 h (vs. 120 h in this study). We suspect that unnoticed faecal ingestion may have been partly responsible for the extreme values.

A capacious large intestine in which meals spend a long time has been correlated with herbivory as these features facilitate the breakdown of cellulose by microorganisms. Bjorndal (1980) demonstrated a cellulytic flora in adult green turtles; Davenport and Oxford (1984) obtained evidence (albeit not conclusive) that such microorganisms were present in post hatchlings too. The absorption efficiency data collected in the present study confirm that yearlings (i.e animals of about 0.7-1.0 kg) can readily digest plant material since 68 per cent of the energy content of meals of *Zostera* is absorbed — a value well within the range reported for large juvenile and adult animals feeding on sea grass (21-71 per cent at 20-35°C; Bjorndal, 1980). This indicates that effective herbivory develops earlier in the life of *Chelonia mydas* than previously recognised, perhaps indicating a phase during which more and more plant material is taken. The rather higher absorption efficiency on a diet of cod flesh (87 per cent) shows that the ability to digest plant material does not diminish the turtles' capacity for exploiting available animal food sources. Energy absorption efficiencies have rarely been reported for reptiles, especially herbivores, but the literature reviewed by Hamilton and Coe (1982) suggests that green turtles are as efficient in their digestion as herbivorous lizards (54.5-69.5 per cent) and markedly more efficient than Aldabran giant tortoises which only achieve 34.5 per cent.

The measured large intestine residence times, the results of the 'iron tag' experiments, and the observation of 'catch up' by spheroids from reingested faeces all indicate that material from several meals is present in the hind gut at the same time, and that mixing of meals takes place. This will be of advantage for digesting plant material, facilitating the inoculation 'new' material with microorganisms from 'old' meals.

Two interesting details of food movement in the gut were revealed by this study. Firstly, it is clear that both post hatchling and yearling green turtles can store food in a distended oesophagus. They do not often do so, and only for a limited period (15-30 min). This contrasts with the abilities of the loggerhead sea turtle *Caretta caretta* (Birse and Davenport, 1987) and the freshwater turtle *Mauremys caspica* (Davenport and Kjørsvik, 1988), both of which can store food in the oesophagus for more than an hour. However, all three cryptodiran species studied in these laboratories have

shown oesophageal storage; Davenport and Kjørsvik suggested that such storage originated in chelonians capable of retracting the head into the shell (which sea turtles are not), possibly in response to the necessity for sudden head retraction during meals interrupted by predators.

Secondly, it was noticed that the food of yearlings often went straight through the stomach into the small intestine; there is little evidence of a sphincter guarding the duodenum. It is doubtful whether adult green turtles eat 'meals' as such in the wild; instead they browse on benthic algae or sea grass beds, in the latter case selecting the young leaves with least lignin (Bjorndal, 1981). Since most digestion takes place in the large intestine there will be little need to retain food in the stomach.

ACKNOWLEDGEMENTS

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ACTIVITY AND THERMOREGULATION IN THREE MEDITERRANEAN SPECIES OF LACERTIDAE

C. POLLO MATEOS AND V. PÉREZ-MELLADO

Department of Animal Biology, University of Salamanca, 37071-Salamanca, Spain.

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ABSTRACT

A study was made of the thermoregulatory development and activity rhythms, both daily and annual, of three species of mediterranean Lacertidae: *Psammodromus algirus, P. hispanicus* and *Acanthodactylus erythrurus*, recording 505 cloacal temperatures (TB). Statistically significant correlations were found between the TB and the TA and TS (temperatures of the body, environment and substrate, respectively) values of the different age and sex classes established in *P. algirus* and *P. hispanicus* but not in some age and sex classes of *A. erythrurus*.

A. erythrurus, mainly the adult males, was the species that showed the greatest thermoregulatory efficiency.

Both *Psammodromus* species remain active from March to October, while the fringe-toed lizard shows an annual activity from May to September.

INTRODUCTION

The activity rhythms, and in particular thermoregulation are less well known aspects in the ecology of the Iberian Lacertidae. In the case of the species examined here, *Psammodromus algirus, Psammodromus hispanicus* and *Acanthodactylus erythrurus*, there are few works that have dealt with these topics; in this sense, only Mellado *et al.* (1985), Busack (1976 and 1978), Pough and Busack (1978), Pérez-Mellado (1981), Seva (1982) and Seva and Escarre (1980) offer some data.

Our aim in the present work was to provide a definition in these species of what could be termed "niche thermal dimension", a parameter that we believe to be of great importance apart from the by now classic definitions of niche for characterising both the autoecology of species and interactions between them.

We felt it essential to determine the daily and annual activity rhythms of the established different age and sex classes (see below) owing to the importance of the three species in communities of Iberian lizards. Regarding *P. algirus*, many basic aspects of its biology remain to be elucidated, in spite of it being one of the most abundant Lacertidae in the southernmost two thirds of the Iberian Peninsula (Arnold and Burton, 1978) and being present throughout the whole of the peninsula with the exception of the extreme northern part (Salvador, 1985). In the study zone, *A. erythrurus* is found close to the northern boundary of its distribution area in the west of the Peninsula such that we felt it interesting to gain insight into its activity cycles and thermoregulatory behaviour in this area. Finally, *P. hispanicus* is undoubtedly one of the least well known Lacertidae regarding its ecology; only recent works have offered data concerning the Spanish *Psammodromus* (Pascual, 1986).

MATERIAL AND METHODS

The study area is located to the south west of the province of Salamanca (Spain) in the neighbourhood of the village of Espeja. The zone features a greater Atlantic influence than the rest of the province, with a sub-humid mediterranean type bioclimate. Sampling was performed from May 1986 to June 1987, with a total number of sampling hours of 85 throughout the months in which the species studied were active. In the case of *P. algirus* and *A. erythrurus*, five age and sex classes were established: adult males, adult females, subadult males, subadult females and juveniles. In this sense, the specimens observed during the years in which they had been born and that had still not gone through a winter season were considered as juveniles; subadults were considered to be the specimens that were observed in the year after they had been born and that had lived through a winter season, and adults were considered to be the specimens detected after two periods of winter lethargy with reproductive capacity. In the case of *P. hispanicus*, we only considered three classes of age and sex: adult males, adult females and juveniles since, according to Pascual (1986) and to our own observations, most of the juveniles of this species reach sexual maturity during the year after hatching, after the winter period.

To determine activity rhythms, a total of 671 observations was made, 197 corresponding to *P. hispanicus*, 287 to *P. algirus* and 187 to *A. erythrurus*; these were made made during the whole of the activity period of the species studied. Using these data, we constructed plots of annual and diurnal activity during the day in different periods of the year according to the behaviour exhibited by the specimens. Regarding this we considered two types of specimens according to their behaviour: a) active specimens, involved in

activities including locomotion, territorial defense, hunting or others and b) specimens showing thermoregulatory activity that in these species is usually heliothermic. The values corresponding to each hourly or monthly segment were obtained applying an index to correct the sampling differences in each period.

A total of 505 cloacal temperatures (TB) were recorded using a Scultheis thermometer, 129 in *A. erythrurus*, 215 in *P. algirus* and 161 in *P. hispanicus* Air (TA) and substrate (TS) temperatures were taken at the same moment as the TB temperatures of the specimens were made; TA was taken at 1 meter above the surface of the soil occupied by the specimen, always in the shade, and TS was taken by placing the thermometer on the substrate, also in the shade.

RESULTS

THERMOREGULATION

A. erythrurus, in all its age and sex classes, showed higher TB values than those of the other two species studied (Table 1). Within the species, the adult males had the highest mean TB but with no statistically significant differences between any of the different age and sex classes (one way ANOVA test, $F_{(4.124)} = 1.65$, n.s.).

The adult females comprise the age and sex class with the highest mean TB values in *P. algirus*, with highly significant differences (one way ANOVA test, $F_{(4.210)} = 7.09$; $P < 0.001$) between all the age classes, except among the adults (Student's t test: subadults between them $t = -3.618$, $P < 0.001$, subadult males-adult males $t = 4.65$, $P < 0.01$; subadult females-females

$t = -4.60$, $P < 0.001$, subadult males-juveniles $t = -2.46$, $P < 0.02$, juveniles-adult males, $t = -2.28$, $P < 0.05$, juveniles-adult females: $t = -2.47$, $P < 0.02$, adult females-juveniles: n.s.).

There were also significant differences between juveniles and adults in *P. hispanicus* ($F_{(4,158)} = 7.166$, $P < 0.005$) but not between adults (adults intra-specimens) $t = -1.38$, n.s.; adults males-juveniles: $t = -3.35$, $P < 0.001$, adult females-juveniles: $t = 1.56$, n.s.).

Correlations were made between TB-TA and TB-TS (see Figs. 1, 2 and 3); only in the case of *A. erythrurus* were coefficients lacking in statistical significance found, which points to the high degree of thermal independence of this species (see corresponding regressions).

HOURLY VARIATIONS AND VARIATIONS WITH MICROHABITAT OCCUPATION

Regarding the hourly time-course of the TB, TA and TS (Figs. 4, 5 and 6), in both *Psammodromus* species, the TB values reached their maxima during the first hours of the morning, probably due to thermoregulatory processes. Following this they fell sharply during the period of activity, to rise gradually thereafter during the middle hours of the day. Regarding the mean values of the TB, TA and TS in the different hourly segments, of the three species we applied the Spearman rank correlation coefficient. The results obtained were as follows: *P. algirus*: TB-TA: rs = 0.8583, $P < 0.01$; TB-TS: rs = 0.5891, $P < 0.05$, *P. hispanicus* TB-TA: rs = 0.5727, $P < 0.05$, TB-TS: rs = 0.6906, $P < 0.05$; *A. erythrurus* TB-TA: rs = 0.60, $P < 0.05$; TB-TS: rs = 0.6363, $P < 0.05$ and hence statistically significant in all cases.

Age class and sex	$\overline{X}$	S	CV	Range	n
* *A. erythrurus*					
adults males	34.20	2.66	7.80	29.5-40	33
adults females	33.41	3.55	10.62	26.5-39.5	26
subadults males	32.54	3.28	10.08	27-37	16
subadults females	32.76	2.55	7.78	27-37.5	19
juveniles	32.66	2.48	7.59	21.5-35.5	35
* *P. algirus*					
adults males	30.89	4.15	13.45	21-38.5	72
adults females	31.27	4.29	13.73	21.5-39.5	47
subadults males	27.19	3.60	13.24	19-32	33
subadults females	30.20	3.04	10.07	22-36.5	31
juveniles	29.23	3.05	10.43	21-38.5	32
* *P. hispanicus*					
adults males	28.94	4.31	14.91	19-38	53
adults females	30.09	3.22	10.69	22.5-36	31
juveniles	31.06	1.87	6.04	21-34.5	77

TABLE 1: Body temperatures of different age and sex classes considered.
$\overline{X}$: arithmetic mean; S: standard deviation; CV: coefficient of variation; n: sample size.
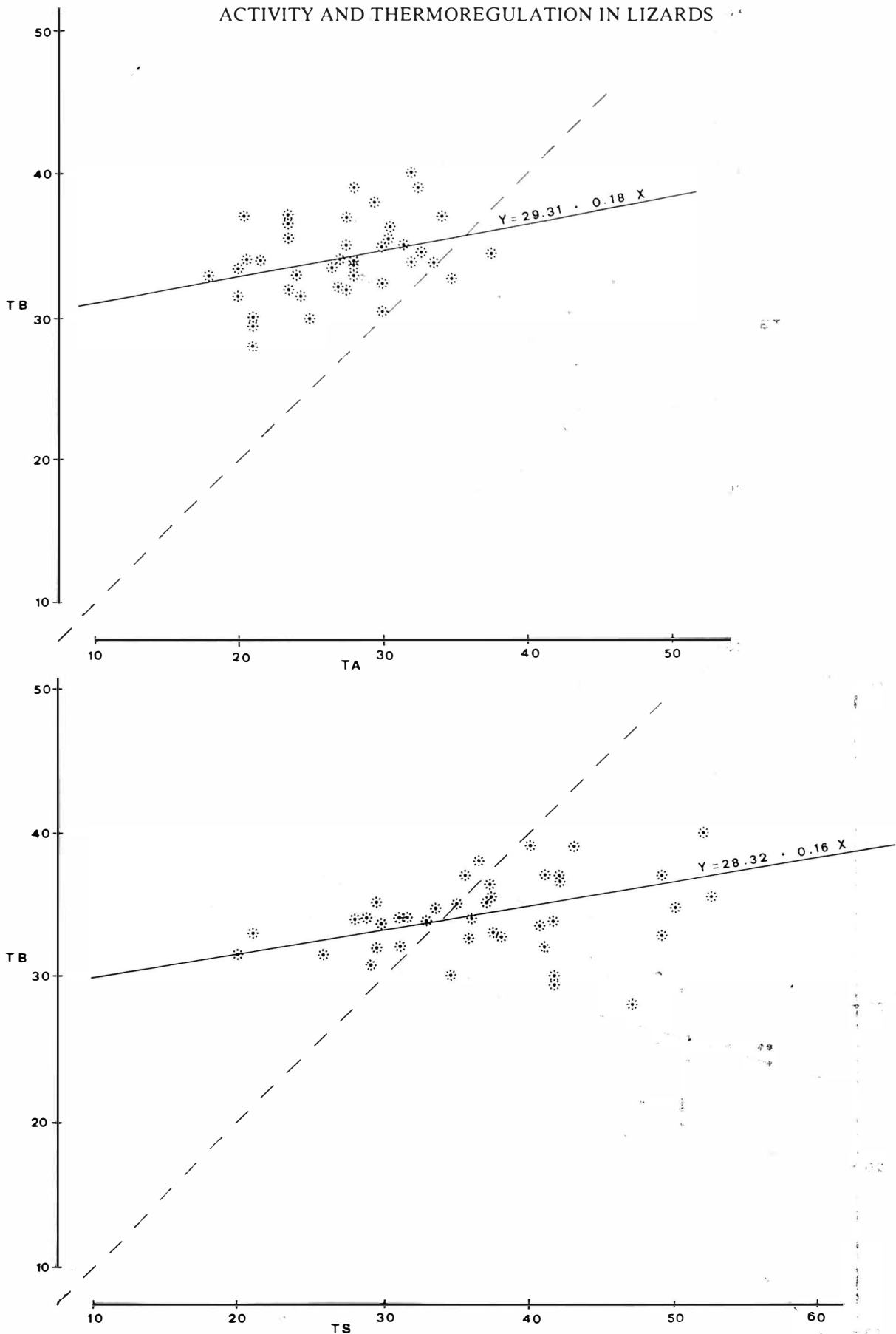
Fig. 1 Several representative examples were chosen of the relationship between body temperatures, environmental temperatures and substrate temperatures, altho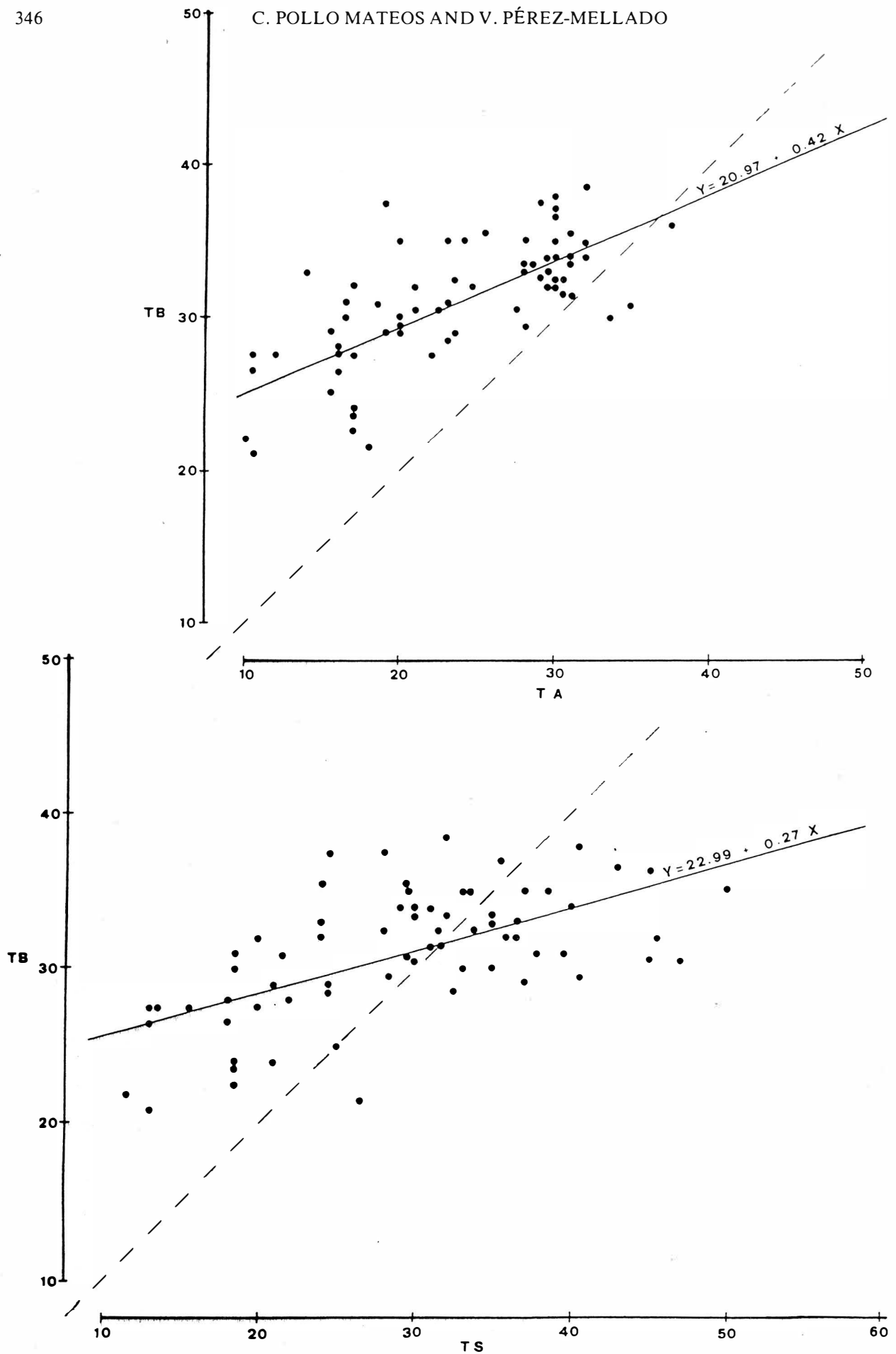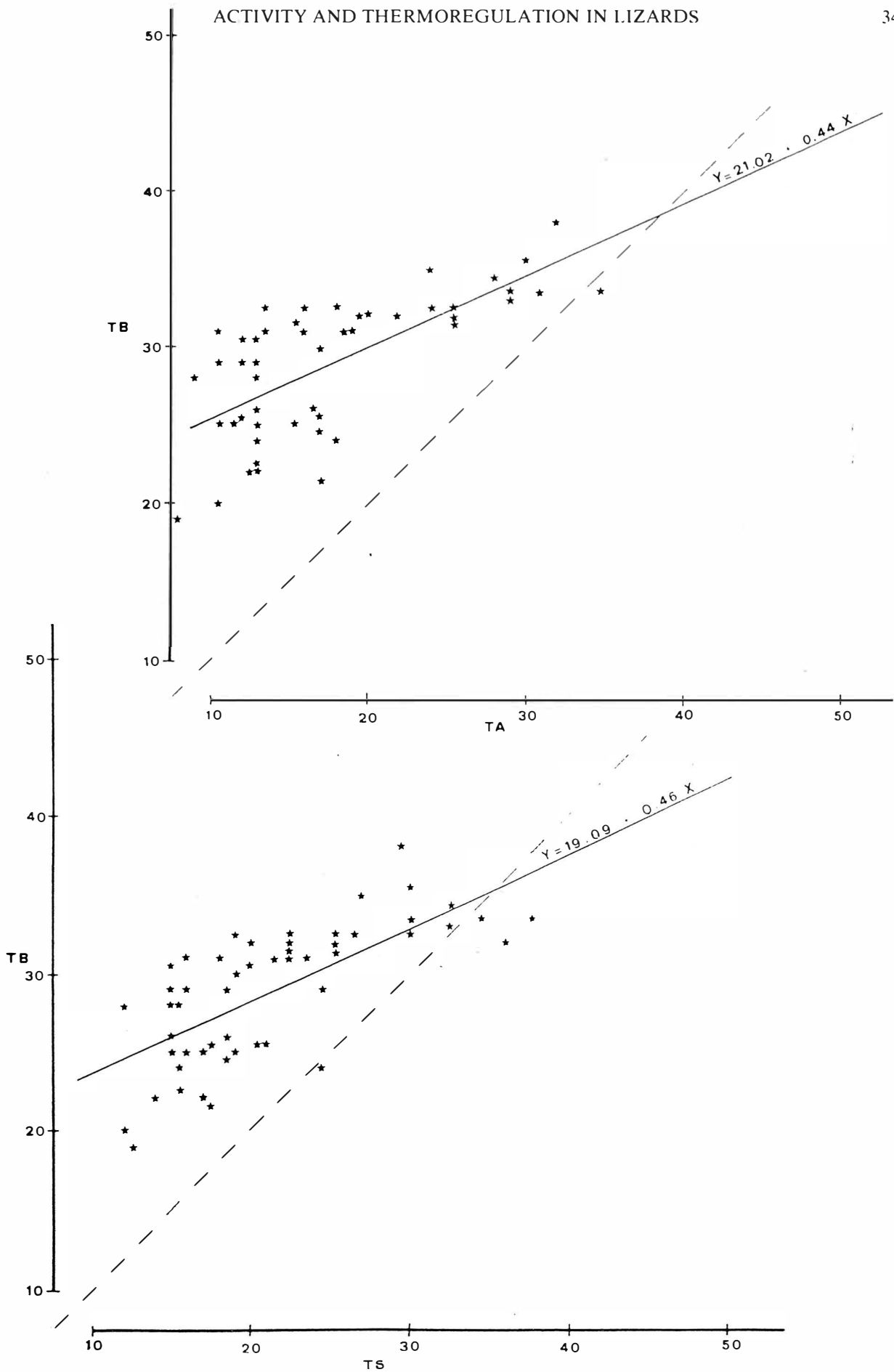ugh analyses were performed on all of the age and sex classes considered. Correlation between Body temperature (TB) and Air temperature (TA) and Substrate temperature (TS) in adults males of *A. erythurus*, both in °C. (TB-TA, r: 0.355, P<0.05; TB-TS, r: 0.438, P<0.02). The dotted line is called the line of perfect poikilothermy (absolute correlation between TB and the other temperature considered).

