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MINI-REVIEW:
THE ORIENTATION BEHAVIOUR OF AMPHIBIANS

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INTRODUCTION

Migrations from one microhabitat to another, during development or reproduction, form part of the life history of most Amphibia. The embryonic and larval development often take place in bodies of water, and larvae regularly move between the sites which provide food, shelter, or other resources. During metamorphosis tadpoles of the terrestrial species orient towards the shore line. Juveniles disperse over the adjacent areas, sometimes reaching places several kilometres distant from their natal site. Adults return to specific breeding sites, sometimes in spectacular mass migrations. These examples demonstrate that amphibians migrate during all developmental stages, if important habitat resources such as food, shelter or mates are spatially separated.

During the past decades many studies presented evidence that migratory amphibians and even some sedentary species exhibit orientation behaviour (reviews: e.g. Adler, Vertebrata Hungarica 21, 7, 1982; Ferguson, Ann. NY Acad. Sci. 188, 30, 1971; Sinsch, Ethology Ecology and Evolution 2, 65, 1990). Displaced individuals are able to relocate known sites (e.g. ponds, home ranges) using a variety of directional cues to accomplish homing. This review summarises the present knowledge on the complex relationships between developmental stage, migratory range and preferred orientation cues.

MIGRATORY BEHAVIOUR

Navigation means long-distance orientation independent of familiarity with the release site (Able, in: Animal migration, orientation and navigation (ed. Gauthreaux), 283, 1981). Therefore, the first step of analysis of orientation behaviour must be directed to the migratory experience obtained by larvae, juveniles and adults. Presently, our knowledge is limited to the scarce data on some terrestrial Anura and Urodela, whereas information on aquatic species and Gymnophiona are absent. The next step of analysis concerns the evidence that amphibians home to specific sites in their habitat. Site fidelity permits the experimental approach to orientation behaviour because the goal of displaced individuals can be predicted and the spatial range of homing response estimated.

Natural migratory range: The spatial experience obtained during larval development ranges from none

in terrestrial-brooding and viviparous species to the size of the natal pond. In stream-breeding species such as *Ambystoma texanum* (Petranka, J. Herpet. 18, 106, 1984) and *Ascaphus truei* (Landreth & Ferguson, Herpetologica 23, 81, 1967) drift may increase the area of familiarity considerably. Generally, the contribution to local knowledge gained during the larval stage appears to be small in most amphibians.

In contrast, dispersing juveniles move up to 800m per night (*Rana pipiens*; Dole, Copeia, 221, 1971) and maximally 35km away from their natal pond (*Bufo marinus*; Freeland and Martin, Aust. Wildl. Res. 12, 555, 1985). Juvenile *Bufo woodhousii* are about six times more vagile than conspecific adults (Breden, Copeia, 386, 1987). Observations on *Bufo calamita* (Sinsch, unpubl.) support this stage-specific difference in migratory activity. At least in these species the local map of adults mainly bases on the migratory experience obtained during the juvenile stage. Further quantitative studies should reveal whether the migratory range of juveniles is generally greater than that of adults.

The migratory range of adults ranges from a few metres in sedentary salamanders to 5.2km and 15km respectively in the frogs *Rana pipiens* (Dole, Copeia, 221, 1971) and *R. lessonae* (Tunner, Austria; pers. communication). The maximum speed of migration is 500m per night in *Bufo bufo* (Gelder, Herpet. J. 1, 111, 1986) and 400m in *Taricha rivularis* (Twitty *et al.*, Proc. Nat. Acad. Sci. US 56, 864, 1966). Thus, all maximum records of migrating adults are considerably lower than those of juvenile amphibians. Adults are undoubtedly able to cover large distances, but most individuals even of wide-ranging species such as *Bufo bufo* (Heusser, Rev. Suisse Zool. 75, 927, 1968) stay within a few hundred metres of their natal site during their whole lifetime.

In conclusion, the natural migratory range of Amphibia amounts to 35km at most, which is far smaller than that of any other vertebrate class. Ectothermy and the water permeability of skin limit locomotory activity to periods of favourable temperatures and humidity and so constrain the migratory range.

Site fidelity: Adults of many salamander and anuran species annually return to the same pond for reproduction, others prefer specific parts of their habitat as home ranges, and some even hibernate at the same site during their whole lifetime. These examples illustrate the meaning of site fidelity: voluntary homing to specific sites following active or passive displacement.

Experimental evidence for homing to breeding ponds or terrestrial nests has been presented in 13 species of Urodela (*Ambystoma maculatum, A. opacum, Aneides aeneus, Desmognathus auriculatus, D. fuscus, D. ochrophaeus, Notophthalmus viridescens, Taricha granulosa, T. rivularis, T. torosa, Triturus alpestris, T. cristatus, T. vulgaris*), and in 16 anurans *(Acris gryllus, Ascaphus truei, Bufo americanus, B. boreas, B. bufo, B. calamita, B. japonicus, B. spinulosus, B. terrestris, B. valliceps, B. woodhousii, Hyla regilla, Pelobates fuscus, Pseudacris triseriata, Rana clamitans, R. temporaria, Scaphiopus bombifrons*). In many species reproductive adults return to their natal pond as shown in *B. woodhousii* (Breden, Copeia, 386, 1987). The homing response seems widely independent of information obtained during experimental displacement provided that the release site is located within the migratory range. Such strong attachment to a specific site indicates that breeding places are a scarce resource in the habitat. In fact, following the construction of an artificial pond within the migratory range of a *B. bufo* population, a large number of individuals broke their former breeding site fidelity and headed directly to the new pond (Schlupp *et al.*, Informationsdienst Naturschutz Niedersachsen 10, 12, 1990). This study shows that breeding site fidelity is not unalterable. The fact that new ponds are rapidly colonised by species with a rather strict breeding site fidelity supports this view.

Home site fidelity has been reported for an additional number of species (Urodela: *Ambystoma talpoideum, A. tigrinum, Eurycea lucifuga, Plethodon cinereus, P. jordani, Salamandra salamandra*; Anura: *Atelopus varius, Bufo hemiophrys, B. marinus, B. punctatus, Dendrobates pumilio, Hyla cadaverina, R. pipiens*). The motivation to return towards a home area may last a few days (*B. hemiophrys*; Breckenridge and Tester, Ecology 42, 637, 1961), one season (*B. bufo*; Heusser, Rev. Suisse Zool. 75, 927, 1968) or a lifetime (*B. woodhousii*; Ferguson, Herpetologica 16, 112, 1960). The extent of home site fidelity is probably a function of the number of suitable home ranges in the habitat.