Fig. 2 Correlation between body temperature (TB) and air temperature (TA) and substrate temperature (TS) in adult male specimens of *P. algirus*, (TB-TA, r: 0.700, P<0.001; TB-TS, r: 0.594, P<0.001).

Fig. 3   Correlation between body temperature (TB) and air temperature (TA) and substrate temperature (TS) in adult male specimens of *P. hispanicus*, (TB-TA, r: 0.686, P<0.001; TB-TS, r: 0.701, P<0.001).
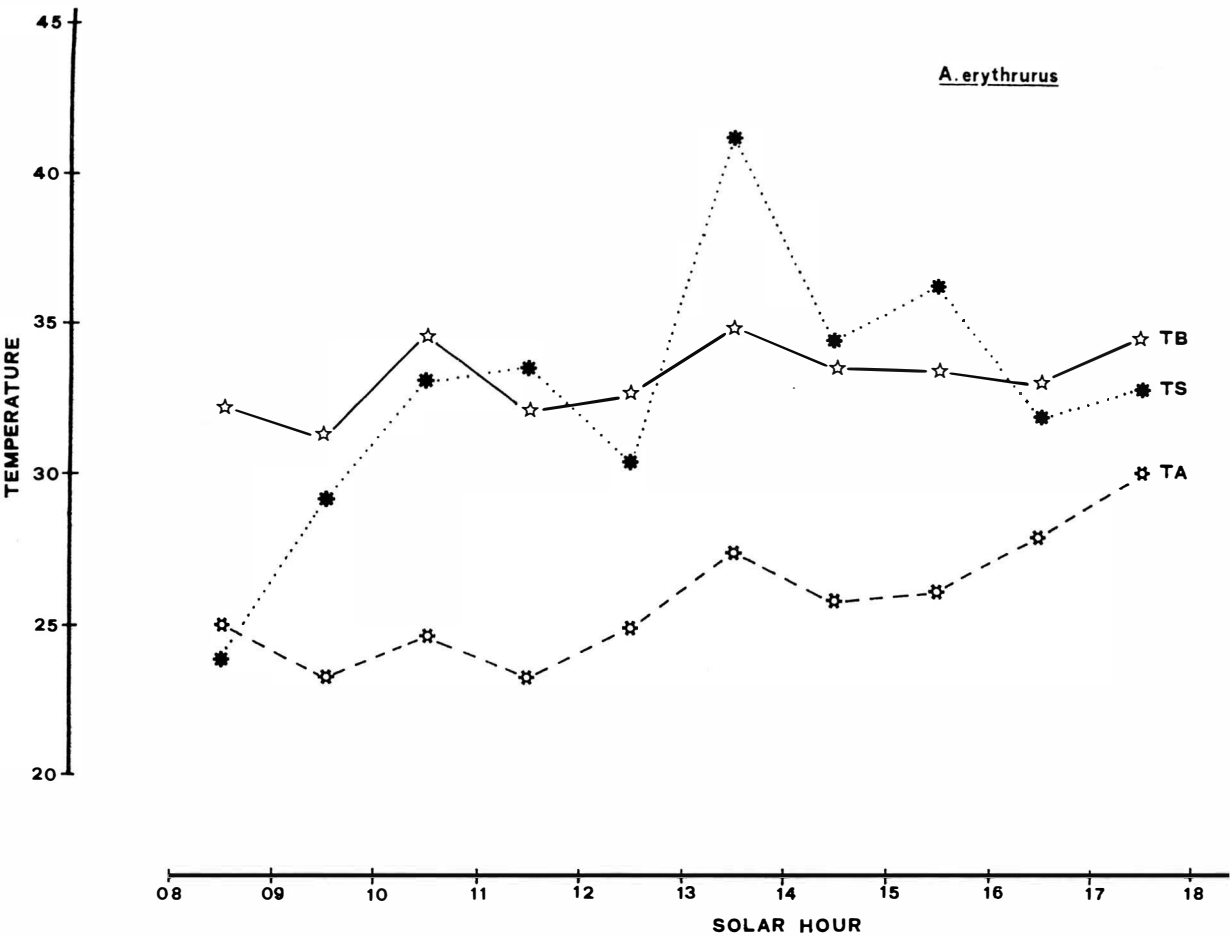
Fig. 4   Hourly variation of TB, TA and TS in *A. erythrurus* for all age classes.
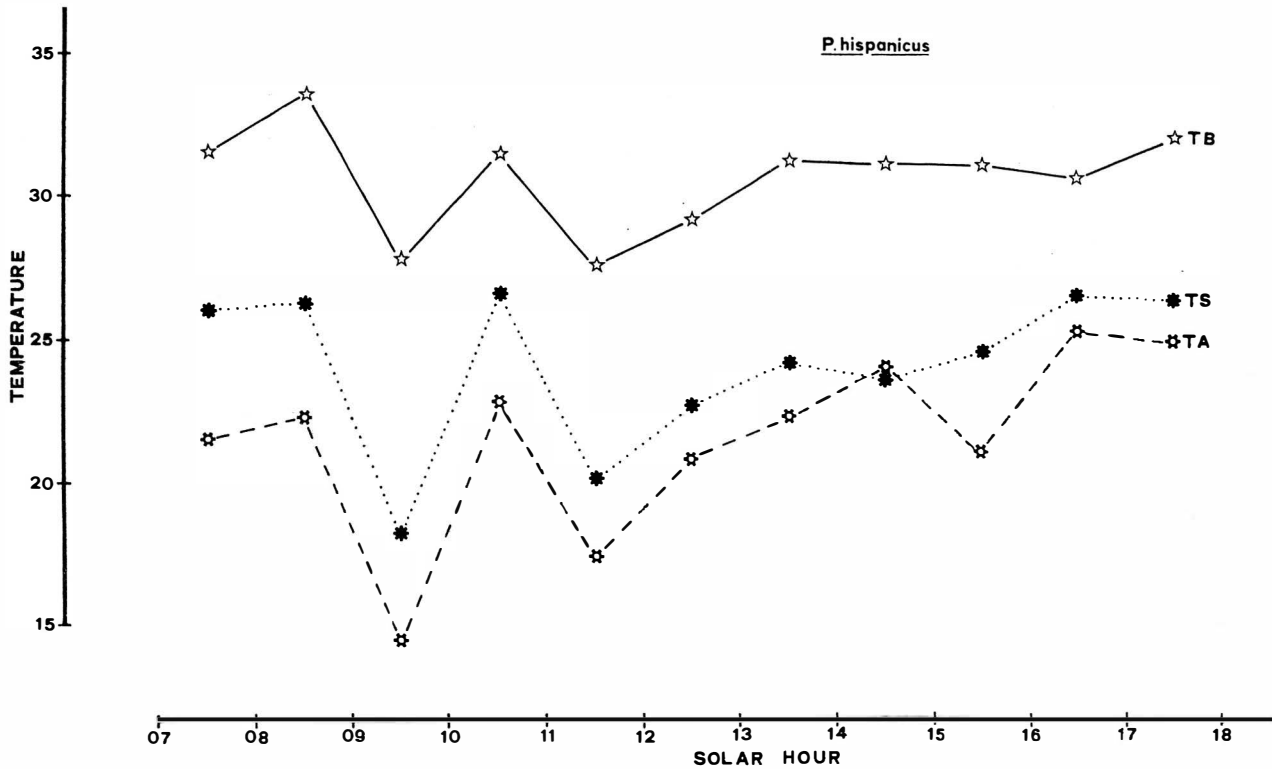
Fig. 5   Hourly variation of TB, TA and TS in *P. hispanicus* for all age classes.
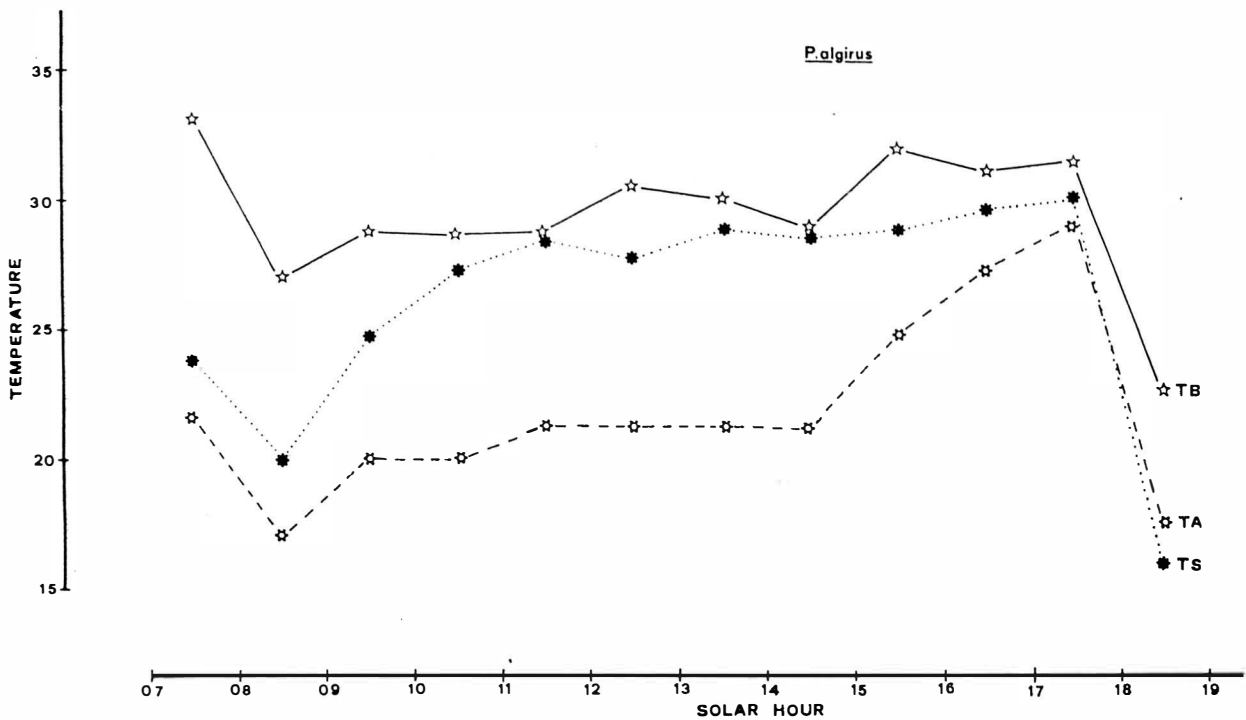
Fig. 6   Hourly variation of TB, TA and TS in *P. algirus* for all age classes.

ACTIVITY

A. erythrurus shows an annual activity period restricted to 5 months, lasting from May to September. By contrast, both *Psammodromus* species have a broader annual period of activity ranging from March to October. *P. hispanicus* has a winter lethargy period in all the populations studied, while *P. algirus* and *A. erythrurus* only show this resting period in areas where the winter season is harsh (Pérez-Mellado, 1982a) although they remain active throughout the year in zones with milder climates (Seva, 1982).

In all three species, the peak activity period in autumn is greater than in spring, undoubtedly due to the appearance of the juveniles. This is specially pronounced in the case of *P. hispanicus* where great activity is shown by this class in this period (autumn), thus allowing some specimens — hatched earlier than their fellows — to reach adult size before the winter lethargy period (Pascual, 1986).

The adults of *P. algirus* and *P. hispanicus* show a bimodal type of activity during the summer months, exhibiting a complete diapause in the middle of the day. By contrast, the adults of *A. erythrurus* show an unimodal activity (Fig. 7a and 7b) throughout the day during all the months in which they are active.

In our study area the subadults and juveniles of this species remain active throughout the day, there only appearing a slight bimodality in activity in the juveniles during the central hours of the day (Fig. 7c and 7d).

In *A. erythrurus*, the activity peak in the morning is higher than that recorded in the afternoon, both in spring and in summer.
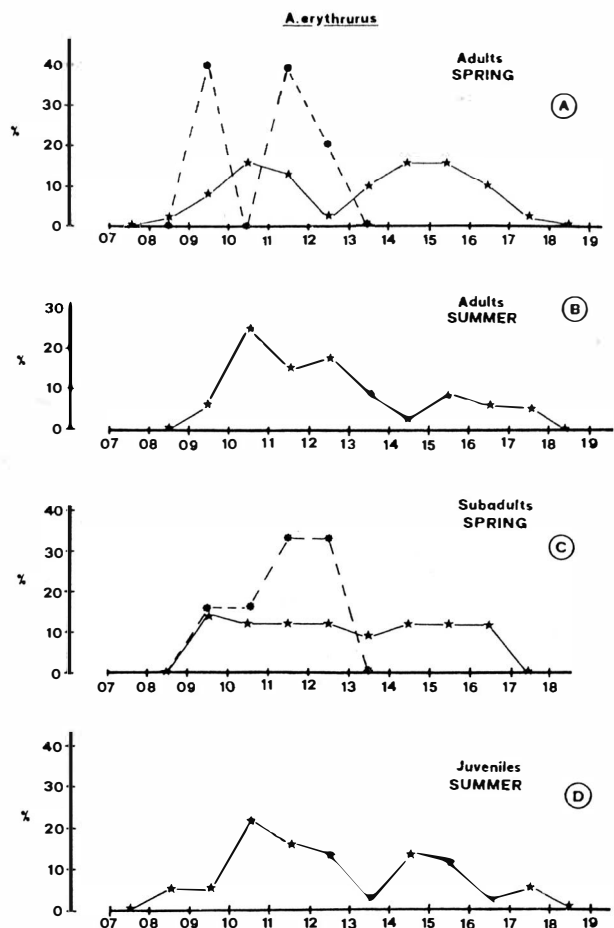
Fig. 7   Behaviour of *A. erythrurus*, throughout the day in different periods of activity, A. Adults, spring; B. Adults, summer; C. Subadults, spring and D. Juveniles, summer. On ordinates, percentage of individuals of the total number observed. Continuous line, active specimens, dotted lines, specimens under thermoregulation.

DISCUSSION

The slopes of the regression lines of *A. erythrurus* and the plots of the hourly time course of TB, TA and TS seem to show that with high substrate temperatures, the lizard exhibits lower TB values; this species must therefore possess a hypothermic mechanism that affords it a certain independence from the temperature of the microhabitats that it occupies. Such a characteristic is shared by other Saurian species that inhabit areas in which sharp differences in temperature occur during the day, such as in the case of deserts and high mountain areas (Heatwole, 1976; Avery, 1979 and Pérez-Mellado, 1981, 1982b). Regarding thermoregulatory behaviour, Seva (1982) has shown that *A. erythrurus* occupies a position close to that of reptiles adapted to life in desert regions, with TB values that are consistently higher than those of TA, as is our own case and which increases in the differences in the first and last hours of the day. This thermal independence, with a continuous daily activity but with brief periods of intermittence, is one characteristic of the thermoregulatory behaviour of reptiles inhabiting open spaces or sites with very sparse vegetation (Avery, *op. cit.*).

In all three species the processes of heliothermia in spring are delayed with respect to summer, where they can be seen at the beginning of the day. During this latter season we were unable to observe thermoregulatory behaviour in *A. erythrurus* (Fig.7b and 7d), probably due to the high temperatures of the microhabitats occupied. *P. hispanicus* shows several thermoregulatory phases in spring one during the first hours of the morning and another later on, at around 12.00 solar time. This seems to allow the lizard to be active very early; later such activity decreases but then gradually increases again towards midday.

The absence of statistically significant differences between the mean TB values and the microenvironmental temperatures of the different media suggest that the heat independence of *A. erythrurus* may be due to physiological causes that are determined genetically. In turn, both species of *Psammodromus* show regression lines that in all cases are statistically significant between TB-TA and TB-TS; this was not the case of *A. erythrurus*. In *P. algirus*, the TS value showed much lower correlations than TA in all the age classes with the exception of the subadult males. In *P. hispanicus* the adult females and the juveniles show a lower TB-TS correlation than TB-TA, opposite to what happens in the adult males in all cases being statistically significant.

The three species can therefore be considered as ectotherms able to control their TB with the thermoregulatory behaviour that they exhibit and hence able to show a broad range of voluntary TBs (eurithermy).

A. erythrurus is found close to the northern limit of its distribution; accordingly, both its annual and daily activity and its thermoregulatory behaviour are strongly affected by microclimatic characteristics which are very different to those of the microhabitats usually occupied by this species in the southern and eastern parts of the Iberian Peninsula. Pough and

Busack (1978) have shown that *A. erythrurus* does not tolerate low temperatures very well, which thus limits its activity. This species therefore exhibits a thermoregulatory behaviour that affords its considerable independence from its microhabitat, characterised by strong fluctuations in TA and particularly in TS.

The other two species, not as affected by the environmental influences of the zone and probably with greater thermal tolerance, show a much greater annual and hourly activity than *A. erythrurus*.

Seva (1982), working on the sandy coast of Alicante, found that *P. algirus* has great thermoregulatory efficiency. This rather rare inhabitat for this species, but common for *A. erythrurus*, demands a finer thermoregulatory performance leading to an inversion of roles between both species with respect of our area.

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OBSERVATIONS ON FOAM-MAKING BY *LEPTODACTYLUS FUSCUS* TADPOLES

J. R. DOWNIE

Department of Zoology, University of Glasgow, Glasgow G12 8QQ, Scotland, UK.

ABSTRACT

Downie (1984) showed that recently hatched tadpoles of the ground nesting frog *Leptodactylus fuscus* make a foam which replaces the original nest foam made by the mating adults, but did not describe how it is made. The present results show that 1) foam-making is a communal activity: single tadpoles do not do it; 2) foam bubbles are made mainly by spitting movements of the mouth, but also by wriggling of the tail; 3) foam is probably stabilised by mucus secreted by buccal glands; precocious secretion by these glands may be an adaptation to foam-making; 4) components of foam making behaviour are shown by other tadpole species out of water, but the complete behaviour is specific to recently hatched *L. fuscus*.

INTRODUCTION

Frogs of the family Leptodactylidae deposit their eggs in foam nests, either in burrows on land, or floating on the surface of water. Downie (1984) reported that in the ground-nesting species *Leptodactylus fuscus* (Heyer, 1968) the hatched tadpoles, which may remain in the nest up to several weeks, depending on when the rains fall, themselves make a foam which replaces the original foam, if the tadpoles remain in the nest long after hatching. Downie noted that the ability to make foam wanes once tadpoles enter water, and also wanes the longer they remain in the nest, but did not report on how the tadpoles make foam, other than to surmise that it is made by whipping movements acting on secretions. The following paper investigates in detail how these tadpoles carry out this unusual activity.

MATERIAL AND METHODS

COLLECTION AND MAINTENANCE OF TADPOLES

Seven foam nests of *L. fuscus* were collected from burrows around the margin of a temporary pool site on the University of West Indies campus at St Augustine, Trinidad, in July 1984 and July 1987. In addition, because nests were hard to find in 1987 (due to tidying up of the site), two clutches of newly-emerged tadpoles were collected from freshly-flooded pools in the same area, removed from water, then placed on the surface of damp tissue in a polythene tub, to stimulate them to make foam.

It proved preferable to use pre-stage 27-28 tadpoles (staged by Gosner, 1960) from foam nests, since this allowed the tadpoles to be accurately aged. Once they reach stage 27-28, they remain at this morphological stage as long as they remain in the nest, but their ability to make foam progressively declines.

Foam-making tadpoles were maintained on the surface of moist tissue paper in small polythene tubs. For later stages, some tadpoles were transferred to tanks and fed on mixed grain powder and fish food.

For comparison, tadpoles of three other Trinidad species were collected: floating foam nests of *Physalaemus pustulosus* were collected from drainage ditches and puddles in St Augustine, and tadpoles hatching from these nests were grown in glass tanks; tadpoles of *Colostethus trinitatis* were collected from Tamana cave; tadpoles of *Bufo granulosus* were collected from puddles in St Augustine (see Kenny, 1969a, for species accounts and Harding, 1983, for nomenclature alterations).

BEHAVIOURAL OBSERVATIONS

To observe tadpole behaviour out of water, tadpoles were removed from foam or from tanks, washed, and placed singly or in groups on the surface of moist tissue in glass petri dishes, with the lids on. The behaviour of the tadpoles was then recorded at regular intervals, as described under Results.

STRUCTURAL ANALYSIS

After washing, tadpoles were fixed in Bouin's fluid (for light microscopy) or 2 per cent glutaraldehyde in phosphate buffer (for electron microscopy). Wax sections were stained with haematoxylin and eosin, or by the Periodic acid — Schiff's (PAS) method. Glutaraldehyde-fixed tissue was post-fixed with 1 per cent osmium tetroxide in phosphate buffer then processed by standard methods for examination with a Phillips 500 scanning electron microscope, or embedded in araldite resin for semithin and ultrathin sectioning. Semithin sections were stained with toluidine blue, and ultrathins with uranyl acetate and lead citrate before examination with an AEI 801 transmission electron microscope.

RESULTS

BEHAVIOURAL OBSERVATIONS

Initiation of foam-making by L. fuscus *tadpoles*

The earliest hatchlings I saw were at Gosner stage 22, estimated as 3.5 days old (assuming egg deposition at the middle of the night). Since Gosner quotes stages 17-20 as hatching time for most species, it may be that *L. fuscus* hatches a little earlier than stage 22, but takes some time to wriggle free of foam. These early hatchlings were not able to make foam. This was established by washing tadpoles of stage 23-24, and, for comparison, tadpoles which had just reached stage 26-27, and placing them in a heap on moist tissue in polythene tubs. Stage 26-27 tadpoles made foam within 12 h; stage 23-24 tadpoles did not (results not shown).

Foam-making is a communal activity

My original observations (Downie, 1984) on foam-making involved many tadpoles placed together in a heap. An obvious question is: can single tadpoles make foam, or is this a group activity? To answer this, I placed washed stage 27-28 tadpoles on the surface of moist tissue in petri dishes in groups of 10, 5 and 3, or as individuals approximately 2cm from one another, then checked for the presence of foam after one and two days. The results are shown in Table 1. Groups as small as 3 did make foam, though less well than larger groups; individuals did not make foam at all.

Number in group	10	5	3	1
Number of trials	5	14	16	52
% showing foam after 1d	100	71	19	0
% showing foam after 2d	100	78	38	0

TABLE 1: Foam-making by groups or individuals of *L. fuscus* tadpoles on damp soil.

How foam is made

To find how tadpoles make foam, groups of 5 or 6 stage 27-28 tadpoles were removed from foam, washed, and placed in a heap on the surface of moist tissue in a petri dish. Using a Wild dissecting microscope, they were then observed at intervals until they had made a substantial amount of foam. The following features were noted:

1) Although a tadpole might occasionally move away from the group for a short time, by active wriggling, groups generally kept together.

2) Movements made by tadpoles included rapid wriggling of the whole body — sometimes several times, in quick succession — and jerking movements of the head or tail alone. Wriggles sometimes moved tadpoles up and over the other tadpoles in the group. Head movements were sometimes preceded by contractions within the pharynx, and usually ended with the mouth spitting out one or several bubbles, ranging from 0.07-0.8mm in diameter. Occasionally, a rapid tail wriggle produced a bubble in the surface moisture film.

3) Bubbles made soon after isolation of the tadpoles were generally unstable, bursting spontaneously or after tadpole wriggling movements. Bubbles made later were more stable. Sometimes, wriggling movements broke larger bubbles into smaller ones.

4) Tadpoles at the top of a heap were more likely to move than those at the bottom, and very commonly, several tadpoles moved together.

As an example, in one group of 5 tadpoles, observed at intervals over a 6 hour period, the first bubbles to be formed all burst quickly. By 2 hours, there were about 10 bubbles, but by 3 hours, 60 or so. In a 10 minute continuous observation period, made at 6 hours, there were 9 episodes of tadpole wriggling and spitting, most involving two or three tadpoles at a time. Only the bottom tadpole in the heap did not move during this time.

The specificity of foam-making behaviour

The observations reported in the previous sections suggest two further questions: 1) Why do isolated individual stage 27-28 tadpoles not make foam, while the same tadpoles in groups do; 2) is the behaviour shown by foam-making tadpoles specific to them?

To investigate the first question, I set up dishes of washed foam-making tadpoles on damp tissue, 5 or 6 to a dish, with the tadpoles either in a heap, or as isolated individuals, in order to look for differences in their behaviour. All tadpole movements were recorded for a number of 5 minute periods starting from one hour after setting up and carrying on for up to 10 hours. The different kinds of movements — head shakes, tail flicks, whole body wriggles — were all counted together simply as 'movements'. The results are shown in Table 2. The movements the tadpoles made are presented in two ways: 1) as the mean number of movement 'episodes' per tadpole in each 5 minute period, irrespective of the number of tadpoles that moved at any one time; a movement episode begins when one tadpole starts to move and continues till that and other tadpoles cease moving. 2) as the mean number of tadpoles that moved during each movement episode. A comparison of the figures for groups and individuals shows both that tadpoles in a group are more likely to move in a 5 minute period than individual tadpoles ($P < 0.001$, Student's t test) and that in any episode of movement, several tadpoles in a group tend to synchronise their movements, whereas isolated tadpoles show no such tendency.

To investigate the second question, I compared the behaviour of foam-making *L. fuscus* tadpoles with that of later stage *L. fuscus*, and that of two other Trinidad tadpole species, *Physalaemus pustulosus* and *Colostethus trinitatis*, chosen because previous studies (unpublished) had shown these tadpoles to survive some time out of water.

Later stage *L. fuscus* and *P. pustulosus* tadpoles were quite active when first removed from water, with wriggling movements and occasional mouth spitting, forming a few short-lived bubbles, but they soon became rather inactive, whether in groups or singly. In both cases, groups tended to stay together. A small

Tadpole type, number and arrangement	Number of observation periods	Mean number of movement episodes/ tadpole/period	Mean number of tadpoles moving/ movement episode
Foam-making *L. fuscus* 5 or 6 in a heap	13	1.38	1.92
Foam-making *L. fuscus* 5 or 6 individuals	11	0.63	1.01
Later stage *L. fuscus* 5 in a heap	4(3*)	0.3	2.5
Later stage *L. fuscus* 5 individuals	3	0.4	1.17
Colostethus trinitatis 5 individuals	14	2.10	1.19
Physalaemus pustulosus stage 30, 5 in a heap	7(4*)	0.14	1.0
Physalaemus pustulosus stage 30, 5 individuals	7(2*)	0.4	1.0

TABLE 2: Analysis of movements made by several species of tadpoles out of water, during a series of 5 minute observation periods. * = observation periods with no movement.

number of 5 minute observations were made after the initial active phase, and these are recorded in Table 2. Overall activity was very low compared to foam-making *L. fuscus*.

C. trinitatis tadpoles behaved very differently. They remained active throughout a 10 hour experiment. Tadpoles did not stay together if set up in groups. Movements were often very active wriggles, even jumps that could carry a tadpole right across the dish. Mouth spitting was not seen. Five minute observation results are shown in Table 2, and demonstrate that these were the most active tadpoles observed. Synchronisation of movement was low, perhaps because tadpoles remained in contact with one another only briefly.

STRUCTURAL OBSERVATIONS

Although foam-making clearly involves the spitting and wriggling behaviour of tadpoles, it is possible that there are histological and physiological specialisations associated with this behaviour. To establish this, it was necessary to compare different stages of *L. fuscus* tadpoles and to compare *L. fuscus* tadpoles with those of other relevant species. The structures examined, as most likely to be involved, were the buccal cavity and the skin.

Buccal cavity

Kenny (1969b) has provided a light microscope description of the buccal mucus-secreting glands of tadpoles, and Wassersug (1976) has reviewed the terminology of these structures. There are two sets of glands: a crescentic band of secretory pits at the posterior limit of the buccal roof; and rows of secretory ridges on the ventral surface of the ventral velum. PAS — stained sections of foam-making tadpoles showed that these glands are all fully active (Fig. 1a) and therefore that they are the source of the mucus-bubbles the tadpoles spit out. However, this may not be a specific adaptation, since tadpoles of most species at stage 27-28 would be in water and feeding using their

buccal glands to trap food. Is it therefore adaptive for these glands to be functional before entering the water? A useful comparison is with hatchlings of *Colostethus trinitatis*. *C. trinitatis* is a dendrobatid, and males carry tadpoles on their backs from terrestrial nests to water. *C. trinitatis* tadpoles from males backs are at about the same stage as *L. fuscus* foam-making tadpoles, but PAS-stained sections of their buccal cavities showed glands which were much less active (Fig. 1b).
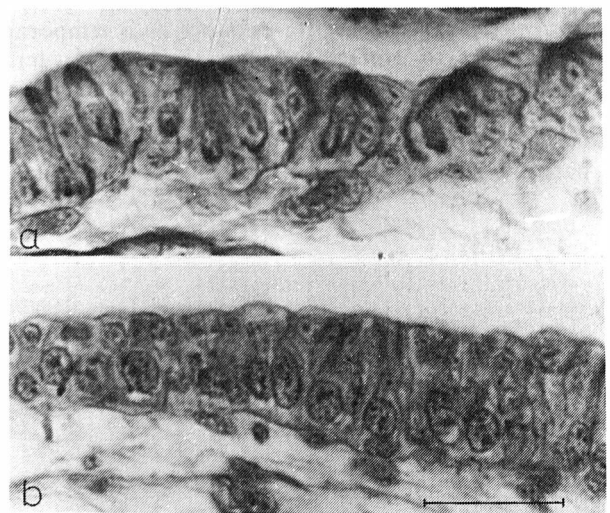
Fig. 1 Secretory pits of the buccal roof, stained PAS and light green. a) *L. fuscus* foam-making tadpole. b) *C. trinitatis* tadpole from an adult male's back. Bar = 20 μm. The dark staining at the apical ends of clusters of gland cells in figure a shows active mucus production. Note the relative lack of staining at the equivalent position in Fig. b.

Skin

Transmission electron microscope sections of foam-making tadpole skin showed numerous mucus secretory droplets, some of them open, lined up at the skin surface, in between microridges. This appearance was not noticeably different from skin of the same
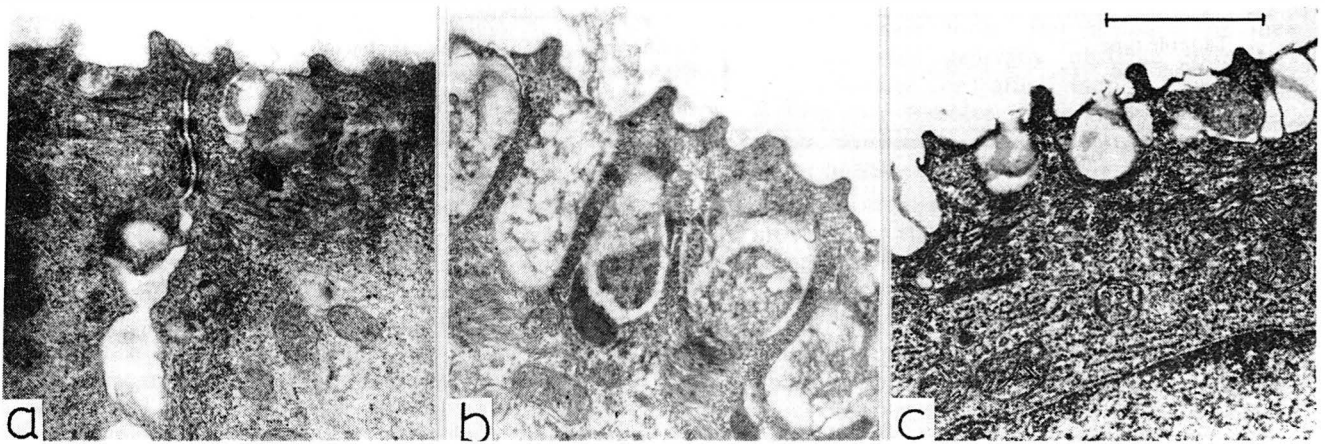
Fig. 2   Transmission electron micrographs of tadpole skin, to show mucus secretory droplets and microridges in section.
a) *L. fuscus* foam-making stage tadpole. b) *L. fuscus* stage 32 tadpole. c) *C. trinitatis* tadpole from an adult male's back.
Bar = 1 μm.

stage from other species examined, or from skin of later stage *L. fuscus* tadpoles. *C. trinitatis* tadpoles from the male's back again offer a useful comparison: their skin was as well supplied with mucus secretory droplets as that of foam-making *L. fuscus* (Fig. 2).

Scanning electron microscopy showed that epidermal surface microridge patterns varied between species, but also between adjacent cells on the same area of skin (results not shown).

Two other skin structures are worth reporting on. Leydig cells are large diameter cells with a clear watery cytoplasm found in larval amphibian epidermis and located in sub-surface layers. Kelly (1966) suggested, on the basis of experiments with the urodele *Taricha torosa* that Leydig cells act as a temporary water store to protect the skin against short-term desiccation. However, of the tadpole species I looked at, only *Bufo granulosus* had prominent Leydig cells; foam-making tadpoles had very few (Fig. 3). Finally, hatching gland cells, located in the frontal region, are

Fig. 3   Toluidine blue stained 1 μm sections of tadpole skin to show Leydig cells — large empty looking cells located beneath the surface of the epidermis. a) *L. fuscus* foam-making tadpole, lacking Leydig cells. b) *B. granulosus* stage 28, with prominent Leydig cells. Bar = 20 μm.

normally active around the time of hatching, and regress over the next few days (Yoshizaki and Katagiri, 1975). Since *L. fuscus* tadpoles do not undergo normal morphological development while in foam, it seemed possible that the hatching gland might not regress, and even that it might have a role in foam production. However, I found that hatching gland regression did occur in foam-making tadpoles, though at a slower rate than in feeding tadpoles. These results will be more fully reported elsewhere.

DISCUSSION

From the behavioural observations made here, it is clear that stage 27-28 *Leptodactylus fuscus* tadpoles make foam primarily by spitting out bubbles from their mouths, and to a lesser extent by the wriggling action of their tails. Wriggling movements are also responsible for breaking larger bubbles into smaller ones, and bursting some bubbles altogether. Since the first bubbles made by newly-washed tadpoles are unstable, whereas later-made ones are longer lasting, it is reasonable to suggest that stability is the result of mucus secreted progressively by the tadpoles the longer they are out of water.

From the evidence, the inability of single tadpoles to make foam is partly due to their lower activity. In groups, tadpoles somehow stimulate each other to be active, probably by being in contact, and the spitting movements are usually associated with overall body wriggling which itself forms some bubbles. It may also be that a single tadpole cannot produce as high a local concentration of bubble-stabilising mucus as a group: this could explain why groups of 10 tadpoles form stable foam more quickly and reliably than groups of three.

Some components of foam-making behaviour were seen in other kinds of tadpoles. *Colostethus trinitatis* tadpoles wriggled more vigorously and more frequently, but they did not stay together, nor did they spit bubbles. *Physalaemus pustulosus* and later stage *L. fuscus* tadpoles initially made spitting movements, wriggled actively and did stay together, but all kinds of movements, particularly spitting soon stopped.
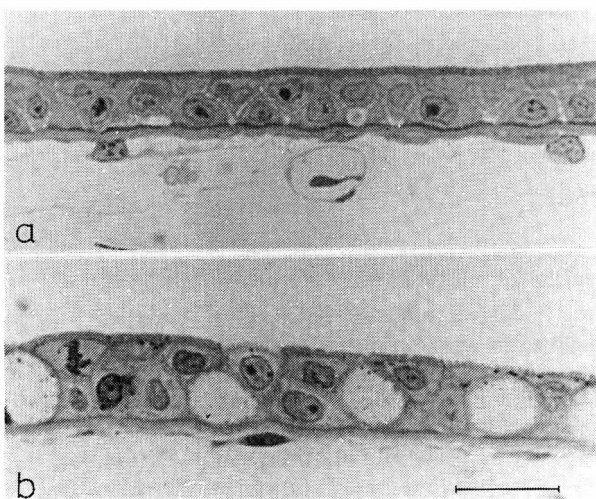
Therefore, though the components of foam-making behaviour are not specific to *L. fuscus* stage 27-28 tadpoles, the overall behavioural repertoire is.

From the histological and ultrastructural evidence, it is likely that the secretion of mucus by *L. fuscus* buccal glands prior to entering water is a specific adaptation to foam-making behaviour. No other feature showed clear evidence of specific adaptation. Mucus secretion by cells all over the skin may certainly help, but occurs generally in tadpoles. Hughes and Wright (1970) have suggested that skin surface microridges help anchor mucus films to skin, though other functions are possible. Since mucus films are as important to tadpoles in water as in foam, there is no reason to suspect that the microridge pattern of foam-making tadpoles should be specifically adapted to this behaviour. Fishelson (1984) has classified microridge patterns in fish epidermis, where they have systematic value, but no similar study has been made on tadpoles, and there is no known functional significance in the pattern variations.