Finally, there are two well-documented cases of hibernation site fidelity. Several individuals of *Salamandra salamandra* hibernated in the same cave for 20 years (Feldmann, Jahrb. Feldherpet. 1, 33, 1987), and some *B. hemiophrys* in the same mould for at least 6 years (Kelleher and Tester, Ecology 50, 1040, 1969).

In conclusion, selection has favoured homing behaviour to specific parts of the habitat instead of random search for new resources by adults. Basic to homing, however, is exploratory behaviour at the juvenile stage to get an idea of the distribution of resources. Considering the scarcity of appropriate localities for reproduction, nutrition, and shelter, homing is obviously a strategy to minimise energetic expenditure for locomotory activity.

Spatial range of homing response: Individuals of several species have been passively displaced to estimate the range of their homing response. The extensive field studies on the newt *T. rivularis* revealed a range exceeding 12.8km (Twitty *et al.*, Proc. Nat. Acad. Sci. U.S. 57, 342, 1967) and a speed of homing of up to 8km per year (Twitty *et al.*, 56, 864, 1966) which have not been matched by any other amphibian. In anurans the range seems smaller: 7 out of 10 displaced toads *B. bufo* oriented towards the 3km distant breeding pond (Sinsch, J. Comp. Physiol 161A, 715, 1987). In both studies the release sites were far outside the adults' migratory range. Nevertheless, it cannot be excluded that migrations during the juvenile stage (*B. bufo*: 2-4 years; *T. rivularis*: 5 years) extended to the release site. Displaced individuals of several other anuran species did not show homeward orientation, if the release site was outside their migratory range.

Amphibians share some common features of homing behaviour: (1) the number of individuals which do not intend to home increases with the displacement distance; (2) the time to determine the correct home direction or to initiate homing also increases with the displacement distance; (3) the motivation to home can persist several years. Nevertheless, it will remain doubtful that amphibians are able to navigate from unfamiliar sites towards a home site, unless the previous migratory experience of the displaced individuals is exactly known.

SENSORY BASIS OF ORIENTATION

Amphibia use a number of different ways to accomplish homing. Path integration as evidenced in the newt *Taricha torosa* (Endler, Behaviour 37, 15, 1970) relies entirely on the uninterupted flow of information during the outward movement. However, it is probably of little importance because the absence of outward journey information does not impair homing. Piloting towards a fixed reference (e.g. breeding chorus) is a form of homing based exclusively on cues which are perceived at the release site. Another possibility which does not require a geographically fixed reference is compass orientation along a preferred direction ('y-axis': Ferguson and Landreth, Behaviour 26, 105, 1966). However, this behaviour only results in homing, if the compass direction leads to a familiar area. The most complex way to home is the map-compass orientation which relies on (1) the determination of the exact position relative to the goal (map-step), and on (2) the calculation of the direction which leads directly to the goal (compass-step; Able, in: Animal migration, orientation and navigation (ed. Gauthreaux), 283, 1981).

Amphibians employ acoustic, magnetic, mechnical, olfactory and visual cues for orientation. The present knowledge mainly bases on studies of those species mentioned before, that means on more or less terrestrial salamanders and anurans, and, with a few exceptions, on adults. The following sections summarise the classes of cues as well as their possible function in the orientation system.

Acoustic cues: Short-distance acoustic communication is widespread among anurans. However, wide-ranging vocalisation is restricted to few species such as *Bufo calamita* (Arak, Nature 306, 261, 1983), *Dendrobates histrionicus* (Zimmermann, Fortschr. Zool. 38, 61, 1990), and *Pseudacris triseriata*

(Ferguson, Ergeb. Biol 26, 128, 1963). Choruses produce advertisement calls which are audible at 500-1000m distance. Nevertheless, homing of *B. calamita* is neither influenced by misleading acoustic information nor by the absence of choruses (Sinsch, Fortschr. Zool. 38, 75, 1990). Moreover, the acoustic transmission of the position of a potential breeding site over large distances implies great energetic expenditure. Therefore, this strategy probably is only used by species which reproduce at unpredictable sites (e.g. temporary ponds). Even in species which employ phonotaxis for long-distance piloting acoustic cues can be replaced by other cues.

Magnetic cues: Orientation based on earth's magnetic field was first demonstrated in *Eurycea lucifuga* (Phillips, J. Comp. Physiol. 121, 273, 1977), later also in *Notophthalmus viridiscens* (Phillips, J. Comp. Physiol. 158A, 103, 1986), *Bufo bufo* (Sinsch, J. Comp. Physiol. 161A, 715, 1987), *B. calamita* (Sinsch, Fortschr. Zool. 38, 75, 1990), *B. spinulosus* (Sinsch, Boletin de Lima 57, 83, 1988), and *Xenopus laevis* (Leucht, Fortschr. Zool. 38, 321, 1990). Evidence in adults is based on deprivation experiments in the field and controlled alterations of magnetic parameters in the laboratory, and in tadpoles of *X. laevis* just on the latter. The effects range from complete disorientation to predictable false directional choice. The inclination of the magnetic field (vertical component) serves as reference for a compass system (Phillips, J. Comp. Physiol. 158A, 103, 1986). Moreover, there are recent indications that magnetoperception may be related to the map-step (Phillips, Science 233, 765, 1986). Yet evidence is still too weak to attempt a final evaluation of the function of magnetic parameters in the orientation behaviour of amphibians. Since toads deprived of magnetic information still home successfully, there obviously exists an alternative map to the proposed magnetic one (Sinsch, Fortschr. Zool. 38, 75, 1990).

Mechanical cues: Water surface-waves (Walkowiak and Münz, Naturwissenschaften 72, 49, 1985), seismic signals (Lewis and Narins, Science 227, 187, 1985) and rheotaxis (Durand and Parzefall, Behav. Processes 15, 285, 1987) are used in several species for short-distance orientation. However, there is no indication that mechanical cues provide directional information for long-distance orientation.