ACKNOWLEDGEMENTS

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OBSERVATIONS ON THE AQUATIC LOCOMOTION OF YOUNG SALT-WATER CROCODILES (*CROCODYLUS POROSUS* SCHNEIDER)

J. DAVENPORT AND M. D. J. SAYER*

Animal Biology Group, Marine Science Laboratories, University College of N. Wales, Menai Bridge, Gwynedd LL59 5EH, N. Wales, UK.

* *Present address: Zoology Department, University of Nottingham NG7 2RD.*

ABSTRACT

Swimming behaviour of young salt-water crocodiles was studied in capitivity by analysis of video films. Resting postures in fresh and salt water, escape responses, jumping and food handling behaviour were investigated.

INTRODUCTION

Although the terrestrial gaits of crocodilians have attracted much attention (see Frey, 1984 for review), their locomotion in water has been less studied. Fish (1984) has investigated the undulatory fast swimming of the American alligator, *Alligator mississippiensis*, while Turner, Tracy, Weigler and Baynes (1985) have correlated burst swimming speed with temperature in the same species. No detailed descriptions of swimming and associated behaviours in true crocodiles appear to have been published, and slow swimming in all crocodilians seems to have been ignored.

The availability of young salt-water crocodiles, *Crocodylus porosus*, in these laboratories, allowed the study of slow, medium and fast swimming in one of the most aquatic of living crocodilians. Resting postures in fresh and salt water, escape responses, jumping and food handling behaviour were also filmed and analysed.

MATERIALS AND METHODS

COLLECTION AND MAINTENANCE

Hatchling *Crocodylus porosus* were supplied by the Conservation Commission of the Northern Territories. They were held in running fresh water at 30°C and fed routinely upon chopped whole fish or squid. Occasionally they were given live food (cockroaches, crickets, shrimp or small crabs). Filming took place intermittently over several months during which period the animals ranged in weight from 70-220 g.

FILMING

All locomotion was filmed with a Panasonic F10 videocamera fitted with a 'high speed' shutter. Such shutters store an image for only 0.001 s during each video field, so freezing movement much more effectively than with a normal video camera. However, the video field frequency (25 fields s^{-1}) is unchanged and filming is only possible under conditions of bright lighting.

Crocodiles were filmed in a large plate glass tank (120cm long, 40cm high, 30cm wide) filled normally with fresh water at 30°C (occasionally sea water was used instead to investigate posture in a medium of greater density). The tank had a 2cm grid marked on the base and one of the long sides; these were backed with paper of neutral colour. The tank was illuminated from above and from each end to minimise shadow formation. The standard zoom/macro lens of the camera system was used, and the camera was mounted either 2m from the side of the tank or 1.5m above the water surface.

PROTOCOL

Swimming crocodiles were filmed from above, from the side and from head on to allow a 3 dimensional picture of locomotion to be constructed. In most cases the animals were allowed to swim spontaneously, but to achieve maximum speed animals were chased with the hand, or briefly restrained.

To study resting postures in fresh water and sea water, crocodiles were left until they quietly floated at the surface in fresh water; they were filmed continuously for about 15 minutes. They were then transferred to sea water and the process was repeated.

To study escape responses, the crocodiles were allowed to settle down in the tank so that they floated at the surface. Any sudden movement above the tank induced an escape reaction. To investigate behaviour during food capture, the animals were offered large cockroaches, some struggling in water, but others climbing on the walls of the tank well above the water surface.

ANALYSIS OF VIDEOTAPE

Motion was analysed by placing acetate sheets over the screen of the video monitor and making fine felt tip drawings from arrested video fields. The 2cm grid background allowed precise positional, size and distance data to be collected.

RESULTS

SWIMMING

When swimming slowly (<0.5 body lengths s⁻¹) the crocodiles use all four limbs, but with little tail motion. Each limb performs a simple drag-based propulsive cycle (Fig. 1). During the effective stroke the digits of the limb are spread to deploy the web (much larger in the case of the hind limbs) which is then pushed backwards at right angles to the direction of swimming (Fig. 2). At the end of the effective stroke the web is folded and brought forward in a recovery stroke. The limbs are synchronised ipsilateraly, so that one forelimb and the hindlimb on the opposite side of the body are on the effective phase of the limb stroke, while the other limbs are recovering (and vice versa). This low speed paddling, of typical tetrapod pattern, gives a steady speed as there is no period when propulsive power is not being generated.

Medium speed swimming (0.5-1.6 body length s⁻¹) is provided by combined action of the tail and limbs (Fig. 3). Propulsive waves pass rearwards along the tail with progressively increasing amplitude.

Fig. 2 A. Detail of movement of right rear limb (viewed from beneath) during slow swimming. Fields 1-6 represent the recovery stroke; fields 7-15 represent th effective stroke. B. Summary of timing of rear limb cycle; numerals represent successive video fields (0.04 s apart). Scale bar = 4cm.
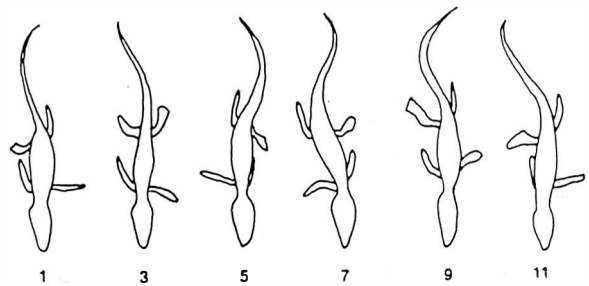
Fig. 3 Medium speed swimming in *Crocodylus porosus* filmed from above. Numbers represent video fields (in this case 0.08 s apart; intermediate fields were omitted for clarity).

Fig. 1 Slow swimming in a specimen of *Crocodylus porosus* ascending from the bottom of a tank. Dotted lines indicate movements of each limb. Numerals refer to video fields (0.04 s apart) following the drawings (all made at field 1).

Faster swimming (1-2 body lengths s⁻¹) is accomplished by the propagation of travelling waves along the body and tail, all limbs being held immobile and close to the body to minimise drag (Fig. 4 A-E). Although it is obvious from this figure that the tail provides the bulk of the propulsion, it is also evident that the propulsive wave originates in the body anterior to the pectoral girdle, and is not simply a post-pelvic wave as described for the alligator by Fish (1984). Table 1 illustrates the relationship between crocodile swimming speed and the speed of propagation of the travelling wave along the tail. In all cases the propulsive wave travels rather more quickly than the animal's swimming speed. At least half to one wavelength (λ) occurs within the tail length at all times and the wave is not truly sinusoidal, since the amplitude increases (and λ decreases) towards the tip of the tail. These observations are in agreement with Fish (*op. cit.*) for *Alligator mississippiensis*.
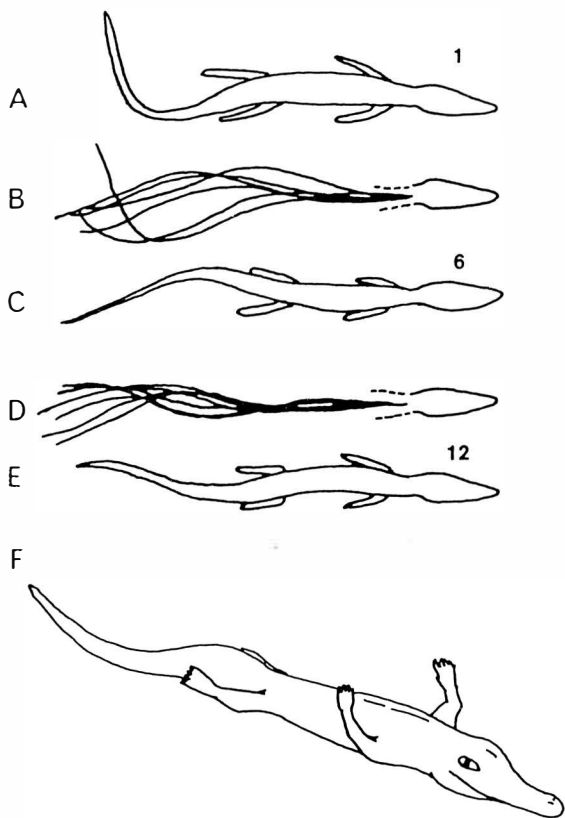
Fig. 4   Fast swimming in *Crocodylus porosus*. A. Posture at video field 1 (filmed from above). B. Drawing to show position of the midline of tail and body in video fields 1-6. C. Posture in video field 6. D. Drawing to show position of the midline of tail and body in video fields 6-12. E. Posture in video field 12. Interval between fields = 0.04 s. F. Posture of fast swimming *Crocodylus porosus* in shallow dive. Note raised fore limbs.

Fig. 4F illustrates the posture of a crocodile swimming rapidly in a shallow dive. Although the hind limbs are always held parallel to the body axis during fast swimming, this is not the case for the forelimbs; during dives they trail in raised position (as in Fig. 4F), during ascents they trail below the body. In both cases the limb positioning may counteract rolling and yawing.

When accelerating rapidly from a slow swimming mode to a fast swimming mode, the crocodiles sometimes go through a brief episode of combined tail beat and hindlimb paddling, but with immobile forelimbs; this lasts for no more than 2-3 leg beats before the fast swimming configuration supervenes. During deceleration the animals either progressively move from fast to medium to slow swimming, or they brake abruptly by extending all 4 limbs with spread webs.
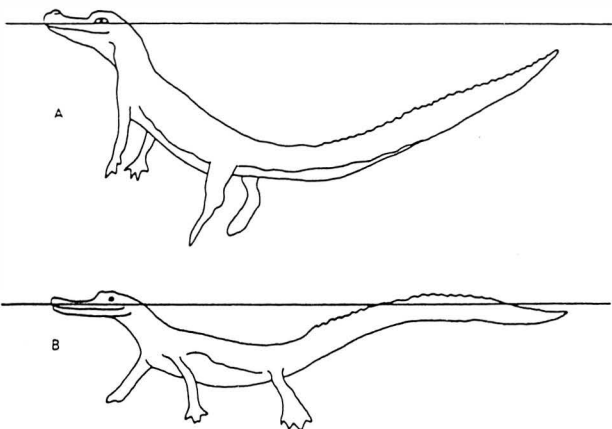
Fig. 5   Surface resting postures of *Crocodylus porosus*. A. In fresh water. B. In sea water.

SURFACE RESTING POSTURE

The surface resting posture of young crocodiles is shown in Fig. 5. This posture is very common in hungry animals (presumably because it allows them to spot insects, fiddler crabs or mudskippers in the wild); recently fed animals usually rest on the bottom. In fresh water the top of the head is held out of water so that the eyes and nostrils are exposed. The body is held at about 45° to the horizontal and the tail projects upwards but does not reach the water surface. All four limbs are extended below the body, the hindlimb webs being widely spread (in preparation for the escape response — see below). In still water the crocodiles remain motionless between breaths. When the animal

Trial No.	Swimming speed (v) (m s^{-1})	Wave speed (w) (m s^{-1})	w/v	Animal length (m)	Swimming speed (body l s^{-1})
1.	0.64	0.92	1.4	0.326	1.96
2.	0.33	0.43	1.3	0.310	1.06
3.	0.36	0.52	1.5	0.290	1.24
4.	0.35	0.38	1.1	0.310	1.13
5.	0.56	0.71	1.3	0.314	1.78
6.	0.57	0.71	1.2	0.312	1.83
7.	0.51	0.60	1.2	0.311	1.64
8.	0.43	0.46	1.1	0.311	1.38
Mean	0.47	0.59	1.3		1.50

TABLE 1: Relationship between swimming speed and tail travelling wave speed during fast swimming in young *Crocodylus porous*.

Species	Body length l m	Velocity v m s^{-1}	Reynolds number	v/l	Reference
Pleuronectes platessa (flatfish)	0.235	1.2	2.8 x 10^5	5	Blaxter & Dickson (1959)
Scomber scomber (mackerel)	0.350	3.0	1.0 x 10^6	9	Blaxter & Dickson (1959)
Aptenodytes forsteri (penguin)	1.000	2.3	1.8 x 10^4	2	Clark & Bemis (1979)
Chelonia mydas (green turtle)	0.110	0.9	9.4 x 10^4	8	Davenport *et al* (1984)
Mauremys caspica (f.w. turtle)	0.100	0.2	2.1 x 10^4	2	Davenport *et al* (1984)
Alligator mississippiensis (alligator)	0.460	1.0	4.6 x 10^5	2	Fish (1984)
Crocodylus porous (crocodile)	0.326	0.6	2.1 x 10^5	2	This study

TABLE 2: Comparison of maximum swimming speeds of aquatic vertebrates.

takes a breath the hind body and tail start to rise; this tendency is opposed by a slight forwards and upwards movement of both hindlimb webs (generating upwards thrust and transferring the centre of gravity forwards), causing the animal to bounce a little, though the head remains motionless. In sea water the surface resting posture is somewhat different, the whole animal being nearly horizontal and the dorsal part of the mid section of the tail projecting above the water surface. The limbs project sideways far more than in fresh water and the animal is less stable laterally, being prone to rolling.

ESCAPE RESPONSE

The escape reaction exhibited by crocodiles startled whilst floating at the water surface is shown in Fig. 6. The animal responds by simultaneously sweeping the spread webs of both hindlimbs (which are fully extended) forwards the upwards. This drives the animal downwards into the water column and transfers the centre of gravity forwards, helping to depress the head. The downward movement causes the tail to bend, but it is also flexed vigorously by the crocodile, the broad side of the tail being directed upwards. This action draws the body further into the water column, helped by the vertebral column adopting a ventral concavity (the animal 'crouches' in the water), and by sideways turning of the head. Within 0.68 s the animal is almost a body length below the water surface, horizontal and with the hindlimbs forward and the tail alongside the body. From this position (field 17 in Fig. 6) the crocodile accelerates away by straightening the tail and kicking back the hind limbs.

JUMPING AND FOOD CAPTURE

To capture insects above the water surface (in this case the glass of the tank, but presumably upon rocks or vegetation in nature) the crocodiles show remarkable jumping ability. Typical sequences are
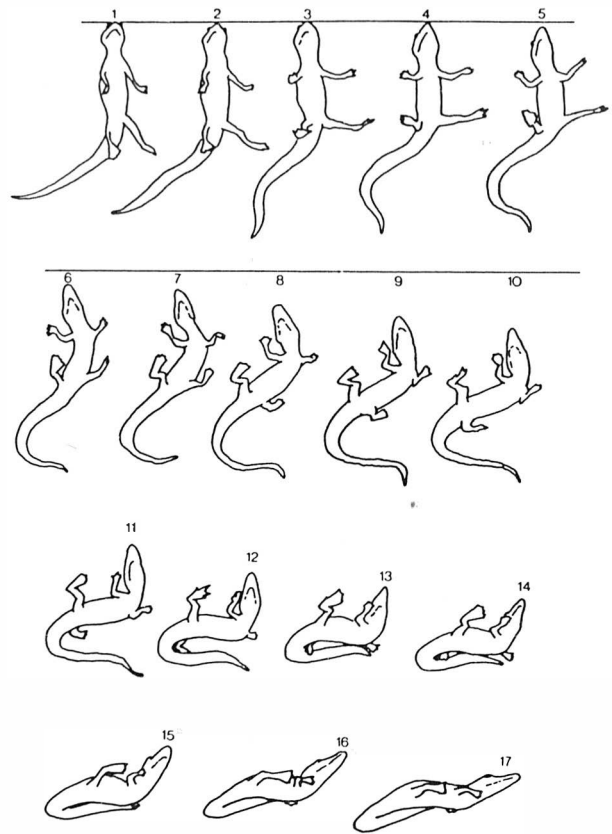
Fig. 6   Escape response of *Crocodylus porosus* startled when resting at the surface. Numerals indicate successive video fields (0.04s intervals). The animal was startled between fields 1 and 2.

shown in Fig. 7, but hatchling crocodiles (unfortunately not filmed) sometimes jumped almost completely out of water to catch cockroaches. In preparation for a jump, the crocodile brings both hind limbs far forward and extends their webs. The tail is bent at right angles
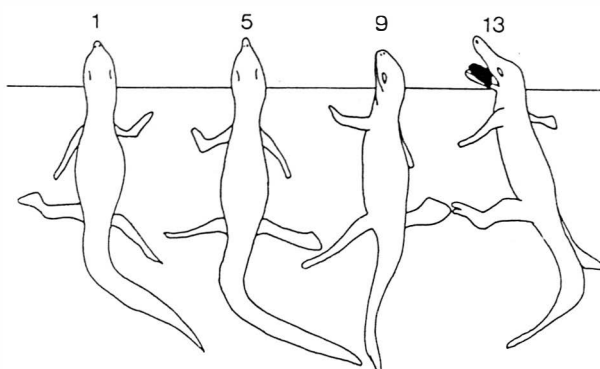
Fig. 8   Water treading during food handling in *Crocodylus porosus*. Numerals represent video field numbers: black object represents insect prey.

Fig. 7   Food capture by jumping in *Crocodylus porosus*. A. Filmed from the side. B. Detail of limb movements. C. Filmed from behind (except that the animal twisted between fields 11 and 12. Numerals indicate successive fields (interval 0.04 s); black objects represent cockroaches. Scale bars = 4cm.

to the body axis. To initiate the jump the hind limbs and tail are simultaneously driven backwards in a propulsive action lasting about 0.08 s. The head is driven upwards and forwards, the mouth starting to open as the snout clears the water. The animal accelerates as more of the body leaves the water, and the mouth gapes wide until snapped shut on the prey. Before jumping the neck and back are bent; both straighten during the jump.

When catching slow moving aquatic prey (e.g. crabs), or insects floating on the water surface, the crocodiles capture them by foot and tail powered lunges, similar in essentials to the jumps described above, but with less acceleration.

FOOD HANDLING AND WATER TREADING

Young *Crocodilus porosus* cannot swallow large food items under water (Davenport, 1987); this would involve opening the water seal between the back of the tongue and palate, causing water to flood into the oesophagus and stomach. Despite this problem the animals often retreat into water to swallow food, even

when it is captured on land. Swallowing is accomplished by adopting a vertical position in the water, by throwing the head back so that the snout points skywards, and by treading water vigorously with all four limbs to keep the whole head out of water (Fig. 8). Food is tossed around in the jaws until the longest axis of the food item is parallel with the body axis and swallowing is accomplished. The water treading (similar in pattern to low speed swimming) is obviously an energetic process. With medium sized prey items (e.g. small cockroaches) the crocodiles often caught several insects before starting a bout of water treading and swallowing.

DISCUSSION

Young crocodiles, like adults, spend most of their time in relative immobility; they are classic wait and strike predators. By use of the limbs and tail, a wide and flexible repertoire of movements are possible. The large hind limbs are of particular importance, their broad webs providing much of the force required to overcome inertia during escape reactions and in attacks on prey. The crocodiles' maximum length-specific swimming speed (v/e) is poor by comparison with other aquatic vertebrates (see Table 2), though their long, slender shape handicaps them to some extent in such comparisons. The peak length-specific swimming speed recorded for the salt water crocodile is close to that recorded for the alligator (Fish, 1984) and their anguilliform fast swimming mode is also generally similar (though we found that propulsive waves involved the body of the crocodiles and were not confined to the tail). The finding that the tail travelling wave is propagated at about 1.3 times the swimming speed also agrees with Fish's findings for the alligator. As Webb (1978) points out (for undulatory swimming in fish), longitudinal tail wave velocity (w) must exceed swimming speed for steady propulsive thrust to be developed, but if w greatly exceeds v, much energy is lost laterally to the wake; propulsive efficiency rises as w falls towards v.