Olfactory cues: Many adult salamanders and anurans use odours as directional cues. However, the effect of anosmia on homeward orientation differs considerably among the species: (1) homing is completely impaired in *Desmognathus fuscus* (Barthalmus and Bellis, Copeia, 632, 1972) and *Plethodon jordani* (Madison, NASA SP 262,485, 1972); (2) initial orientation towards home is greatly reduced, but homing is still possible in *Taricha rivularis* (Grant *et al.*, Science 160, 1354, 1968), *Notophthalmus viridescens* (Hershey and Forester, Can. J. Zool. 58, 266, 1980), *Bufo boreas* (Tracey and Dole, Copeia, 693, 1969), and *B. bufo* (Sinsch, J. Comp. Physiol. 161A, 715, 1987); (3) homeward orientation is only affected during the simultaneous absence of visual cues in *B. valliceps* (Grubb, Copeia, 674, 1970). In toads of the

genus *Bufo* the importance of olfactory cues for initial orientation increases with the size of the migratory range (Sinsch, Fortschr. Zool. 38, 75, 1990).

The chemical nature of the olfactory cues is completely unknown. During the breeding migration guiding odours originate at least partly from the breeding pond itself as evidenced in *Rana temporaria, Bufo bufo, B. woodhousii, Pseudacris clarki*, and *P. streckeri* (e.g. Grubb, Anim. Behav. 21, 726, 1973). Although olfaction is undoubtly involved in the orientation of many amphibians, its specific function is unclear. Odours may serve for piloting along gradients of familiar odours (Adler, Photochem. and Photobiol. 23, 275, 1976) or as sources of a local map (Sinsch, Ethology Ecology and Evolution 2, 65, 1990).

Visual cues: Vision is used for the perception of directional cues in tadpoles (Justis and Taylor, Copeia, 98, 1976), in juveniles (Tracy, Copeia, 145, 1971), and in adults (Landreth and Ferguson, Nature 215, 516, 1967). The cues involved are either fixed visual landmarks (e.g. shore lines, forest silhouettes) or periodically 'moving' celestial cues (e.g. sun, moon, stars, skylight polarisation patterns). In Amphibia, not only the lateral eyes perceive such cues but also extraocular photoreceptors of the pineal complex (Adler, Photochem. and Photobiol. 23, 275, 1976). The interaction of both sensory systems has been demonstrated in *Acris gryllus* (Taylor and Ferguson, Science 168, 390, 1970): eyeless frogs and frogs with covered pineal complex orient as untreated individuals, whereas eyeless frogs with covered pineal complex orient randomly. Analogous experiments with *Ambystoma tigrinum* (Taylor, Anim. Behav. 20, 233, 1972) yielded the same result indicating similar sensory mechanisms in Urodela and Anura.

The role of visual cues in homeward orientation apparently differs among the species and depends on the class of cues. Fixed visual landmarks can serve for piloting as evidenced in the toad *B. bufo* (Heusser, Rev. Suisse Zool. 76, 444, 1969). Celestial cues are used as references for time-compensated compass systems (Adler, Vertebrata Hungarica 21, 7, 1982). The ability of larval and adult amphibians to use the axis (e-vector) of linearly-polarised light for orientation and the visibility of skylight polarisation even when the sun's position cannot be determined directly suggest that the reference of the sun compass probably is the e-vector and not the sun itself. In nocturnal amphibians star or lunar compasses have been demonstrated (Plasa, Z. Tierpsychol 51, 112, 1979), but their contribution to orientation is probably low because most individuals migrate in rainy nights under cloud cover. Finally, fixed visual landmarks are potential map sources as indicated by the findings that (1) visual landmarks can apparently supplant olfactory cues in *B. valliceps* (Grubb, Copeia, 674, 1970), and that (2) blindfolded *B. spinulosus* were completely disoriented, although they were not deprived of magnetic and olfactory cues (Sinsch, Boletin de Lima 57, 83, 1988). Generally, visual cues are more important for the orientation of species with a small migratory range than for that of wide-ranging species.

Multisensory system of orientation: An important feature of the orientation behaviour of amphibians is the integration of many potential cues into a redundant system which leads them safely to their goal even if the availability of cues changes during migration. The apparent contradiction to the principle of parismony is probably consequence of (1) differences in the availability of potential cues among different biotopes inhabited by the same species, (2) the necessity to reach a breeding site at a fixed time (e.g. explosive breeders), and (3) the increased risk of losing life during a prolonged search for the goal. The natural migratory range, the diel activity period and the type of breeding site influence considerably the selection of normally-used cues for initial orientation. The ranking of the sensory input obtained from the potential cues into a specific hierarchy optimises the available information in every habitat. Thus, the interspecific differences in orientation behaviour are probably modifications of the same basic system.

PROSPECT

The concept of a multisensory orientation system in Amphibia (Ferguson, Ann. NY Acad. Sci. 188, 30, 1971) has stimulated research specifically with regard to the identification of directional cues and perceiving sensory systems. Presently, we know that amphibians usually prefer certain cues for initial orientation but also that they use every available source of information to back up their orientation system. A major future task will be the analysis of the neuronal base of ranking the sensory input to filter out reliable directional information. Moreover, the system of magnetoperception has still not been identified. Besides the neurophysiological approach, future field studies will contribute considerably to our understanding of orientation, if they consider the interactions of migratory range, habitat and preferred orientation cues during the complete life history of the studied species.

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SUMMER ACTIVITY PATTERNS AND THERMOREGULATION IN THE WALL LIZARD, *PODARCIS MURALIS*

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ABSTRACT

Body temperature of active *Podarcis muralis* from Noreña (Asturias; Northern Spain) during summer averages 33.8°C (SD = 2.0, n = 116), and similar values were found in other close populations (grand mean: 33.8°C, SD = 2.3, n = 171). There were no significant differences neither in body temperatures between populations nor between sex/age groups within populations. Daily activity pattern is bimodal, with depressed activity during the warmer hours at the midday. This pattern of activity, as well as the significant negative correlation between the percentage of lizards at sun and the environmental temperatures, are indicative of behavioural thermoregulation. The standard deviations of the mean body temperature and the slopes of the regressions of body temperature on environment temperatures are indicative of a relatively imprecise thermoregulation. Populations from the highest altitudes show a higher variability in body temperature and a greater dependence on the thermal environment.