Fish (1984) described the alligator as a low swimming speed, low acceleration and low efficiency organism, and cited the work of Schaller and Crawshaw (1982) on the caiman *Caiman crocodilus*,

and of Pooley and Gans (1976) upon the Nile crocodile *Crocodylus niloticus* to extend this hypothesis to crocodilians in general. These latter two studies demonstrated that adult crocodilians fished by snapping their jaws (sometimes with tail and foot powered lunges) at fish which had either strayed within range, or which had been herded into swallow, enclosed water. Our results for *Crocodylus porosus* generally support Fish's hypothesis, except in the case of the ability of hatchlings and juveniles to jump almost completely out of water to catch insects. It is increasingly clear that most crocodilians are insectivorous when young (Cott, 1961; IUCN, 1982), so it is probable that other species have the same jumping ability. Aquatic animals which jump out of water, either to catch prey or to avoid predators, exploit the much lower viscocity of air, which permits greatly enhanced acceleration.

Two features of aquatic movement in *Crocodylus porosus* merit further consideration; the frequent use of simultaneous movements of the hind limbs when rapid movement is required (whether forwards, as in jumps, or backwards, as in the escape response), and the involvement of the vertebral column in lunges and jumps. Both features may be related to the unique (amongst living reptiles) galloping ability of crocodiles upon land (Cott, 1961; Zug, 1974; Webb and Gans, 1982). Galloping involves the synchronous movement of the hind limbs and out of phase synchronous movement of the fore limbs, combined with alternate bending of the vertebral column into a strong ventral arch (when the hindlimbs are brought forward), and straightening of the arch during the propulsive phase (when the hind limbs are thrust backwards). When a young *Crocodylus porosus* jumps out of water to catch an insect, the limb and back movements correspond to half of the gallop stride described for the same species by Zug (1974); only the involvement of the tail in aquatic propulsion is different.

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ACTIVITY AND HOME RANGE OF THE LIZARD *LACERTA AGILIS L.*

A. M. NICHOLSON AND IAN F. SPELLERBERG

Biology Department, The University, Southampton, England SO9 5NH.

ABSTRACT

During a three-year period of research on the lizard *Lacerta agilis*, observations on activity and home range area were obtained for two seasons. It was found that *L. agilis* had overlapping home ranges. The home range area of *L. agilis* was found to be smaller than would be predicted from studies on the relationship between the size of various lizard species and home range areas.

INTRODUCTION

The ecology of the lizard *Lacerta agilis* has been well researched, particularly its habitat requirements in England (House and Spellerberg, 1983a; Dent and Spellerberg, 1987). The habitats of this lizard species has also been studied in other countries including Russia (Tertyshnikov, 1970; Jablokov, 1976), Germany (Glandt, 1979), Luxembourg (Parent, 1978), and Sweden (Andren and Nilson, 1979). A review of *Lacerta agilis* habitats is contained in House and Spellerberg (1983b) and some aspects of management are described in Corbett and Tamarind (1979). One aspect of the habitat requirements of this species that continues to be of interest to both conservationists and ecologists is area or space.

One way to investigate the space or area requirements of a species is to examine data on activity and home ranges. A home range is the entire area within which an individual moves (Rose, 1982) and data on the area of home ranges may be used as a basis for assessing how lizards use their resources. The aim of this paper is to present and assess such data which could later be used for the management, restoration and creation of habitats for the protected *L. agilis*.

METHODS

This research and other aspects of *L. agilis* ecology was undertaken over a period of three years at two study sites (A and B) in Dorset, England. Site A was approximately 0.5 ha on an area of open heathland near a National Nature reserve. Site B was heterogeneous in nature and included parts of a disused railway site, a bog and small lake and a mixed deciduous woodland. The vegetation of site B was composed of large areas of coarse grasses, bracken, brambles and typical early colonisers of disturbed ground.

Lizards were caught by hand and individual lizards were identified by clipping some claws to a predefined code. The characteristic dorsal markings and the various patterns on the lizards were also recorded in drawings. Adults were defined as those lizards that had experienced two winters, sub-adults were lizards that had experienced only one winter. Data on activity and home range area was accumulated during two years of the field work in addition to other aspects of the ecology of this species being researched over the three years.

In order to assess levels of activity, lizards were caught by hand and also permission was obtained to trap *L. agilis* on site A with the use of pitfall traps (glass jars, 150mm deep and 70mm diameter at the base) set out in a grid. The pitfall traps were kept dry and were checked every day for lizards. During the first pitfall trapping programme, 66 traps were set in a grid of 5 metres. In the following year, 109 traps were positioned on a 7 metre grid over the central part of the study site and a 10 metre grid on the edge of the study site. Home range areas were calculated using the convex polygon method (Southwood, 1966). As it was known that the accuracy of home range area estimates are affected by the number of sightings used, a correction factor was used as part of the analysis.

RESULTS

SPRING EMERGENCE

During the research, the earliest date for emergence recorded for one season was 1st March (week 9) but most male *L. agilis* were first seen in the first two weeks of April (weeks 14, 15). Males were first sighted on average two weeks before females. Following emergence from overwintering sites (holes in banks or disused burrows of small rodents) the most predominant form of male behaviour was basking and this usually took place within a metre of the overwintering site. Only during warm spring days were the males seen to forage and feed. By mid-April, male lizards had left the vicinity of the overwintering sites but the same sites were used by other individuals as an overnight refuge. Shortly after this local dispersal of males, the first females were sighted (15th April).

ACTIVITY AND SOCIAL BEHAVIOUR

The total number of male lizards caught in pitfall traps was, for most months, greater than the number of female lizards caught (Fig. 1). This difference between sexes was clear in the second season but less clear in the first season when trapping commenced. If the sex ratio is near 1:1 (and there is no reason to believe otherwise) then it would appear that male lizards are usually more

active than female lizards. For the first few months of the pitfall trapping, sub-adults were caught in fewer numbers than were male or female lizards and it was only towards the end of the second season that comparatively high numbers of sub-adults were trapped.

Observations on behaviour of males during the spring suggested that there was a dominance hierarchy amongst the males (Nicholson, 1980). In all but one of nine male-male interactions observed, the smaller male

Fig. 1   Rates of capture of male (△), female (■) and sub-adults (●) *L. agilis* in pitfall traps at study site A. a = first season with 66 traps. b = second season with 109 traps.

lizard withdrew and in all cases the interaction between conflicting males was terminated abruptly by withdrawal. Social interaction between females was not observed in the field. Although actual mating was not observed, identification of individuals involved in courtship suggested that males are polygynous (Nicholson, 1980).

HOME RANGE AREA

The uncorrected and corrected home range areas for individual *L. agilis* are shown in Table 1. Included in this Table are some individuals for which home range area was estimated more than once but on different occasions. These data indicate that the estimate of home range area is affected by sample size and a detailed analysis of this aspect is provided in Nicholson (1980).

Mean uncorrected (and corrected, Jennrich and Turner, 1969) home range areas for male and female lizards (excluding those based on only three sightings and also those observations made in the first year when the trap grid was small) are given in Table 2. The difference between the mean corrected home range areas of males and females was not significant at Site A ($t = 0.32$, $p = 0.8$) but was for Site B ($t = 2.97$, $P < 0.05$). The mean corrected home range area for female lizards was significantly smaller at Site B compared to Site A ($t = 2.61$, $P < 0.05$) but there was no significant difference between the male lizards from the two study sites ($t = 0.63$, $p = 0.5$).

HOME RANGE OVERLAP

During this research, it became evident that there was overlap between home range areas. The degrees of home range overlap (that percentage of an individual

Site	MALES				FEMALES			
	Time period over which observations made	Number of captures or sightings	Polygon home range (m²)	Corrected home range (m²)	Time period over which observations made	Number of captures or sightings	Polygon home range (m²)	Corrected home range (m²)
	June-Oct	7	113	578	July-Aug	9	384	1492
	Aug-Sept	6	75	439	May-Aug	7	78	400
	June-July	3	63	1454	July-Aug	5	525	3890
	April-July	14	775	2135	*May-July	3	50	1163
A	April-Aug	25	1155	2230	April-July	5	169	1250
	April-Aug	12	780	2400	April-July	8	431	1866
	June-July	3	161	3751	*June-July	7	641	3309
	May-July	6	75	438	June-July	17	654	1565
	*June-July	6	325	1901	One year	8	233	1007
	One year	17	950	2273	One year	4	63	679
	One year	5	478	3538	One year	7	600	3060
	April-June	16	1396	3455	May-June	6	120	701
	May-June	6	150	879	May-July	12	59	182
	April-May	12	161	495	May-June	12	61	188
	April-May	10	904	3183	May-June	3	79	1843
	April-July	12	314	966	One year	5	105	776
B	April-July	10	725	2553	April-May	5	81	599
	April-July	6	675	2921				
	April-May	5	183	1356				
	April-May	7	41	210				

TABLE 1: Home range area for *L. agilis*.   * Denotes a sub-adult individual.

Study Site	Sex	No. of Lizards	Home range areas (m²)	
			Uncorrected	Corrected
A	0	7	648	2130
A	0	7	398	1819
B	0	9	505	1779
B	0	5	85	489

TABLE 2: Mean home range areas for *L. agilis*.

home range shared by lizards; Ferner 1974) should be estimated for each individual lizard but that can be done however only if the exact boundaries of the home range are known. However, an index of the extent of overlap within a population can be calculated if the population density and the mean home range size is known and if it is assumed that the lizards distribute their home ranges evenly over the study site. At Site A the population density was estimated as being one male lizard per 800m². On this basis and in the light of several assumptions, it was calculated that male *L. agilis* at Site A had a home range overlap of 75 per cent. This high degree of overlap was supported by observations of the use of overnight refuges. For example, during the course of one season as many as nine *L. agilis* used one particular overnight refuge.

DISCUSSION

The most notable and characteristic feature of the spring emergence behaviour was that males appeared before females (see also Nuland and Strijbosch, 1981) and basked for much of the time unless the weather was particularly warm. It would appear therefore that foraging could only be undertaken on warm days when insolation levels resulted in a lizard's body temperature reaching the preferred body temperature level or mean voluntary temperature (Spellerberg, 1980).

The costs of partitioning a lot of time to basking in the early spring when weather conditions are not always favourable are at least two-fold: one cost is the extra energy spent on raising body temperatures compared with the lesser amount of energy utilised by remaining inactive in a burrow; a second cost is exposure to predation. The benefits of this spring basking behaviour would therefore need to be high so as to balance such costs. In reptiles, many biochemical and physiological processes have been shown to be temperature related (Huey and Slatkin, 1976) and spermatogenesis is one such temperature dependent process (Licht, 1965).

The activity of *L. agilis* in a temperate climate is of course seasonal and one reproductive cycle occurs each year within a few months. It would seem therefore that male *L. agilis* direct some energy towards spermatogenesis in the early spring and although the total amount energy could be small (in relation to all other spring energy expenditure), the fact that the lizards need to complete the process of spermatogenesis as soon as possible during periods of unfavourable weather would seem to imply high costs which are not balanced by energy gains from feeding. Evidence for this latter point was obtained in the form of data on

weight loss amongst male lizards during the spring (Nicholson, 1980).

The seasonal level of activity (based on animals caught in pitfall traps) showed a predictable pattern with highest levels of adult activity occurring in June, July and August. In one year, male *L. agilis* seemed to be consistently more active than females but there is no evidence to suggest a reason for the apparent high level of male activity. The incidence of lizards caught in pitfall traps was highest on days when insolation was at its greatest (Nicholson, 1980) and this is explained by the activity of lizards being largely temperature dependent.

The uncorrected home range area of individual lizards as calculated by the convex polygon method was in all cases strongly related to the number of sightings. Although for this reason, a correction factor (Jennrich and Turner, 1969; Rose, 1982) was used, both uncorrected and corrected estimates have been given for comparative reasons. Mean corrected home range areas have been reported for *L. agilis* in Sweden (Olsson, 1986). Whereas the mean home range area for 29 male lizards was 1110m² the mean area was only 156m² for 19 females. Olsson's field work was undertaken in the spring and it is interesting to note that, in reference to the work reported here, small home ranges were found for female *L. agilis* (Table 1) during the spring (Nicholson, 1980). Small home range areas have been reported for *both* sexes of *L. agilis* in Russia (Tertyshnikov, 1970). In plantation compartments where trees had not reached the thicket stage, Dent (1986) found the mean uncorrected home range areas to be 1681m² for five males and 1100m² for 10 females (recalculated for comparative purposes from Dent's data and omitting data for lizards where there was less than six sightings for the calculation of the home range area).

In this study it was found that female home ranges were much smaller than those of males on study site B whereas on study site A there was little difference in home range size between the sexes. More recent studies (see above) describe statistically significant larger home ranges for males compared to female home ranges. Such differences are possibly related to social behaviour and in particular the reproductive behaviour of the females. In this study, the small home ranges of female lizards occurred throughout the breeding season and up to egg-laying, suggesting that these small home ranges are characteristic of gravid females.

Assuming that corrected results give a more accurate estimate of the actual home range area than uncorrected results, then the home range area of male *L. agilis* in some habitats could be near 2,000m². A home range area of near 2,000m² for a lizard of this size (9-10 g, 7-9cm snout-vent length) is not surprising and indeed this is smaller than would be predicted from the comparative data on lizard home range size and body weight provided by Turner *et al.* (1969). Furthermore, and in view of information on movement and the homing ability of this species, it is possible that all the above figures for home range size are underestimates. For example, in the present study, some individuals travelled hundreds of metres during the course of a season and one male lizard on one occasion took only

29 minutes to travel 43m. Arising out of some research on the homing behaviour of *L. agilis* and *L. vivipara* (Strijbosch *et al.*, 1983) it was found that 81.5 per cent of individual *L. agilis* displaced by 70m returned within a few days.

A small lizard species with a home range area of several hundred square metres could not effectively defend resources in a territorial manner in habitats where the structure and density of vegetation limits visibility to no more than a few metres. It is therefore not surprising that no evidence of territorial behaviour was found for male or female lizards. However, a high degree of home range overlap amongst the male lizards could be the basis for a dominance hierarchy amongst the males.

The home range or territory of any lizard must be large enough to contain all those resources necessary for survival throughout different times of the year. For *L. agilis*, these resources include certain prey types and abundance of prey (Nicholson, 1980), egg laying sites, overwintering sites used at night and during periods of unfavourable weather and conditions suitable for thermoregulation. Any one of these resources or a combination of these resources could be critical in determining the area (and indeed shape) of an individual lizard's home range and for *L. agilis* it is not known which resources affect home range size. However, it is interesting to note that inverse relationships between the one resource of food abundance and lizard territory size have been analysed and described by Rose (1982). Although Rose analysed territories of lizards, it would not be unreasonable to suggest that in some species of lizards, food abundance is a critical factor in determining home range size. Also, if such resources affect lizard population density, then we could expect small home ranges to occur where there was high population density.

There is little evidence to support this conclusion but House and Spellerberg (1983a) did find that population density of *L. agilis* was varied and that highest population densities occurred where vegetation structure was most diverse. Glandt (1979), working in Germany, has also drawn attention to the importance of vegetation structure in *L. agilis* habitats. Although home range size was not investigated by House and Spellerberg, it is possible that diverse vegetation structure could support high prey abundance resulting in both small home range size and high population density.

ACKNOWLEDGEMENTS

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DIET AND REPRODUCTIVE BIOLOGY OF THE ROTTNEST ISLAND BOBTAIL, *TILIQUA RUGOSA KONOWI* (LACERTILIA, SCINCIDAE)

GLENN M. SHEA

Department of Veterinary Anatomy, University of Sydney, New South Wales, Australia, 2006.

ABSTRACT

Diet and reproduction in *Tiliqua rugosa konowi* were examined by dissection of museum specimens. *Tiliqua r. konowi* attains a smaller size than other races of *T. rugosa*. Adult males and females were similar in size. Reproduction was seasonal, both testis length and ovarian follicle diameter peaking in early Spring (September). One or two young were born in late summer (February). The diet included large quantities of both plant and animal material, as in other subspecies, and contained a high proportion of *Acanthocarpus preissii* seeds and piedish beetles (Tenebrionidae) in spring and summer.

INTRODUCTION

The occurrence of *Tiliqua rugosa* on Rottnest Island, 18km off the south-west coast of Western Australia, was first noted by Werner (1910) and Glauert (1929), although it was Mertens (1958) who described this insular population as a subspecies, *T. r. konowi*, on the basis of its smaller size and darker coloration than adjacent mainland populations. Although the subspecific status of this population has been accepted without question by several authors (Worrell, 1963; Storr, Smith and Johnstone, 1981; Cogger, 1983), nothing has been published on its natural history apart from observations on drinking following rain (Sadleir, 1958). Two named subspecies of *T. rugosa* occur on the mainland, *T. r. rugosa* west of Balladonia and Zanthus, Western Australia, and *T. r. asper* east of Caiguna and Rawlinna, Western Australia, with a third unnamed subspecies north of the Murchison River, Western Australia (Mertens, 1958; pers. obs.).

As part of a taxonomic revision of the genus, I examined all of the specimens of *T. r. konowi* (n = 63) in the collection of the Western Australian Museum (WAM), and took the opportunity to gather data on body size, reproduction and diet from this material.

MATERIALS AND METHODS

Snout-vent length was measured on all material. Specimens were sexed by gross examination of gonads through a single ventral midline incision over the abdomen. Diameter of largest ovarian follicle and testis length were measured, and a subjective estimate of testis condition made: 1. flattened, elongate and narrow; 2. laterally expanded but flaccid; 3. turgid. Minimum size at maturity was based on the smallest specimens with ovarian follicles $\geq$5mm or turgid testes $\geq$12.5mm long and opaque vasa deferentia, and all specimens greater than this size assumed to be mature. The stomach and colon were opened and any digesta removed for examination and sorting under a dissecting microscope.

RESULTS

The smaller size described for this subspecies by Mertens (1958) is a valid diagnostic character (adult SVL 201-260mm, $\bar{x}$ = 231.5, SD = 14.56, n = 55 *vs* 209-300mm, $\bar{x}$ = 252.4, SD = 19.32, n = 96 for *T. r. rugosa*; Mann-Whitney U test, z = 6.02, P<0.001). Mature males were similar in size to mature females (SVL $\delta\delta$ 205-251mm, $\bar{x}$ = 233.3, SD = 12.99, n = 23 *vs* $\varphi\varphi$ 201-260mm, $\bar{x}$ = 230.2, SD = 15.72, n = 32; Mann-Whitney U test, z = 0.81, P>0.05). Gravid females (SVL 213-250mm, $\bar{x}$ = 232.8, SD = 11.14, n = 12) were not different in size to other females.

Tiliqua rugosa konowi, like other *Tiliqua* (Cogger, 1983; Shine, 1985), is viviparous, with litter sizes (based on enlarged yolking ovarian follicles $\geq$12mm, unshelled oviducal eggs or embryos) of 1-2 ($\bar{x}$ = 1.3, SD = 0.49, n = 12). There was no significant correlation between maternal SVL and litter size (r = 0.27, n = 12), nor was there a significant difference in SVL between females with one *vs* two young (Mann-Whitney U test, z = 0.81, P>0.05). Gravid females females had litters of one.

Female reproductive activity was strongly seasonal. Enlarged yolking ovarian follicles were present in females collected on 7 September (n = 2) and 1 November (n = 1), oviducal eggs were present on 22 January (n = 3), while well developed embryos were present in February (n = 2). Other females collected between January and early September (n = 16) had

ovarian follicles ≤9mm in diameter, with the larger follicles occurring in the later months (Fig. 1).
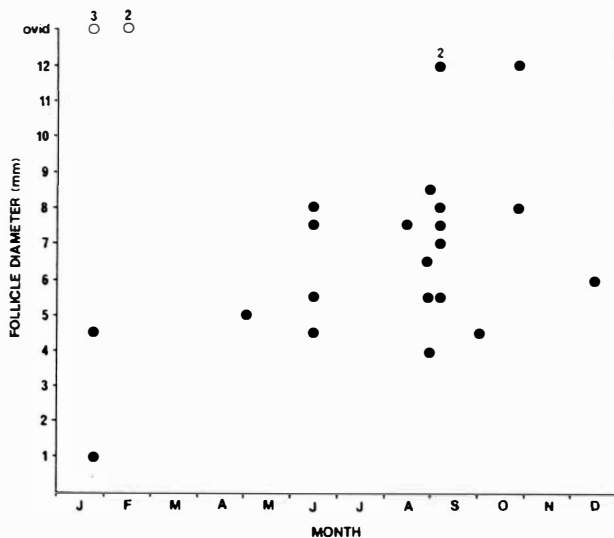
Fig. 1 Seasonal variation in diameter of largest ovarian follicle (dots) and presence of oviducal eggs (open circles) in *Tiliqua rugosa konowi*.