INTRODUCTION

Since the pioneer study by Cowles and Bogert (1944), finding that desert reptiles behaviourally regulate body temperature, many aspects of reptilian thermoregulation have been examined, so that thermal ecology represents currently a major topic in reptilian research. Many studies have shown that, under a variety of environmental conditions, most diurnal lizards are able to regulate their body temperature within relatively narrow limits during the active periods (see review in Avery, 1982).

The mean body temperature, calculated by averaging the temperatures recorded from active animals in the field, is commonly used as a measure of the thermal status of a species. However, field body

temperatures can vary widely in association with seasonal acclimation, habitat shift, size or sex (e.g. Patterson and Davies, 1978; Bowker *et al.*, 1986; Van Damme *et al.*, 1986), and therefore the mean body temperature may not be the only relevant trait for understanding thermoregulation. A better statement of the method and extent of temperature regulation also requires information about the thermal environment and the behaviour and activity patterns involved in thermoregulation (Huey, 1982).

The objective of this study was to examine the thermal biology and the behaviour and activity patterns associated with temperature regulation for a population of the wall lizard (*Podarcis muralis*) near the southern edge of its distribution range.

MATERIAL AND METHODS

This study was conducted at Noreña (Asturias; Northern Spain; 43° 23' N, 5° 40' W) from late June to early August in 1988. Thermal data were recorded from 116 lizards captured by noosing, taking care to minimise heat flow during handling and excluding data from animals that were chased or handled excessively. In addition, data from 55 lizards from other locations or years were considered for comparative purposes.

Body (cloacal) temperatures of lizards were measured to the nearest 0.2°C with a Schultheis mercury thermometer within 10 s of capture. Measurements of air temperature (10 cm above the ground) and substrate temperature were also taken at the time and point of capture of each lizard with the same instrument by shading the bulb. All temperature records concern active animals during the daylight hours.

Lizards were sexed and snout-to-vent length (SVL) measured, from which three age/sex groups were determined: subadults (born during the previous year; SVL from 35 to 45mm), adult males and adult females (SVL >50mm). Young of the year specimens appears from the second half of the study period, but were too small to accommodate the thermometer without

damage (SVL, 22 to 32mm), and therefore they will not be considered in this study.

In order to assess daily activity patterns, I performed a fixed transect along the study plot, repeated at hourly intervals throughout the daylight hours in two different days. Number of active lizards, environmental temperatures, and location in sun or shade (including here the sun-shade mosaic) for each lizard sighted without previous disturbance were recorded.
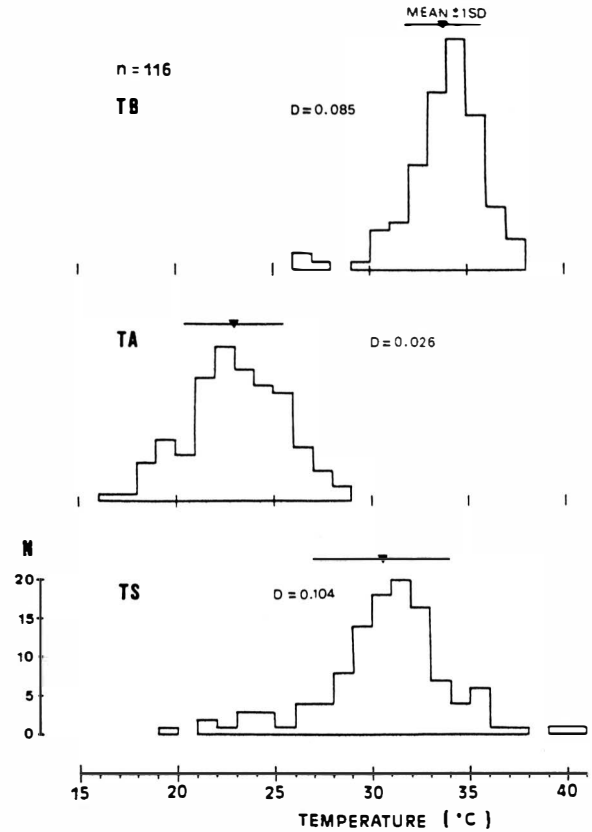
Fig. 1 Frequency distributions of temperatures of body (TB), air (TA), and substrate (TS) for *P. muralis* from Noreña-1988. At each histogram are indicated mean ± standard deviation and the statistic for the Kolmogorov-Smirnov test of normality (D, p<0.01 in all cases).

		Mean ± 1 SD	Minimum	Maximum	N
MALES	TB	33.65 ± 2.63	26.00	37.20	39
	TA	22.24 ± 2.25	16.60	26.60	39
	TS	29.75 ± 3.81	19.00	37.20	39
FEMALES	TB	33.87 ± 1.69	30.40	37.40	36
	TA	23.19 ± 2.72	17.80	28.40	36
	TS	30.16 ± 3.69	21.20	39.80	36
SUBADULTS	TB	33.93 ± 1.64	30.00	37.00	41
	TA	23.53 ± 2.25	19.00	28.40	41
	TS	31.42 ± 2.75	26.20	40.20	41
OVERALL	TB	33.82 ± 2.02	26.00	37.40	116
	TA	22.99 ± 2.45	16.60	28.40	116
	TS	30.47 ± 3.48	19.00	40.20	116

TABLE 1: Descriptive statistics of thermal variables for *P. muralis* from Noreña-1988. TB: Body Temperature; TA: Air Temperature; TS: Substrate Temperature. All temperatures in °C.

Fig. 2   Plot of body temperature against substrate temperature for lizards from Noreña-1988, showing the regression line and the isothermal line (body temperature equal to substrate temperature). Large points indicate more than one data.
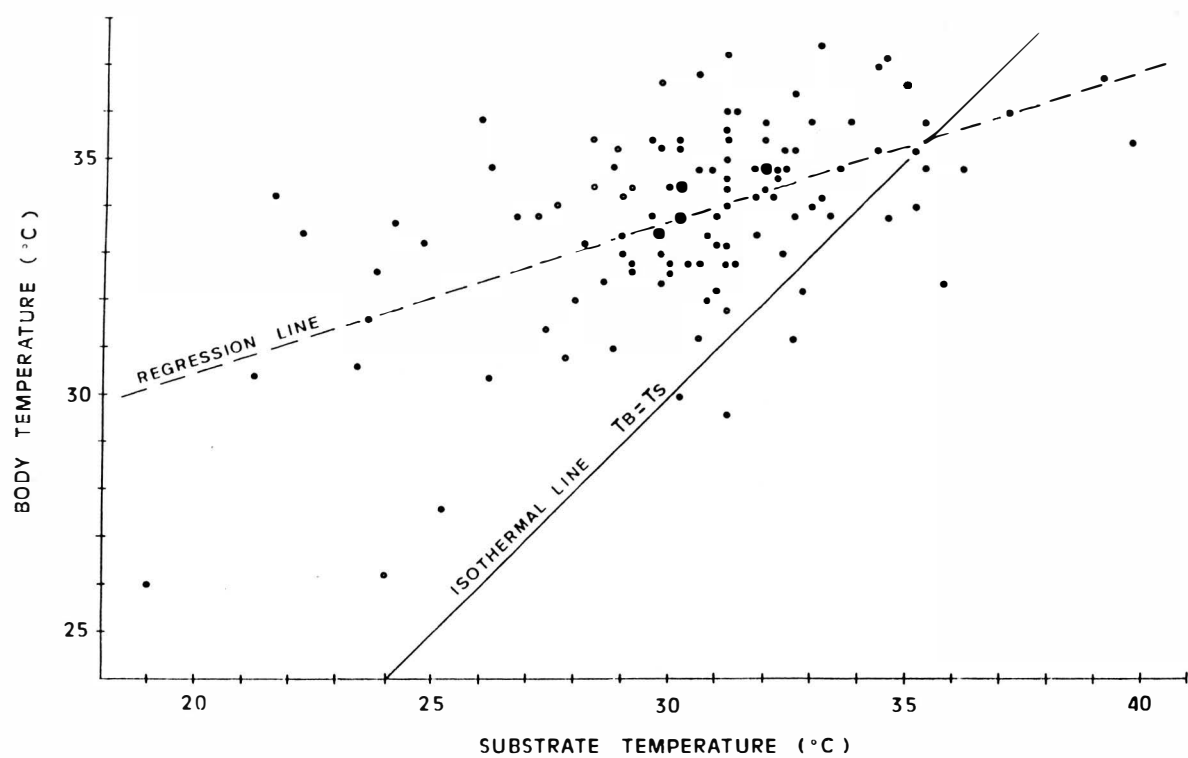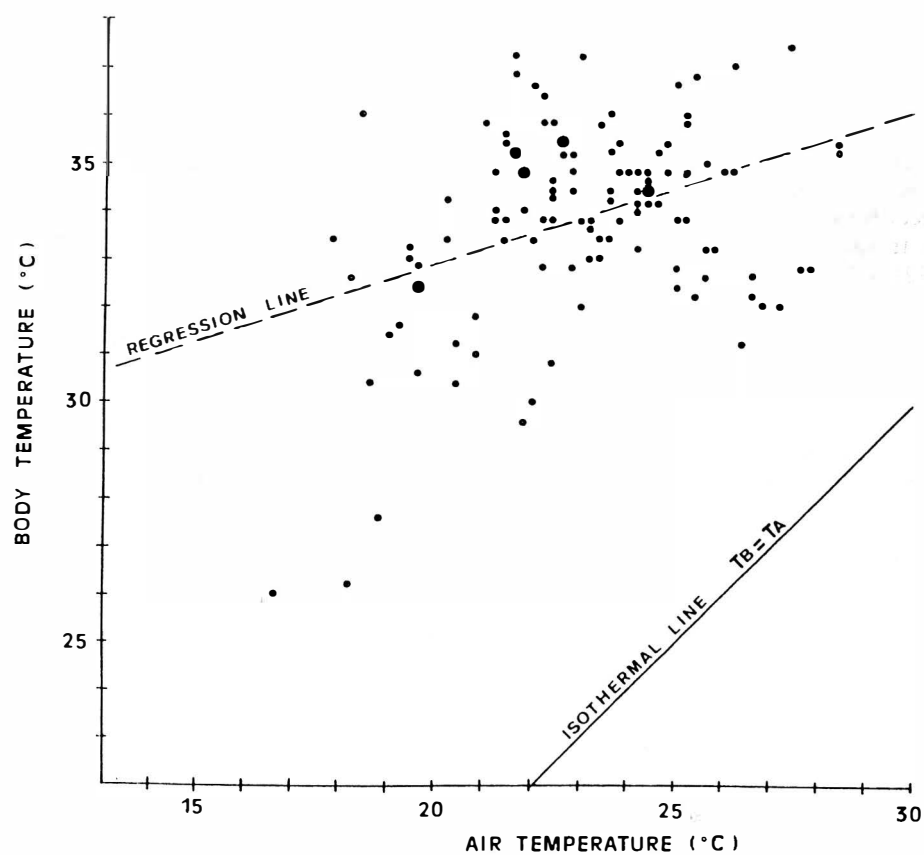

Fig. 3   Plot of body temperature versus air temperature. All considerations as in Fig. 2.

RESULTS

Body and environmental temperatures for 116 captured lizards, separated for subadults, adult males and adult females, are given in Table 1. Mean cloacal temperatures (°C, $\pm$ 1 SD) were 33.93 $\pm$ 1.64 (N = 41) for subadults, 33.65 $\pm$ 2.63 (N = 39) for adult males, and 33.87 $\pm$ 1.69 (N = 36) for adult females. No significant differences were found in the mean body temperature for the three age and sex groups (one-way ANOVA, F = 0.207; d.f. 2,113; p = 0.813); thus, data were pooled for further analysis. Overall mean body temperature was 33.82 $\pm$ 2.02 (N $\pm$ 116). Maximum values were rather constant for all the age/sex groups, rarely surpassing 37°C. Differences in substrate temperature among groups were non-significant (ANOVA, F = 2.573; p = 0.081), whereas mean air temperature showed marginally significant differences (ANOVA, F = 3.064; p = 0.051), air temperature at point of capture for adult males being slightly lower than that for subadult specimens (Student-Newman-Keuls test; p <0.05). Pooled frequency distributions for the three thermal variables are normally distributed (Kolmogorov-Smirnov one-sample test, Siegel, 1956; p <0.01 in all cases; see Fig. 1), and show that lizard temperature was somewhat higher and fluctuates less than that of the physical environment (Fig. 1).