Male reproductive activity paralleled the female cycle. Males with laterally expanded turgid to flaccid testes were collected between 26 March and 23 November, testicular length increasing throughout this period, whereas most males collected in January had thin, narrow testes (Fig. 2).
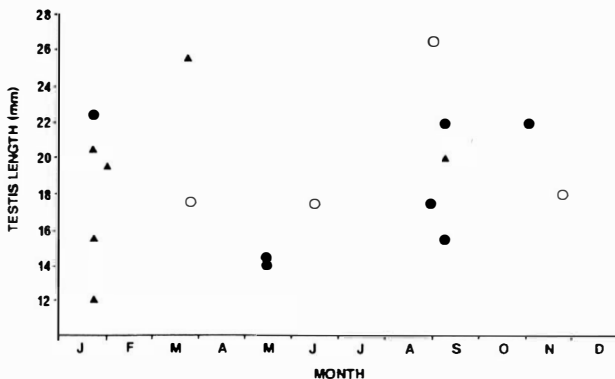
Fig. 2 Seasonal variation in testis length and condition in *Tiliqua rugosa konowi*. Condition categories used are flattened, elongate and narrow (triangles), laterally expanded but flaccid (open circles) and turgid (dots).

No food items were found in stomachs examined. However, the dilated colon usually contained large amounts of digesta. Of 49 colons with identifiable food items, 47 (96%) contained some plant material, this being by far the major component in 35 (71%). Seeds from the perennial herb *Acanthocarpus preissii* (Dasypogonaceae) were a major contributor to colon contents, occurring in 27 (55%) specimens. The presence of these seeds was seasonal, restricted primarily to the period October to March, when they were present in 15 of 20 (75%) colons. All 11 specimens

collected 22 January 1958 contained *A. preissii* seeds, the number in the colon (not including rectum) varying from 9 to over 200. Other species of seed were also frequently present (11 of 49 cases; 22%). Non-seed plant material was mostly herbage, from both monocots and dicots, although small amounts of moss were present in four cases, and single small mushrooms in two cases. Herbage appeared to be poorly digested, with most leaf material entire and even whole new growth tips present.

The majority of identifiable animal material in colons consisted of piedish beetles (Tenebrionidae) of two species (60 small (length approximately 1cm) in 17 colons, 16 large (length approximately 1.5cm) in 9 colons) and snails. The presence of piedish beetles was strongly associated with *Acanthocarpus preissii* seeds, with only one colon having piedish beetles but no seeds. Snails and shell grit were present in 29 colons. In at least 10 of these, whole snails were present, while in the remaining cases, the grit may have been ingested as grit.

Other identifiable animal material included beetles of other species (17 specimens in 9 colons, including *Promecoderus* sp. (Carabidae), *Onthophagus duboulayi* (Scarabaeidae) and unidentified Melolonthinae (Scarabaeidae)), millipedes (Diplopoda) (4 in 4 colons), insect larvae, at least some lepidopterous (19 in 6 colons), roaches (6 in 6 colons), small amounts of arthropod fragments, including some crustacean and arachnid material (6 colons), and apparent carrion (3 mammalian caudal vertebrae in 2 colons, and a small tuft of hair with about 80 dipterous pupae in another). Some seasonal variation in the animal component of the diet was apparent, with insect larvae (mostly hairy caterpillars) only present in late autumn and winter, and piedish beetles only in summer.

Nematodes of several species were present in 35 of 49 colons (71%).

DISCUSSION

Timing of reproduction in *T. r. konowi* is similar to that in mainland *T. rugosa* populations (Bamford, 1980; Bourne, Stewart and Watson, 1986; Bourne, Taylor and Watson, 1986), and agrees with the common pattern of mid or late spring mating and summer or early autumn birth in viviparous squamates in temperate Australia (Shine, 1985). Litter size is similar to that of *T. r. rugosa* on the adjacent mainland (1-2, x̄ = 1.35, n = 20, Bamford, 1980; 1-2, x̄ = 1.56, n = 18, pers. obs.), although litter size in both subspecies is lower than in *T. r. asper* (1-3, x̄ = 2.2, n = 9, Bull, 1987; x̄ = 2.8, n = 6, Bourne, Stewart and Watson, 1986).

Although *T. rugosa* has been widely reported to be omnivorous (e.g., Worrell, 1963; Cogger, 1967, 1983; Bustard, 1970; Swanson, 1976; McPhee, 1979) there are few specific data on the diet of any population. Bamford (1980) examined the diet of two mainland populations of *T. rugosa*, representing both *T. r. rugosa* (Spectacle Swamp, W. A.) and *T. r. asper* (Eyre, W. A.). His results were broadly comparable with the present

	T. r. rugosa	T. r. asper	T. r. konowi
Weevils	17	35	<1
other Coleoptera	4	12	70
Hymenoptera	6	1	2
Ornithoptera	4	5	—
Blattodea/ Hemiptera	<1	4	5
Insect larvae	68	43	15
Diplopoda	1	—	3
Arachnida	—	—	2
Crustacea	—	—	2
Unidentified arthropods	—	—	2

TABLE 1: Numerical analysis of arthropod prey items in three subspecies of *T. rugosa*. Values are percentage of total number of arthropod prey items. Data for *T. r. rugosa* and *T. r. asper* from Bamford (1980), from gut contents and scat analysis respectively; data for *T. r. konowi* from present study.

study, although statistical comparisons are impossible due to the different methods of dietary analysis employed. As in the present study, plant material was the major component of the diet (in terms of wet weight), although seeds were only a minor dietary component in *T. r. rugosa*. The majority of animal material consisted of insects and snails, with insect larvae being most common in winter. However, the major insect prey in the two mainland populations were weevils (Table 1) compared with piedish beetles in

T. r. konowi. It is not known whether this merely reflects prey availability. Anecdotal records of food items in mainland *T. rugosa* populations are also largely in agreement with these findings (Table 2), although suggesting a greater degree of herbivory.

The small adult size of *T. r. konowi* compared to mainland populations would appear to be of very recent origin, as Rottnest I was last isolated from the mainland only 7000 years ago by sea level changes (Abbott, 1978), and populations on the adjacent mainland coast and nearby Garden I (Robinson, Maryan and Browne-Cooper, 1987; WAM R89982, SVL = 263mm; WAM R89996, SVL = 280mm) do not appear to differ significantly from other populations of *T. r. rugosa* in adult size or morphology. Recent studies (Schwaner, 1985; Shine, 1987) have hypothesised that large and small adult body size in tiger snakes (*Notechis*) on other continental shelf islands of southern Australia relative to mainland populations is due to limitations in prey availability. However, given the wide dietary range and trend to herbivory in *T. rugosa*, and the relatively diverse vegetation and physiography of Rottnest I (Storr, 1962; Storr, Green and Churchill, 1959), this hypothesis does not appear to apply to *T. r. konowi*.

ACKNOWLEDGEMENTS

Anon (1892)	*Styphelia* berries, fungus
Chapman and Dell (1980)	seeds, dragonfly, grasshopper (Acrididae), beetle (Carabidae: *Calosoma schayeri*), bugs
Cole (1930)	*Lycium ferocissimum* berries
Dell and Chapman (1979)	weevils, Acrididae, plant remains, old rabbit bones
Frauca (1966)	dandelions, other plant material
French (1901)	*Wahlenbergia gracilis* flowers
Frith (1962)	Mallee Fowl (*Leipoa ocellata*) egg
Keighery (1984)	*Astroloma macrocalyx* fruits
Longley (1944)	mushrooms
Loveridge (1934)	large weevil
Mattingley (1909)	*Arctotheca calendula* flowers
Meredith and Cann (1952)	succulent plants, yellow flowers (*Dodonaea. Arctotheca calendula*, dandelions)
Peters (1973)	yellow flowers
Satrawaha and Bull (1981)	snails (*Helicella virgata*), carrion, *Lycium ferocissimum* flowers and berries, beetles
Serventy (1970)	dried boletus-type fungus, dessicated carrion, *Arctotheca calendula* flowers
Shugg (1983)	*Patersonia* flowers
Simpson (1973)	small yellow flowers, *Pogona barbata* and rabbit carrion
Sullivan (1927)	roach, *Eucalyptus* leaves, flower buds
Tubb (1938)	*Myoporum insulare* and *Gasoul crystallinum* seeds
Turner and Doery (1981)	orchid flowers
Waite (1925)	*Leptomeria* berries, toadstools

TABLE 2: Literature records of specific food items for *T. rugosa*.

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THE DISTRIBUTION IN ENGLAND OF THE SMOOTH SNAKE (*CORONELLA AUSTRIACA* LAURENTI)

Results of the British Herpetological Society Survey, 1984-7

A. C. Braithwaite, J. Buckley, K. F. Corbett, P. W. Edgar, E. S. Haslewood, *G. A. D. Haslewood, T. E. S. Langton, W. J. Whitaker

*28 Old Fort Road, Shoreham-by-Sea, Sussex BN43 5RJ.

ABSTRACT

The British Herpetological Society (BHS) contracted with the Nature Conservancy Council during the years 1984-7 inclusive to determine the distribution and population characteristics of the smooth snake *Coronella austriaca* Laurenti in England. 14-19 BHS members, assisted by other persons, surveyed likely areas by direct observation and by searching under metal sheets (tins) and debris. Snakes were identified by descriptions, measurements, drawings or photographs and their occurrence marked on maps; they were usually sexed by relative tail length. Weather conditions at the time of sighting were recorded. BHS members surveyed altogether 196 sites and found not less than 261 snakes on 86 sites. The survey measured 118 males, 64 females and 58 immature (less than 42cm total length) snakes: the remaining 21 were not measured. Evidence of breeding (gravid and/or immature snakes) was found on 40 sites. Implications for conservation are considered. A map shows the approximate limits of *Coronella* occurrence and 10km squares in which snakes were found. The text includes observations on mating, times of birth, length of snakes and persistence in small areas.

INTRODUCTION

The smooth snake *Coronella austriaca* Laurenti is the rarest British reptile. Smith (1951) indicated its distribution by dots on a map showing populations in two separated regions; A Dorset/Hants/Wilts and B Hants/Surrey (with two observations in Sussex). Frazer (1983) reproduced a Biological Records Centre map based on a 10km square grid. Particularly since about 1970, there have been massive losses of the dry heathland habitat type preferred by the smooth snake (Nature Conservancy Council, 1983) with, presumably, decrease also in its population. To obtain more systematic and up-to-date information, the Nature Conservancy Council (NCC) offered the British Herpetological Society (BHS) a contract to make a survey of suitable habitats in and peripheral to areas A and B to establish the distribution and status of *Coronella* populations. The survey ran from 1984-7.

METHODS

Personnel. For each survey year, the BHS formed a *Coronella austriaca* team (CAT) for fieldwork. Numbers for each year were: 1984, 15; 1985, 17; 1986, 19; 1987, 14.

Organisation and methods of survey. By discussion, the CAT and NCC selected sites to be surveyed during each season: an agreed list was given to each member. Members communicated findings as these were made. Surveys of sites were curtailed as soon as evidence of breeding (gravid snakes or juveniles) was obtained.

The CAT found smooth snakes by searching under flat or corrugated iron sheets ('tins') and other debris and also by direct observation. On most sites, members laid tins unobtrusively: these were not laid where there was much public access or where owners refused permission. Members prepared maps of almost all sites, showing the positions of numbered tins, if laid.

Recordings. CAT members recorded findings of smooth snakes and their circumstances in a booklet containing pages as Fig. 1; weight was usually omitted. A code for scale clipping was devised but most observers did not use this method, preferring instead to identify snakes by measurements and by drawings or photographs of the head and proximal dorsal patterns (Fig. 2), a method employed by Goddard (1981) for small *Coronella* specimens. Some observers also recorded scale abnormalities and damage.

Smooth snakes can be conveniently sexed because the tail in females is shorter than in males, the percentage ratio vent-tail length/total body length being about 20-22 in males and 16-17 in females. The CAT used this method or subcaudal scale counts throughout the survey. The accuracy of these methods for sexing has been assessed by van Gelder *et al.* (1988).

Sites were visited as often as time and opportunity allowed, and at the end of each season information recorded was, for each site: number of tins, number of visits, smooth snakes found, individual observers. The CAT paid particular attention to readily accessible sites for which it had no previous *Coronella* records. In general the team surveyed dry heathland areas, but many of these included wet heath, grassy places and conifer tree plantations.
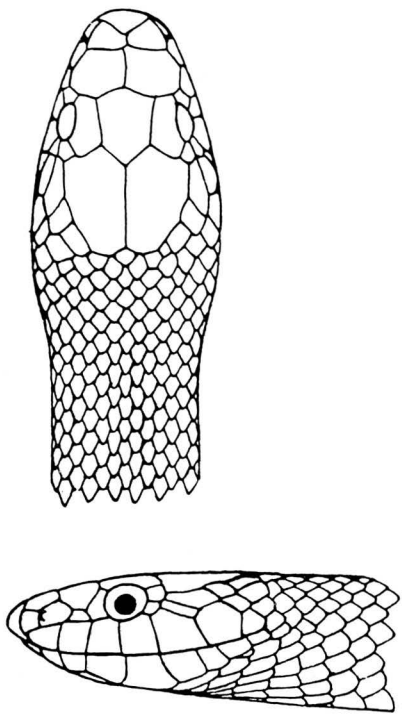
TIN No.	GRID REF.
CLIP No.	SITE
O.A.LENGTH (mm)	DATE
V.T.LENGTH (mm)	TIME
WEIGHT (g)	SUN: STRONG/OCC'/NONE
MALE/FEMALE/JUVENILE	SHADE TEMP (DEG.C)
FIRST CAPTURE/RECAPTURE	CLOUD /8
PRE SLOUGH/POST SLOUGH	WIND: STILL/LIGHT/STRONG
	WIND DIRECTION
	RAIN Y/N
	PREVIOUS RAIN Y/N
NOTES	

Fig. 1   Field record sheet used by BHS smooth snake survey 1984-7.
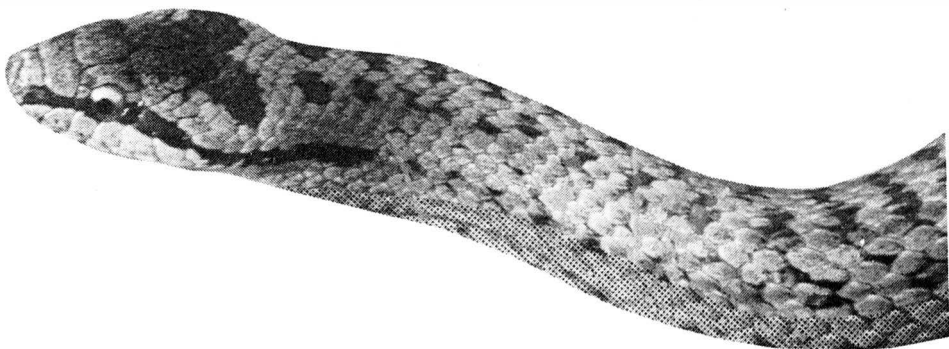
Fig. 2   Forepart of *Coronella austriaca* from area A (see text). Head and proximal dorsal patterns together with measurements of total length and vent-tail length were sufficient to identify smooth snakes found on the BHS survey 1984-7.

RESULTS

Ordnance survey boundaries within which the CAT found smooth snakes are shown as areas A and B in Fig. 3. The vertical line at OS 440 represents the limits of sightings (in 1986) as supplied by A. H. Gent (see DISCUSSION). The team found no smooth snakes in Sussex or Wilts.

A 'site' was defined arbitrarily as a heathland area through which a smooth snake might be expected to travel until checked by difficulties such as roads, urbanisation, mining, cultivation etc. The CAT surveyed 196 sites; 140 in area A (Fig.3), 22 in area B (Fig. 3), 10 peripheral to A and 24 peripheral to B

(including 4 in Sussex). Evidence of breeding (gravid or immature snakes) was found on at least 36 sites in region A and 4 in region B. The number of visits was determined by accessibility (e.g. military sites could be visited only with permission and when activity was minimal), opportunity and desirability (see METHODS). Tables 1 and 2 show the extent to which sites were furnished with tins and surveyed.

The number of new sites surveyed in each season, minimal numbers of smooth snakes seen for the first time and the proportions found under tins are shown in Table 3. Sloughs, snakes not caught, doubtful sightings and recaptures are not included.
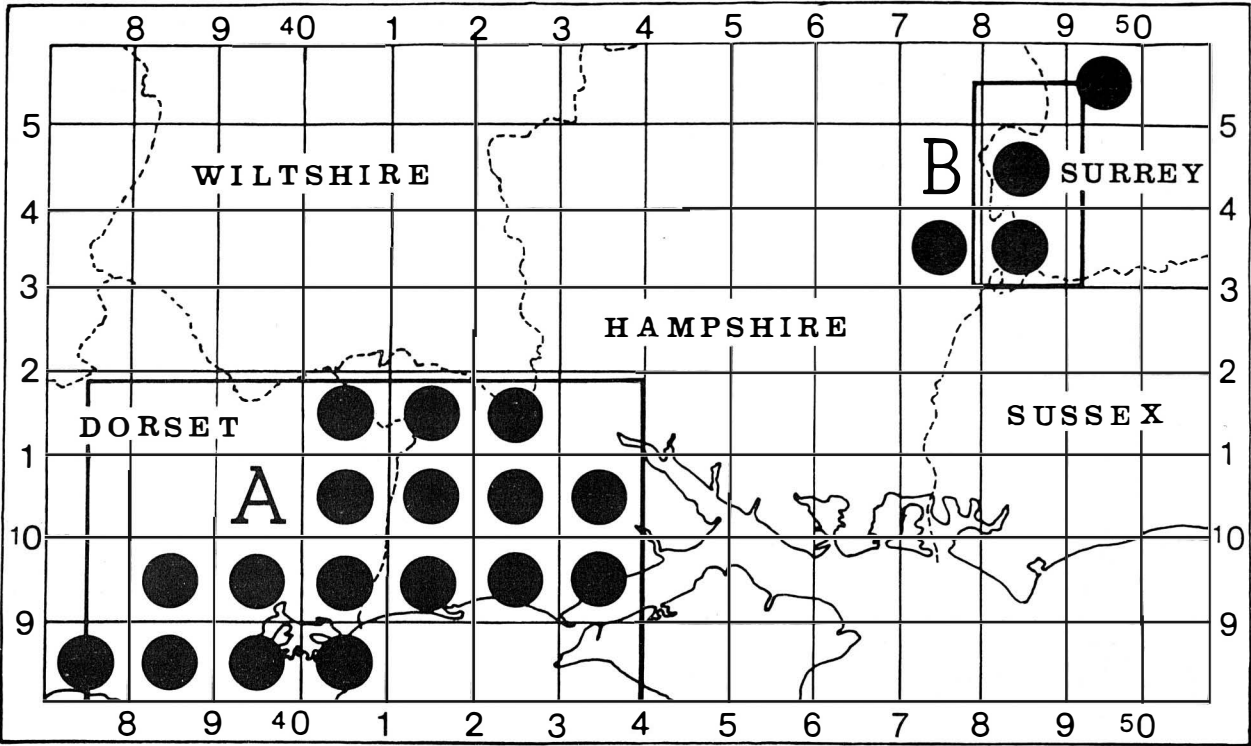
Fig. 3   Approximate limits of the range of occurrence of *Coronella austriaca* as found by the British Herpetological Society smooth snake survey 1984-7. The map shows Ordnance Survey gridlines at 10km intervals. The line at 440 represents the limit as found by A. H. Gent (see text). A solid circle (●) in a 10km square indicates that at least one smooth snake was found in that square. Records in 2 10km squares were supplied by the New Forest Study Group. Broken lines are county boundaries.