Plots of body temperature versus substrate and air temperature are given in Figs. 2 and 3. Body temperature exceeded that of the substrate under cold conditions (96.4 per cent of cases for substrate temperatures lower than 33.8°C, which corresponds to mean body temperature of lizards), whereas under warmer conditions most of the cases lie below the isothermal line (64.3% for substrate temperatures higher than 33.8°C; Fig. 2). In the plot of body temperature against air temperature all the points lie above the isothermal line (Fig. 3). There were no significant difference between the slopes of the regressions of body temperature on air (b = 0.316; Standard Error: 0.072) and substrate temperature (b = 0.320; SE: 0.046; ANCOVA, F = 0.056; d.f. 1,228; p>0.1).

Fig. 4 shows the daily activity pattern, as number of lizard active and percentage exposed to full sun at hourly intervals throughout the day. In the summer months, *P. muralis* shows a bimodal activity pattern, being more active in the morning (main interval from 0800h to 1000h a.m.) and in the afternoon (1500h to 1800h p.m.), and remaining relatively inactive at the midday (1100h to 1400h).
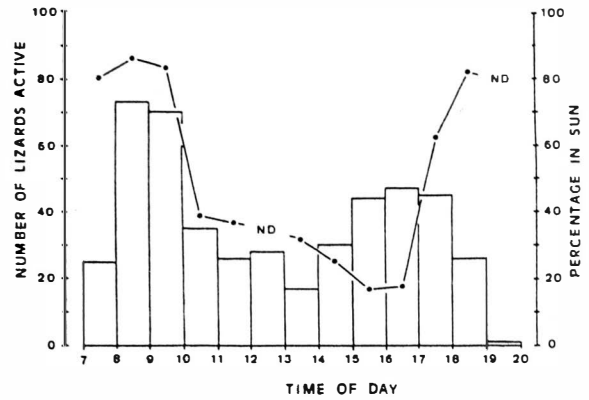
Fig. 4 Number of lizard active (histogram; two transect gathered) and percentage of animals observed in sun at different times of day. ND indicate fewer than 15 valid records for sun/shade location in that interval.
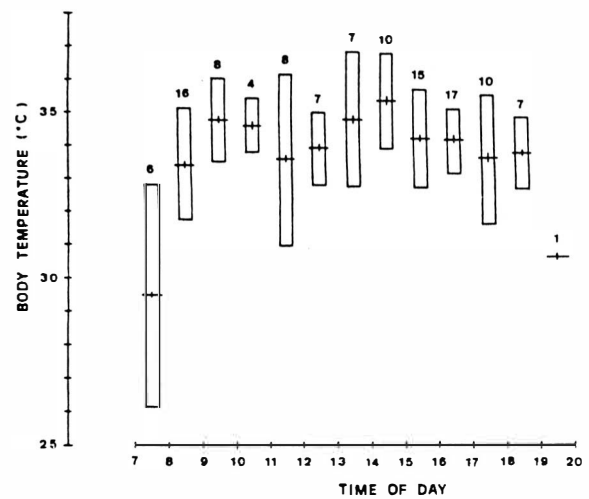
Fig. 5 Body temperatures (mean and standard deviation) of lizards active at different times of day. Sample size is indicated for each hourly interval.

The highest frequencies of lizards in full sun occurred early morning, when more than 80 per cent basked in open places, then decreased progressively until reaching a minimum between 1500h and 1700h (about 17 per cent in sun), and then increased to 80 per cent of active lizards in sun during late afternoon. There was a significant inverse correlation between per cent of lizards in open sun and both the air (r = –0.747; p<0.01) and the substrate temperature (r = –0.623; p<0.05).

Locality-Year	Body Temperature (Mean + 1 SD)	b	r^2	F ratio	N
Noreña - 1988	33.82 $\pm$ 2.02	0.320	0.302	49.34**	116
Noreña - 1989	34.41 $\pm$ 2.36	0.280	0.186	2.97 ns	16
Colunga - 1988	34.55 $\pm$ 1.25	0.198	0.264	3.22 ns	13
Caleao - 1989	33.26 $\pm$ 3.39	0.459	0.307	10.62*	26

TABLE 2: Mean field body temperature (°C), slope (b) and amount of variance explained by the regression on substrate temperature for different populations of *P. muralis*. ** — p<0.001; * — p<0.01; ns — p>0.05

Fig. 5 displays the mean body temperatures of lizards grouped at hourly intervals throughout the day. Body temperatures were remarkably constant between 0800-0900h and 1800-1900h (F = 1.245; d.f. = 10, 98; p = 0.272) but early morning (0700-0800) and late evening (1900-2000) temperatures were sustantially lower.

Field body temperatures of *P. muralis* from other localities or years (Table 2) showed no differences between groups (ANOVA; F = 1.229; d.f. 3,167; p = 0.301). However, both standard deviation of mean body temperature and slopes of the regressions of body temperature on substrate temperature were lower for a population from higher altitude (Caleao, 850m) than for a lowland population (Colunga, at sea level), showing the population from Noreña (300m) intermediate values.

DISCUSSION

Body temperature of active *Podarcis muralis* during the summer averages 33.82 ± 2.02°C in the main population studied, and similar values have been found in some close populations (overall average: 33.83 ± 2.28°C; n = 171). Our data agree with the figures presented by several authors reporting field body temperatures for *P. muralis* (Avery, 1978) and also for other more southerly *Podarcis* species (*P. sicula*, Avery, 1978; *P. hispanica*, Busack, 1978; Pérez Mellado, 1983; Bowker, 1986; *P. bocagei*, Pérez Mellado, 1983; *P. pityusensis*, Pérez Mellado and Salvador, 1981). The resemblance between *Podarcis* species is emphasised when their body temperatures are compared with those of other iberian lacertids, ranging from 29.3°C in *Lacerta monticola* (Argüello and Salvador, 1988) to 38.8°C in adult *Acanthodactylus erythrurus* (Pough and Busack, 1978). Thus, body temperature seems to be a conservative trait within the genus *Podarcis*, whose origin and radiation are quite recent (Arnold, 1973).

A distinct bimodal daily activity pattern, as shown by *P. muralis* seems to be a common pattern for diurnal lizards during the warm summer months (see, e.g. Pianka, 1977). This pattern, as well as the negative correlation between the proportion of lizards at sun and the environmental temperature, is indicative of behavioural thermoregulation (Huey *et al.*, 1977; Waldschmidt, 1980), and suggest that shuttling between sun and shade is a significant way to achieve an accurate control of body temperature. In fact, lizards maintain their body temperatures within relatively narrow limits and above that of the physical environment throughout the daylight hours, except for the first and latest one-hour intervals, as in this extremes the thermal environment likely precludes an accurate thermoregulation.

No differences were found in mean body temperatures of different populations (or years) of *P. muralis* examined in this study. Precision of thermoregulation, however, as indicated by standard deviation of the mean body temperatures did vary. The use of the slope of the linear regression of body temperature on ambient temperature has some theoretical advantages (see Hertz and Huey, 1981; Huey, 1982) and provides similar results in this case, with lower slopes (implying less dependence of body temperature upon ambient temperature) in the lowland than in the highland populations. Contrary to the finding by Hertz and Huey (1981) in *Anolis*, slope was not inversely related to altitude, but the population from the highest location showed higher variability and dependence on thermal environment.

In general, according to the standards made by Bowker (1980, 1986) and Bowker and Johnson (1984), the studied populations of *P. muralis* exhibit low body temperatures and large standard deviations (coefficients of variation from 3.62 per cent to 10.19 per cent) and might be considered as thermophobic and relatively imprecise thermoregulators. Even during the times of day in which environmental temperatures would allow for a more precise thermoregulation, variability of body temperature was equally high (e.g. Noreña-1988: for 36 lizards caught from 10h to 15h, the time of depressed activity when mean substrate temperature was 32.31 ± 2.79°C, the standard deviation of mean body temperature was 1.82, very close to the overall figure). This agree with predictions driving from the cost-benefit models as developed by Huey (1974) and Huey and Slatkin (1976): although constant body temperature provide physiological advantages, increased precision of temperature regulation could increase costs in energy, time and risk of predation, among others (see review in Huey, 1982), so that excessive thermoregulation could lower fitness.

REFERENCES

Argüello, J. A. and Salvador, A. (1988). Actividad, selección de hábitat y temperaturas corporales de *Lacerta monticola* en una localidad de la Cordillera Cantábrica (Sauria: Lacertidae). *Rev. esp. Herpetología*, **3**, 29-40.

Arnold, E. N. (1973). Relationships of the Palaearctic lizards assigned to the genera *Lacerta, Algyroides* and *Psammodromus* (Reptilia: Lacertidae). *Bull. Br. Mus. nat. Hist. (Zool.)*, **25**, 291-366.

Avery, R. A. (1978). Activity patterns, thermoregulation and food consumption in two sympatric lizard species (*Podarcis muralis* and *P. sicula*) from central Italy. *J. Anim. Ecol.*, **47**, 143-158.

Avery, R. A. (1982). Field studies of body temperatures and thermoregulation. In *Biology of the Reptilia*, vol. 12, *Physiological Ecology*, 93-166. Gans, C. and Pough, F. H. (Eds.) London: Academic Press.

Bowker, R. G. (1984). Precision of thermoregulation of some African lizards. *Physiol. Zool.*, **57**, 401-412.

Bowker, R. G. (1986). Pattern of thermoregulation in *Podarcis hispanica* (Lacertilia: Lacertidae). In *Studies in Herpetology*, 621-626. Rocek, Z. (Ed.), Prague.

Bowker, R. G. and Johnson, O. W. (1980). Thermoregulatory precision in three species of whiptail lizards (Lacertilia: Teiidae). *Physiol. Zool.*, **53**, 176-185.

Busack, S. D. (1978). Body temperatures and live weights of five Spanish amphibians and reptiles. *J. Herpetol.*, **12**, 256-258.

Cowles, R. B. and Bogert, C. M. (1944). A preliminary study of the thermal requirements of desert reptiles. *Bull. Am. Mus. Nat. Hist.*, **83**, 261-296.

Hertz, P. E. and Huey, R. B. (1981). Compensation for altitudinal changes in the thermal environment by some *Anolis* lizards of Hispaniola. *Ecology*, **62**, 512-521.

Huey, R. B. (1974). Behavioural thermoregulation in lizards: importance of associated costs. *Science*, **184**, 1001-1003.

Huey, R. B. (1982). Temperature, physiology and the ecology of reptiles. In *Biology of the Reptilia*, vol. 12, *Physiological Ecology*, 25-91. Gans, C. and Pough, F. H. (Eds.). London: Academic Press.

Huey, R. B., Pianka, E. R. and Hoffman, J. A. (1977). Seasonal variation in thermoregulatory behavior and body temperature of diurnal Kalahari lizards. *Ecology*, **58**, 1066-1075.

Huey, R. B. and Slatkin, M. (1976). Cost and benefits of lizard thermoregulation. *Quart. Rev. Biol.*, **51**, 363-384.

Patterson, J. W. and Davies, P. M. C. (1978). Thermal acclimation in temperate lizards. *Nature*, **275**, 646-647.

Pérez Mellado, V. and Salvador, A. (1981). Actividad y termoregulación estival de *Podarcis pityusensis* Boscá, 1883 (Sauria: Lacertidae) en Ibiza y Formentera. *Amphibia-Reptilia*, **2**, 181-186.

Pérez Mellado, V. (1983). Activity and thermoregulation patterns in two species of Lacertidae: *Podarcis hispanica* (Steindachner, 1870) and *Podarcis bocagei* (Seoane, 1884). *Cienc. Biol. Ecol. Syst.*, **5**, 5-12.

Pianka, E. R. (1977). Reptilian species diversity. In *Biology of the Reptilia*, vol. 7, *Ecology and Behaviour*, 1-34. Gans, C. and Tinkle, D. W. (Eds.). London: Academic Press.

Pough, F. H. and Busack, S. D. (1978). Metabolism and activity of the Spanish fringe-toed lizard (Lacertidae: *Acanthodactylus erythrurus*). *J. Therm. Biol.*, **3**, 203-2-5.