Number of visits	Number of sites
1	21
2	7
3	12
4	10
5	17
6	10
7	20
8	13
9	9
10	7
11-20	52
21-30	13
31-40	2
41-50	1
?	2

TABLE 1: Number of visits paid to sites on BHS smooth snake survey 1984-7.

Number of tins	Number of sites	Numbers of snakes
0	30	6
1	4	0
2	15	2
3	24	13
4	19	22
5	23	22
6	18	39
7	9	24
8	5	2
9	10	13
10	8	6
11-20	22	77
21-30	3	25
Debris only	4	4
?	2	6
Total	196	261

TABLE 2: Number of sites having from 0-30 tins and smooth snakes found on sites on BHS smooth snake survey 1984-7.

Note The numbers of tins shown in the first column are approximate for many sites contained debris, including tins as defined, which was searched but not numbered on maps.

Four sites yielded sloughs but no snakes. 86 sites (43.9% of the total surveyed) yielded at least 1 snake. Taking sloughs as proof of reptiles, 90 sites (45.9% of the total) had smooth snakes. Sexually mature smooth snakes have been defined as those not less than 42cm long (NCC, 1983). CAT members measured 118 males and 64 females in this category. They found 58 snakes classed as immature by the above definition; 21 snakes

were not measured. Evidence of breeding (gravid and/or immature snakes) was found on 40 sites.

Tables 4 and 5 show recorded numbers of smooth snakes found in calendar months and times of day during the four years of the survey. These figures

Season	No. of sites newly visited	No. of snakes newly seen	No. of snakes in area A (Fig. 3)	No. of snakes in area B (Fig. 3)	No. under tins	% under tins
1984	47	38	36	2	23	60.5
1985	49	73	68	5	57	78.1
1986	56	67	61	6	58	86.6
1987	44	83	76	7	77	92.8
Total	196	261	241	20	215	82.4

TABLE 3: New sites and smooth snakes found for the first time and their occurrence under tins on BHS survey 1984-7.

Month	Year 1984	1985	1986	1987	Total for 4 years
March	0	1	0	0	1
April	4	0	1	1	6
May	5	12	14	8	39
June	7	13	4	11	35
July	4	8	10	13	35
August	9	13	21	6	49
September	8	23	27	15	73
October	2	4	2	1	9
November	0	3	0	0	3

TABLE 4: Numbers of smooth snakes found in calendar months of the years 1984-7 during BHS survey.

Hours	Year 1984	1985	1986	1987	Total for 4 years
9-10	1	8	1	0	10
10-11	2	12	8	3	25
11-12	5	8	8	6	27
12-13	4	9	9	5	27
13-14	5	5	11	6	27
14-15	5	5	10	10	30
15-16	2	10	8	5	25
16-17	6	10	11	11	38
17-18	4	5	3	3	15
18-19	3	2	4	1	10
19-20	0	2	1	0	3

TABLE 5: Hours (British Summer Time = GMT + 1) between which smooth snakes were found on BHS survey 1984-7.

include recaptured reptiles and, of course, reflect the presence of observers as well as that of snakes. The figures in Tables 4 and 5 are thus not comparable with results of systematic searches on defined sites such as reported by Goddard (1981).

We do not wish, for security reasons, to specify which sites yielded the largest numbers of snakes, but the CAT concluded that two areas of greatest populations were in the neighbourhoods of Hurn in the Avon Valley and of Wareham, Dorset. The survey in the New Forest was limited by an agreement not to

intrude in areas of field research by Southampton University and by reluctance of the Forestry Commission to permit the laying of tins. However, the CAT was able to have the numerous observations of A. H. Gent of Southampton University in this region: these are not included in Tables 1 and 2. The CAT survey was also inadequate on the Studland Peninsula: tins were removed by unknown persons from one site. The CAT also knew that *Coronella* records were continually made in this region by the Warden. A fire in February 1986 destroyed the surface vegetation of

much of a large Studland heath: later in the same year an observer found a fresh *Coronella* slough on the blackened land.

As well as defining the smooth snake's range and mapping its occurrence on sites the CAT made incidental observations as detailed below.

(1) Mating of *Coronella* in Britain in the wild has been recorded only once, in May (NCC, 1983). At 1735 hours BST on 9th August, 1987, on a site in area A, under a tin, a CAT member found a male smooth snake (length about 50cm) holding the head of a female (length 47cm) crosswise. The snakes were briefly bagged: on removal for measurement the male again held the female, who opened her cloaca and exuded a little fluid. The snakes were released together and at 1825 hours they moved under the tin, making a sound interpreted as a renewed grasp of the female by the male. The head ends of the snakes were out of view under the tin: the male was loosely twined round the female and rubbed the visible part of her body; the vents were positioned together. At 1830 hours, the snakes were picked up to check that the hemipenis was inserted: as the snakes were firmly attached, this was assumed. The snakes were left mating. The weather was warm and sunny.

(2) On 29th July, 1985, an observer found a gravid smooth snake and this was recaptured on 2nd November, apparently soon after it had given birth. On 9th November 3 newly-born *Coronella* were found close to where the above female had been seen: the snakes were coiled together just behind a tin and one of them was under this tin about 2.5 hours later. On 10th November the same 3 snakes with 2 other new-born were found basking and, later, all under this tin. On 16th January, 1986, BHS members found three partially decomposed new-born smooth snakes under the same tin. This incident may be relevant to current views on *Coronella* breeding and is considered under DISCUSSION.

(3) On 5th September, 1986, a gravid smooth snake was found under a tin on a Dorset site: its total length was 79.2cm and vent-tail length 8.5cm. The tail was truncated. The measurements give an unacceptable percentage tail/total length ratio of 10.7. On the assumption that the intact snake had a minimal female percentage tail/total length ratio of 16.0, simple algebra shows that the undamaged reptile would have been more than 84cm long. This considerably exceeds the length of the longest British smooth snake known to us, i.e. one found basking on another Dorset site in the presence of 7 BHS and NCC personnel on 14th July, 1984; this, also gravid, measured 72.5cm.

(4) CAT members found snakes under tins in all except hot weather conditions at times between 22nd April (1987) and 10th November (1985). Some individual reptiles repeatedly returned to the same tins, even in successive seasons: they were clearly not deterred by the handling they received. For example, the same snake was under the same tin on a Hants site in 1985, 6 and 7. A tin on a Dorset site harboured the same reptile twice in 1985 and twice in 1986. Another snake in Dorset was caught 5 times in an area of about 0.1ha; a second, 3 times.

DISCUSSION

Method of survey. The survey was as thorough as time and opportunity allowed. BHS members' previous knowledge of suitable sites was essential in selecting those to be examined each season. Some of the CAT were experienced snake spotters; others quickly became proficient. Table 3 clearly shows that laying tins increased the chances of finding snakes, with the considerable advantage in this type of survey that these could yield snakes in most weather conditions. The lower percentage (60.5) of snakes found under tins in 1984 (Table 3) is partially explained by frequent searches made in limited Surrey/Hants areas in that season, resulting in the detection of more snakes lying out in the open than was usually the case during the survey. Measurements as set out in Fig. 1, together with drawings of the head and proximal dorsal markings proved sufficient to identify all snakes found, even in successive seasons; the CAT encountered no cases of ambiguity.

Birth of young. In normal years smooth snakes are born between August and October inclusive. It has been suggested that some females may retain young over winter and give birth in the following spring: this behaviour has not been confirmed in the wild (NCC, 1983). During the present survey, gravid reptiles were found well into October, still basking. As described under RESULTS an apparently recently born clutch was found alive on 10th November (1985). The daytime temperature may have been too low for these animals to feed or seek hibernacula and unusually severe night frosts of about $-5°C$ occurred at that period. It is not surprising that 3 of these snakes were later found dead at the place of their original discovery. It seems that some females may produce young well into the normal hibernation period.

Sex ratio. Goddard (1981) was unable to find any difference in the proportions of the sexes at different ages of *Coronella* in populations he studied. He also found a 1:1 sex ratio in hatchlings. Street (1979) commented that male snakes are encountered more frequently than female. The CAT survey results agree with this. This imbalance is perhaps an artefact of the sampling technique. Goddard (1981) could find no significant difference between the home ranges of male and female *Coronella* on two sites. This aspect of the CAT survey needs further study. Van Gelder *et al.* (1988) pointed out that tail/length ratios and subcaudal scale counts do not in all cases clearly establish sex.

Population. It is important not to exaggerate the quantitative significance of this survey as the CAT conducted it. The sites as arbitrarily defined varied greatly in size from, for example, the banks of a disused light railway about 10m apart and extending for about 300m to wide heathland areas of up to 200ha. All heathland sites, with the exceptions mentioned in RESULTS, known to BHS members in and close to areas A and B were covered by the survey although some large sites were no more than sampled. It is highly improbable that any likely *Coronella* habitat in the above category entirely escaped search. Sites usually did not consist of uniform heathland; many

had been partly damaged by fire and were fragmented by wet areas, tracks and mown fire-breaks. Tins were not uniformly laid but put on what seemed to layers to be promising places, for example sunny slopes, ridges and banks and were hidden from casual observation. At many New Forest sites where aspect or topography looked favourable, vegetation and soil type did not. Results indicated that the New Forest *Coronella* populations were in areas isolated by sub-optimal habitat. In most cases tins were placed only on a small proportion of a site. Tins varied in size and, presumably, in attractiveness to reptiles. For these reasons, and others, we can by no means claim that the CAT found a fair sample of the smooth snake population. Goddard (1984) suggested that the total UK population of smooth snakes might be '26,656-53,312'. He obtained this figure by assuming that the total heathland area of central southern England (in 1976) had the same population density as he found on two sites in the New Forest. We find it difficult to take this estimate seriously, especially since Goddard's sites were in areas known to have good *Coronella* populations. As stated above, the BHS survey was organised and quite thorough; over 4 years it produced a minimal total of 261 different snakes, to which we may add 126 specimens from the New Forest recorded in 1984-6 during a survey by A. H. Gent. Figures of 1000-3000 adults (in 1974) and BHS estimates in 1983 of 2000 adults have been suggested (NCC, 1983). Results of the present survey seem to indicate that the total *Coronella* population is numbered in thousands rather than tens of thousands. The point is important for if Goddard's (1984) estimate was of the right order, there need be much less concern for the snake's survival.

Implications for conservation. Knowledge of actual numbers remaining on the declining heathland habitats is of much less importance than knowing whether the populations are viable and breeding. The CAT team found breeding evidence for only 40 sites (20.4% of the total surveyed; 46.5% of those with snakes). On several sites only a single mature snake was found: these might be no more than survivors of relict populations. Although habitat associations were not the prime aim of the survey the importance for conservation of an understanding of such associations can scarcely be overstated. We hope that further analysis of the survey records will provide material for more research on this topic and what follows are preliminary remarks. On many sites the preferred habitat of the densest populations of *Coronella* appeared to be deep stands of mature dry heather (*Calluna vulgaris*). These stands were usually more than 20 years old, in three instances between 30 and 40 years old and, characteristically, with basal pads of bryophytes and lichens within the heather bushes. Five of the six densest populations in SE Dorset, the three densest from the Hants/Surrey Weald and the only apparent surviving population from N Surrey all fitted this category. A correlation between mature heather and good smooth snake populations has also been noted in the New Forest. One exception was a younger stand of dry heath seemingly enhanced by many old piles of rubble, slates and general debris which the

snakes used as refuges: on another site snakes were found under metal plates some distance from heathland. The conclusion of an affinity with maturer dry heath is in accord with that previously deduced (NCC, 1983). Because tins were generally not laid in shaded and hence treed parts of heaths, we cannot comment on the snakes' possible use of open woodland or woodland edge habitats.

Of course the type of habitat described above is widespread on lowland UK heaths, so well described by Webb (1986). What, then, is the explanation for the remarkably limited areas in which the smooth snake occurs, areas which have remained more or less constant for well over a century (Smith, 1951)? Some CAT observers stated that they could recognise differences between Dorset and Surrey *Coronella* examples: however these differences were not precisely noted. An investigation by biochemical methods into the genetic patterns of smooth snakes from different areas might help to define *Coronella* races. The snake's distribution suggests that climate is an important factor in its survival and that the reactions between it and its environment must, in the UK, be delicately balanced. The still largely mysterious biology of *Coronella austriaca* in Britain presents problems of the greatest interest and this alone makes a strong case for the conservation of this snake wherever it may still be found.

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BOOK REVIEWS:

(1) *Frogs and Toads of the World.* Chris Mattison (1987). 191pp. Blandford Press. £12.95.

On first sight the title suggested a bland 'coffee-table' book, but I was to be pleasantly surprised. Chris Mattison has covered a wide range of topics including anatomy, taxonomy, behaviour, ecology, zoogeography and relationships with man. This wide range of subjects in a single volume inevitably has resulted in each topic being dealt with at a superficial level, which can be frustrating at times. Conservation for instance is discussed in one page. I suspect, however, that this book is aimed at newcomers to the subject, and it does succeed in presenting a wide range of facts in an interesting and readable text. For those whose interest has been captured there is an extensive bibliography, although several important books on the British species are omitted.

The factual information presented in the book reflects many of the recent advances made in herpetological research, and I noted only a few minor mistakes in the text. The reason a copy of this book will find its way onto my bookshelf lies in the quality of the illustrations. This is a lavishly illustrated book, with eye-catching photographs of several tropical tree-frogs. I am sure this useful book will introduce many young naturalists to the study of herpetology.

Brian Banks

(2) *Community Ecology and Salamander Guilds.* Nelson G. Hairston, Sr. (1987), x + 230pp. Cambridge Studies in Ecology, Cambridge University Press. £27.50 (cloth).

Recent years have seen new volumes on community ecology appear on the bookshelves with remarkable regularity. This is at least partly due to the high rate at which new discoveries about species interactions are being made and new models of community organisation are being proposed. Moreover, opinions as to how communities are constructed are almost as diverse as some of the communities themselves. Thus new syntheses of the state of the field are published frequently, summarising the latest developments and viewpoints across a wide taxonomic spectrum. Nelson Hairston's book makes a refreshing change in that it concentrates on just one group of organisms, and attempts to put the considerable literature on salamander ecology into perspective with regard to community ecology as a whole. The author has been studying salamander ecology for over 40 years so there is no-one better-qualified to take on this task.

The introductory chapter, entitled 'Challenges to community theory', sets the scene by describing the various theoretical models used in community ecology. Hairston emphasises the case for using salamanders to study community organisation throughout the book, and in this chapter points out that unlike some other groups, salamanders meet many of the assumptions demanded by community

theory and are therefore particularly appropriate organisms for study. The author's own extensive work on the salamanders of the Appalachians are introduced here. Like many other areas of biology community ecology is burdened with a jargon of its own, and the term 'guild' refers to a group of species that use a set of environmental resources, such as food or space, in a similar way. As the guild concept appears central to Hairston's work, perhaps it could have been introduced before the end of chapter 1, and employed more consistently throughout the book to avoid confusion with the supposedly equivalent term of 'salamander communities'.

The question of how stable are salamander populations is dealt with in the next chapter. The author compares the variation in salamander population size from year to year with that observed in other groups, and concludes that salamander populations display a high degree of constancy. As stability appears to be related to the longevity of adult animals, Hairston dwells on the importance of determining age structure and generation time in salamander populations. It is convenient that size or other morphological variables can be used to determine age in many North American species fairly reliably. The only method for ageing European newts with any degree of reliability is by counting growth rings in longbones, and I found it rather curious that this method was not mentioned here.

The variety of life histories found in salamanders are dealt with in the following chapter and these are discussed in a systematic fashion in the order Ambystomatidae, Salamandridae and Plethodontidae. The only comprehensive data on the life history of a salamandrid is that provided by Bell (1977) for *Triturus vulgaris* and Hairston quotes extensively from this author's work. However, Bell's analyses should be accepted with some caution as the age-size relationship which this author assumed to hold may be open to question.

Most of the work carried out on salamander guilds has been on one of three main categories — pond inhabiting salamanders (*Triturus, Ambystoma, Notophthalmus*); terrestrial salamanders (*Plethodon*); and streamside salamanders (*Desmognathus*), and Hairston devotes a chapter to each of these groups. Amongst pond-dwelling salamanders there are complex interactions involving both competition and predation at adult and larval stages. A fact not often appreciated is that over half of all salamander species are entirely terrestrial. In chapter 5 the author describes his own painstaking experiments on competition in the terrestrial salamanders *Plethodon jordani* and *P. glutinosus.* The field results are consistent with laboratory observations of aggression and territoriality, and it is concluded that the distribution of salamanders on the mountain ranges may be determined by the level of interspecific aggression. Hairston carried out similar exhaustive salamander-removal experiments

on streamside salamanders of the genus *Desmognathus*. Again, there are complex interactions between species of this genus and the relative importance of competition and predation seems to be related to the body sizes of the species concerned. The penultimate chapter deals with experimental tests for evolution in salamander communities, and Hairston returns to his eight-year translocation experiment in the Appalachians. By transferring species between two mountain ranges he neatly demonstrates how aggression may have evolved to increase competitive ability on one range but not on the other.

In the final chapter Nelson Hairston looks ahead, and discusses the various possibilities for salamanders in future ecological research. Interestingly, he sites *Triturus* as being one of the most promising genera for studying pond-dwelling guilds.

For any researcher about to enter the field of salamander ecology this book should be at the top of the reading list. The relative importance of competition and predation in structuring communities is an ecological hot potato, and as Hairston acknowledges, 'the bitterness of a scientific dispute is inversely related to the probability of a clear solution'. Although a clear solution may not be in sight, this book contains some of the most unequivocal evidence of competition and predation produced to date. As in any book which reviews complex experiments on organisms which may be unfamiliar to the reader, frequent summaries are particularly useful and I found the syntheses at the end of each chapter invaluable in clarifying what had gone before. The reference list must be the most extensive on salamander ecology produced to date and the volume is illustrated by figures and tables reproduced from original papers.

Nelson Hairston is to be congratulated on producing this book and for carrying out such long and exhaustive field experiments so successfully. The book also brought home one point which I find slightly worrying. Research in Europe has obviously lagged behind that in North America, and the rigorous experimental approach and testing of theoretical models has hardly been taken up at all. Perhaps it would be too easy to lay the blame at the door of short-term research grants and the current pressure for quick results. Let us hope that Hairston's prediction that the genus *Triturus* will eventually become 'irresistible to British and European ecologists' will be borne out.

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Richard Griffiths

(3) *Handbuch der Paläoherpetologie, Teil 17C Anomodontia.* G. M. King (1988). Gustav Fischer Verlag, Stuttgart & New York, xii, 174pp., ISBN 3-437-30438-6. No Price Given.

The *Handbuch der Paläoherpetologie* is a multi-part work which has been published at irregular intervals

since 1979. The entire work will eventually cover all the fossil taxa of amphibians and reptiles and provide detailed summaries of current knowledge, referring particularly to taxonomy and morphology. The majority of volumes published so far, including the one reviewed here, have been written in English, the remainder in German.

Volume 17 covers the mammal-like reptiles; part 17A on Pelycosauria by R. Reisz has already been published, part 17B on the theriodonts is in preparation and part 17C, reviewed here, covers the Anomodontia. The author adopts a cladistically based classification of the Suborder Anomodontia which differs from other recently published classifications (e.g. Kemp, 1982, Carroll, 1988). She includes in the Anomodontia, the Dinocephalia and Dicynodontia at infraordinal rank. Her classification of both groups is derived sequentially from cladograms; this has obviated the need to propose several new taxonomic names but has resulted in a reduction in rank of many preexisting valid taxa.

The book is laid out on the general *Handbuch* bauplan. A brief historical introduction is given for each group, together with accounts of general osteology, functional anatomy, origins and evolution, mode of life, geographical and geological distribution. A complete bibliography of all the systematic literature and substantial reference to papers on other topics, such as functional morphology, is included.

The main sections of the book are devoted to a systematic review of the two infraorders. Brief diagnostic characters are given for superageneric taxa and detailed diagnoses are presented at generic level. The species contained in each genus are listed together with details of repository, locality and horizon.

The author has compiled a thorough and badly needed revision of synonymy at species level. The dicynodonts, especially, are a group in which species names have proliferated, for example the synonymy of *Oudenodon bainii* runs to nearly a full page, and it is very valuable to have all the information listed in one compact source. Unfortunately, diagnostic information is not given at species level, doubtless because of space — this part is some 50 per cent larger than part 17A — but this a real omission which detracts from the overall usefulness of the book as a source of reference. It is certainly a source of frustration for anyone who might be trying to identify and curate material in museum collections for example.

The book is adequately but not generously illustrated. I found it extremely irritating to discover that there are no figure references in the text. This is bad enough where figures and appropriate text occur on the same or facing pages but where they do not, the only indication as to whether a species is figured or not is found in the index at the back of the book. I cannot imagine why such basic information was omitted from the text; it is an extremely weak point in otherwise clearly presented information.

This is a very comprehensive and authoritative book; despite the shortcomings noted above it is destined to be the standard work on amonodonts and it is an essential reference volume for anyone with an

interest in the group. It should be in every university and museum library although I doubt it will reach many personal bookshelves because of the prohibitive price of the *Handbuch* series.

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Kemp, T. S. (1982). *Mammal-like reptiles and the origin of mammals.* Academic Press, London. 363p.

Angela C. Milner

(4) *Visual behavior in salamanders. Studies in brain function. Vol. 14.* Gerhard Roth (1987). Spring-Verlag.

The title is both broader and narrower than the contents of this book. The visual behaviour discussed by Roth is principally that of prey capture, and very dramatic some of it is. Species of the genus *Bolitoglossa* which range from NE Mexico to the Amazon basin stick out their tongue a couple of cm within 4ms. This rapid projectile can be directed laterally as well as frontally allowing these salamanders to catch bees and flies on the wing. The visual system is designed to operate at very low light levels. Prey can be caught successfully when there is less light than that found on a moonless and cloudy night.

Much of the book is devoted to the eye and to the visual system which make such feats possible. It includes a long and useful survey of the anatomy of the central nervous system, and there is full coverage of the current state of physiological understanding. If you need an encyclopaedic account of vision in sala-manders, you will find this a useful monograph. But, sad to say, all this detail does not yet make a coherent story. The book's especial strength lies in the emphasis it places on the behavioural, anatomical and physiological differences to be found within the amphibia. In the long run, it may well be that the most important lessons to be learnt from the study of amphibian prey capture will be drawn from an imaginative use of this comparative approach.

T. S. Collett

(5) *Phylogenetic relationships of the lizard families. Essays commemorating Charles L. Camp.* Edited by R. Estes and G. Pregill (1988). Stanford University Press, California. 631pp. Illustrated. 80 US dollars.

During recent years there has been an upsurge of interest in the evolution of lepidosaurian reptiles — *Sphenodon*, the Squamata, and their extinct relatives — and this has been stimulated by the use of the cladistic method for expressing phylogenetic relation-ships. This book partly represents the proceedings of a symposium held in Tennessee in 1982 to commemorate the late Professor C. L. Camp, a distinguished palaeontologist and the author of a seminal paper on the classification of lizards (1923); R. Estes gives an excellent appreciation of him. Like all symposia, it is difficult to review except at inordinate length, and here one can do little more than indicate the scope and general approach of this important work. Owing to the

fact that some of the papers originally presented at the 1982 symposium have been published elsewhere in the meanwhile, the volume contains no proper coverage of the auguimorphan lizards, which include the anguids, heloderms and varanids; this is a pity, since these forms are among the most interesting groups of lizards, especially in view of their possible (though contro-versial) relationship with the ancestors of snakes.

The various papers deal with such topics as the overall relationships of lepidosaurs and their fossil relatives (Gauthier *et al.*: Carroll), evolution within the Squamata (Estes, *et al.*), iguanid phylogeny (Etheridge and de Queiroz), classification of eublepharid geckos (Grismer), evolution of Scincomorpha (Presch), lizard limb musculature (Russell), and tongue morphology (Schwenk).

These papers contain an enormous mass of detailed information, particularly regarding the skeleton, and many excellent figures. The emphasis is on characters of systematic interest rather than upon functional anatomy, a concomitant of the cladistic approach which will lead morphology into even greater disrepute than it currently 'enjoys' among other kinds of biologists. Furthermore, the work makes minimal concessions to the general herpetologist; for example, one looks in vain for any summary of the cladistic method or for a glossary of its wretched jargon. Elitism! One is is just supposed to know, though one doubts if the subject is taught in any university in the United Kingdom.

Having said all this, there can be little doubt that the work will for many years be consulted by the specialist in reptilian morphology, and one has nothing but praise for the authors of these esoteric articles. Yet one cannot help wondering just how useful this type of publication in a huge, expensive book of this kind will prove to be in the wider context of scientific advance. University libraries, at least in the UK, where 'classical' zoology is everywhere in the retreat, are unlikely to buy it, and it is beyond the pocket of most of us, ill-paid academics. Would it have been better if the articles had been published separately in journals which will remain much more generally available? But perhaps this would strike at the heart of the grant-aided, prestige-symposium philosophy. One wonders.

Angus d'A. Bellairs

(6) *The evolution of the amphibian auditory system.* Fritsch, B., Ryan, M. J., Wilczynski, W., Hetherington, T. E., Walkowiak, W. Eds. (1988). John Wiley & Sons, New York. 705pp.

This book is a collection of research reviews derived from a workshop, held in March 1986 at the University at Bielefeld, FGR, to summarise information on all aspects of the amphibian auditory system. The volume focuses on unifying principles. This is also expressed in an introduction, which forms the first of 28 well-balanced chapters: 'The amphibian auditory system as a model for neurobiology, behavior, and evolution' (W. Wilczynski and M. J. Ryan).

Writing this review in a tropical environment at the Amazonian field station 'Panguana', Peru, with at

least 70 sympatric frog species demonstrating a bright variation in behavioural — especially acoustic (and reproductive) — patterns, I find it difficult to address any anuran as a 'model system' from any vantage point. However, it has been elegantly proven by this workshop that the amphibian auditory system justifiably has received extensive international attention among researchers in the fields of neurobiology, anatomy, physiology, developmental biology, ethology, neuro-ethology and evolutionary biology. And as S. Rand points out 'we are closer to understanding communi-cation in frogs than in most groups of organisms because the investigators of frog communication have exploited a wide variety of approaches'. The many techniques and approaches and their findings are the subject of this stimulating book, which no biologist working on amphibian acoustic systems should miss.

The introductory chapter is followed by an overview of 'Evolutionary relationships of the amphibians' (W. E. Duellmann). Chapters 3 to 6 review the peripheral auditory system: 'Evolution on the stapes in paleozoic tetrapods: conservative and radical hypotheses' (R. E. Lombard and J. R. Bolt), 'Structure and function of the amphibian middle ear' (A. P. Jaslow, T. E. Hetherington and R. E. Lombard), 'The amphibian inner ear' (E. R. Lewis and R. E. Lombard) and the 'Physiology of the Anuran eighth nerve' (H. H. Zakon and W. Wilczynski). Chapters 7 to 12 provide information for central auditory areas: 'The eighth nerve of amphibians: peripheral and central distri-bution' (U. Will and B. Fritsch), 'Organisation and Projections of the area octavolateralis in amphibians' (U. Will), 'Brainstem auditory pathways in anuran amphibians' (W. Wilczvnski), 'Forebrain auditory pathways in ranid frogs' (T. J. Neary), 'Frequency tuning in the anuran central auditory system' (Z. M. Fuzessery) and 'Central temporal coding' (W. Walkowiak). Physiological aspects of sound localisation are given special attendance in Chapters 13 and 14 — although these topics are only marginally within the scope of this volume — : 'Behavioral aspects of sound localisation' (J. Rheinländer and G. Klump), 'Mechanisms of sound localisation in anurans' (J. J. Eggermont). Chapters 15 to 18 review the development of the amphibian auditory system, including changes that occur during metamorphosis: 'Metamorphic changes in the middle ear' (T. E. Hetherington), 'Metamorphic changes in the octavolateralis system of amphibians' (B. Fritsch, U. Wahnschaffe and U. Bartsch), 'Postmetamorphic changes in the auditory system' (W. P. Shofner) and 'Regeneration in the amphibian auditory system' (H. H. Zakon). Be-

havioural aspects are summarised in Chapters 19 to 24: 'An overview of anuran acoustic communication' (S. Rand), 'The effect of social interactions on anuran voval behavior' (K. D. Wells), 'Acoustic properties used in call recognition by frogs and toads' (H. C. Gerhardt), 'Neuroethology of anuran call recognition' (W. Walkowiak), 'The effects of noise and auditory processing and behavior in amphibians' (P. M. Narins and R. Zelick) and 'Peripheral and central mechanisms of vocalisation' (H. Scheider). Finally selected topics in the evolution of amphibians are treated in the last four chapters: 'Phylogenetic and ontogenetic origin of the dorsolateral auditory nucleus of anurans' (B. Fritsch), 'Evolution of auditory pathways in the amphibia' (C. A. McCormick), 'Frog calls and speciation: The retrograde evolution of homogamic acoustic signalling systems in hybrid zones' (M. J. Littlejohn) and 'Constraints and patterns in the evolution of anuran acoustic communication' (M. J. Ryan).

The book is very well edited and contains 204 informative figures. Typographic errors are few. There is adequate cross-referencing between the articles and the many recent references are a sign of the topicality of the subject (51 out of 70 citations in H. C. Gerhardt's chapter are from the 1980s!).

As only 6 out of 28 chapters deal with true evolutionary aspects the term 'evolution' seems somewhat misplaced in the title. Its inclusion may be eye-catching yet misleading. In his excellent chapter M. J. Littlejohn asks 'if we are to learn something of the evolution of bioacoustic systems, where should we look? Also what should be looked for?' The present book together with Ryan's case study on a single frog species (The túngara frog. A study in sexual selection and communication. University of Chicago Press, 1985) form the most sound basis from which to start. But there is still a long way to go before we understand the evolutionary forces influencing calling and hearing in frogs. I consider ecoacoustics, co-evolution or genetic coupling of calling and hearing, costs and benefits of vocal behaviour, sexual selection as well as call structures in hybrid zones to be fruitful topics for further insights into the evolutionary shaping of the various acoustic patterns. Let us rise to the task: Lab and field investigators unite not so much to look for 'a' model, but to understand the varieties of patterns found at inter- and intraspecific levels of those fascinating organisms we call salamanders, frogs and toads. An excellent approach has been made with this book, now it is time to take the leap.

W. Hodl

FIRST WORLD CONGRESS OF HERPETOLOGY

Canterbury, United Kingdom • 11-19 September 1989

THE CONGRESS will be held at University of Kent and in Canterbury. H.R.H. Prince Philip, President of the World Wildlife Fund, will serve as Patron of our Congress and Professor Angus d'A. Bellairs as Honorary President. The Congress will also serve as the official 1989 meetings of Societas Europaea Herpetologica, Herpetologists' League, and Society for the Study of Amphibians and Reptiles. It will be co-hosted by the Zoological Society of London, Fauna and Flora Preservation Society, Societas Europaea Herpetologica, and The British Herpetological Society.

The Scientific Program, subject to modification, is listed below. Plenary speakers and Convenors are now being invited. *Persons who wish to participate in events should contact the Convenors,* whose names and addresses may be obtained from the Secretariat (see below). There will be poster sessions open to all persons but no oral contributed papers. All presentations will be in English, but discussions can be in other languages.

PLENARY LECTURES

THE STATE OF HERPETOLOGY • EVOLUTION AND ECOLOGY OF PARTHENOGENESIS • BIOGEOGRAPHY OF SOUTH AMERICA • INTERNATIONAL CONSERVATION • SEXUAL SELECTION • SYSTEMATICS AND PHYLOGENY • PALEOHERPETOLOGY • ECOLOGICAL PHYSIOLOGY • COMMUNITY ECOLOGY • BIOLOGY OF SALAMANDERS

SYMPOSIA (S), WORKSHOPS (W) and ROUNDTABLES (R)

Conservation
S.1. CONSERVATION AND MANAGEMENT OF SPECIES
S.2. EFFECTS OF POLLUTION ON HERPETOFAUNA
S.3. CAPTIVE MANAGEMENT
S.4. HEALTH AND DISEASE
R.1. IUCN HERPETOLOGY SPECIALIST GROUPS
R.2. CONSERVATION PROBLEMS

Behavior
S.5. SEXUAL SELECTION AND COMMUNICATION
S.6. ENVIRONMENTAL SEX DETERMINATION
S.7. ORIENTATION, NERVOUS SYSTEM AND SENSES
R.3. OPTIMAL SIZES OF EGGS AND CLUTCHES
R.4. MIMICRY AND PREDATOR-PREY BEHAVIOR

Ecology
S.8. LONG-TERM STUDIES
S.9. SNAKE ECOLOGY AND BEHAVIOR
S.10. ADAPTATIONS TO EXTREME ENVIRONMENTS
S.11. AMPHIBIAN COMMUNITY ECOLOGY
S.12. HERPETOFAUNAS: EXPLORATIONS AND STUDIES
R.5. THE ECOLOGY OF THE TUATARA
W.1. SKELETOCHRONOLOGY
W.2. FIELD METHODS AND BIOTELEMETRY

Evolution
S.13. EVOLUTION AND PHYLOGENY OF FROGS
S.14. ORIGIN OF AMPHIBIA AND REPTILIA
S.15. PALEOHERPETOLOGY
S.16. ISLAND HERPETOFAUNAS
S.17. LIFE HISTORY EVOLUTION OF TURTLES
R.6. BIOGEOGRAPHIC REVIEW OF THE CONTINENTS
R.7. CAECILIAN BIOLOGY AND EVOLUTION

Systematics and Genetics
S.18. MOLECULAR SYSTEMATICS
S.19. CYTOGENETICS
S.20. PARTHENOGENESIS AND HYBRIDOGENESIS
S.21. SYSTEMATICS AND PHYLOGENY
S.22. BIOLOGY AND GENETICS OF PIPIDAE
R.8. PHYLOGENY AND CLASSIFICATION OF LIZARDS
W.3. MOLECULAR TECHNIQUES
W.4. AMPHIBIAN LARVAE
W.5. PHYLOGENETIC ANALYSIS

Physiology and Development
S.23. ENERGETICS
S.24. ECOLOGICAL PHYSIOLOGY
S.25. FUNCTIONAL MORPHOLOGY
S.26. REPRODUCTIVE PHYSIOLOGY
S.27. DEVELOPMENTAL PROCESSES

General Topics
R.9. FIELD RESEARCH AND NATIONAL REGULATIONS
R.10. AMATEUR CONTRIBUTIONS TO HERPETOLOGY
R.11. MEDICAL AND RESEARCH ASPECTS OF VENOMS
W.6. PHOTOGRAPHIC TECHNIQUES

EXCURSIONS: Pre- and post-Congress trips are planned to Europe, Russia, the Mediterranean, Belize, Honduras, the Amazon, Ecuador, various sites in Africa, Indian Ocean, Pakistan, Malaysia, China and Australia, each led by professional herpetologists. Day or half-day trips to Darwin's home, London, Cambridge, Oxford and Paris are also planned.

FIRST CIRCULAR: The complete program and full details of excursions, including prices, are given in the First Circular, available from the Secretariat. This includes a Provisional Registration Form. Registration begins January 1988; £90 fee covers abstract book and program, refreshments, and costs of hiring meeting rooms and equipment. *Advance registration is strongly encouraged* for planning purposes and to insure that you receive all other announcements promptly.

SECRETARIAT: Address all inquiries to: First World Congress of Herpetology, Ecology Research Group, Rutherford College, University of Kent, Canterbury, Kent CT2 7NY, UK. *Telephone: (0227) 764000, ext. 3501. Telex: 965449.*

THE HERPETOLOGICAL JOURNAL

INSTRUCTIONS TO AUTHORS

1. The *Herpetological Journal* publishes a range of features concerned with scientific herpetology. These include: full papers (no length limit); reviews and mini-reviews (generally solicited by the editor); short notes (with a single data set); controversies, under 'Forum' (details available from editor); and book reviews. Faunistic lists and letters are not published.

2. *Two* copies of all submissions, and illustrations, should be sent to the Editor.

3. Papers should be concise with the minimum number of tables and illustrations. They should be written in English and spelling should be that of the *Oxford English Dictionary*. Papers should be typed or produced on a good-quality word processor, and double-spaced with wide margins all round. Good quality paper is essential for the top copy. Except for short notes, papers should be divided into sections. The first sub-head will be centred in capitals, the second shouldered in lower case, and the third run on in italics. Footnotes are not permitted.

4. For all papers the title should be followed by the name(s) of the author(s) and the address or name of the Institution in which the work was done. For major papers a short abstract is required before the body of the paper. Acknowledgements should be included before the list of references.

5. The usual rules of zoological nomenclature apply.

6. Tables are numbered in arabic numerals, e.g. Table 1; they should be typed on separate sheets and divided by horizontal lines.

7. Line drawings and half-tones are numbered in sequence in arabic numerals, e.g. Fig. 1. If an illustration has more than one part each should be identified as (a), (b), etc. The orientation and name of the first author should be indicated on the back. They should be supplied for uniform reduction by one-half on A4 size paper to fully occupy the width of the paper. Drawings should be in Indian ink on good quality tracing material, Bristol board or faintly *blue*-lined graph paper; photographic prints may be submitted. For half-tones high quality glossy prints are required. All labelling should be applied to illustrations using stencils or transfers. A metric scale must be inserted in micrographs, etc.; a figure for magnification in the legend is not acceptable. Legends for illustrations should be typed on separate sheets.

8. References in the text should be given as in the following examples: Smith (1964) stated . . ., observed by Smith (1964s, b), Smith & Ones (1963). For three or more authors, the complete reference should be given at the first mention, e.g. (Smith, Jones & Brown, 1972), and *et al.* used thereafter (Smith *et al.*, 1972). For the list of references *the full title or standard abbreviations of the journal must be given.* The following examples will serve to illustrate the style and presentation used by the Journal.

    Bellairs, A. d'A. (1957). *Reptiles*. London: Hutchinson.

    Boycott, B. B. & Robins, M. W. (1961). The care of young red-eared terrapins (*Pseudemys scripta elegans*) in the laboratory. *British Journal of Herpetology* **2**, 206-210.

    Dunson, W. A. (1969a). Reptilian salt glands. In *Exocrine glands*, 83-101. Botelho, S. Y., Brooks, F. P. and Shelley, W. B. (Eds). Philadelphia: University of Pennsylvania Press.

    Dunson, W. A. (1969b). Electrolyte excretion by the salt gland of the Galapagos marine iguana. *American J. Physiol.* **216**, 995-1002.

9. Final acceptance of a paper will depend upon the production by the author of a typescript and illustrations ready for the press. However, every assistance will be given to amateur herpetologists to prepare papers for publication.

10. Proofs should be returned to the Editor by return post. Alterations must be kept to the correction of errors; more extensive alterations will be charged to the author.

11. 25 offprints are provided free of charge. Further copies (minimum of twenty-five) may be purchased provided that they are ordered at the time the proofs are returned.

12. All submissions are liable to assessment by an ethical committee, and publication may be refused on the recommendation of this committee. Contributors are therefore encouraged to justify killing or vivisection carefully in relation to their work.

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