Siegel, S. (1956). *Nonparametric statistics for the behavioural sciences*. Tokyo: McGraw-Hill Kogakusha.

Van Damme, R., Bauwens, D. and Verheyen, R. F. (1986). Selected body temperatures in the lizard *Lacerta vivipara*: variation within and between populations. *J. Therm. Biol.*, **11**, 219-222.

Waldschmidt, S. (1980). Orientation to the sun by the iguanid lizards *Uta stansburiana* and *Sceloporus undulatus*: hourly and monthly variations. *Copeia* 1980, 458-462.

THE DISTRIBUTION AND BREEDING SITE CHARACTERISTICS OF NEWTS IN CUMBRIA, ENGLAND

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ABSTRACT

The distribution and breeding site characteristics of the smooth newt, *Triturus vulgaris*, the palmate newt, *T. helveticus* and the warty newt, *T. cristatus* were investigated in Cumbria. *T. helveticus* was the commonest species on the acidic rocks in the Lake District, but was not found in limestone areas. *T. cristatus* was seldom found without the commoner *T. vulgaris*, and there was no evidence of the former preferring larger, deeper ponds than the latter.

T. vulgaris and *T. cristatus*, unlike *T. helveticus* were rarely found in water with pH<6. *T. vulgaris* was usually found in water relatively rich in metal ions, while the reverse was true for *T. helveticus*.

Newts were found in ponds in a wide variety of terrestrial habitats, but most often in rough pasture land.

INTRODUCTION

Three species of newt occur in Britain, the smooth newt (*Triturus vulgaris*) the palmate newt (*T. helveticus*) and warty newt (*T. cristatus*). Studies of newt breeding site characteristics have indicated certain differences in the ponds chosen by the different species. Cooke and Frazer (1976) found that the smooth newt tended to be found in water with relatively high concentrations of metals, while the reverse was true for the palmate newt.

Yalden (1986) noted that in the Peak district newts showed a distinct geographical separation between the species. *T. vulgaris* and *T. cristatus* occurred mainly on the carboniferous limestone in ponds of pH>7.0, while *T. helveticus* was mainly found on the millstone grit and shales in more acid ponds of pH<7.0. Other studies (Beebee, 1977, 1981, Green, 1984) have indicated the importance of certain terrestrial habitat types around newt ponds, notably the presence of dense vegetation.

The county of Cumbria provides an ideal area in which to examine these ideas. The varied geology and diversity of land use provide study ponds on acid and basic rocks in a variety of habitat types. Such a survey also provided an opportunity to assess the status and prospects of amphibians in an area with relatively few records (Arnold, 1973).

METHODS

During the summer of 1986 a survey of 235 ponds in the county of Cumbria was undertaken. All previously recorded *T. cristatus* sites were visited. Other ponds noted on 1:25000 scale Ordnance survey maps were chosen in an attempt to find sites on many different habitat types and geological substrates in order to determine any associations between them and use by newts. However the survey cover above 350m was limited because of the difficulties of access.

Each of these selected sites was sampled to determine which species were present. All sites were netted and the length of time devoted to each site was related to its size, so larger sites took longer to investigate satisfactorily. Any amphibians seen in and around the ponds were noted. The surface area, maximum depth, and amount of shading were noted. The presence of fish and other likely predator species was also recorded. All the sites containing newts were subject to further analysis. The elevation of each pond was taken from Ordnance Survey maps. The geology of the pond site was also ascribed using 1:50000 drift geology maps with local in-field differences noted.

The terrestrial habitat types found within 100m of the ponds containing newts were identified and the areas taken up by each type estimated using 1:25000 maps and infield observations. Any habitat type occupying >50 per cent of the total was considered to be dominant.

49 of the 166 sites containing amphibians were investigated in more detail. Newts were sampled by 15-minute pond netting; the percentage of open water (i.e. that not covered by algae or weed) was also estimated. Water samples were taken from each pond, pH was measured with a PYE UNICAM PW 9418 metre and the samples were also analysed for Sodium, Potassium and Calcium content using a Corning 400 flame photometer. Water hardness was also measured, 50ml of the water sample were titrated with 0.01m

hydrochloric acid, using methyl orange and phenolphthalein indicators. Alkalinity and hardness was expressed as mg/l $CaCO_3$.

RESULTS

Fig. 1A-1C show the distribution of the three newt species, *Triturus vulgaris* was the most widespread newt species. The common frog (*Rana temporaria*) was however the commonest amphibian, occurring in 57 per cent of all sites (see Table 1).

Species	No. of ponds used	% of ponds used
Rana temporaria	133	57
Bufo bufo	40	17
Triturus vulgaris	56	24
Triturus helveticus	31	14
Triturus cristatus	32	15

TABLE 1: The number and percentage of ponds occupied by amphibians in a survey of 235 ponds.

The percentage of sites containing *T. cristatus* is likely to be overestimated, mainly because previously recorded sites were visited. The comparative figure for the random search phase revealed the species in 7 per cent of all ponds. *T. helveticus* was less common than *T. vulgaris*, but this may be due to the small number of ponds sampled on high fells.

Only 8 sites contained all three newt species, but all the *T. cristatus* sites contained at least one other newt species. It was found with *T. vulgaris* in 30 of 32 ponds, confirming the similarity in their national distribution (Arnold, 1973).

Only two sites were found to contain both *T. cristatus* and *T. helveticus* without *T. vulgaris*, a species combination which appears to be rare nationally. Only two sites were found to contain all five species of amphibian.

57 of the 235 sites contained at least one fish species, but only 23 of the 166 amphibian sites contained fish, a significant difference ($X^2 = 4.8$, df = 1, $p<0.05$). Of these only seven had newts, all of which were *T. vulgaris*.

		T. cristatus	T. vulgaris	T. helveticus
Elevation	Mean	114m	122m	155m
	range	8-310m	8-310m	10-506m
Surface area	mean	910m²	1,400m²	460m²
	range	12-10000m²	12-15000m²	10-5000m²
Maximum depth	mean	0.68m	0.87m	0.55m
	range	0.2-1.5m	0.2-2.5m	0.2-1.5m
% Open water	mean	47%	53%	49%
	range	2-98%	2-98%	5-90%

TABLE 2: Physical characteristics of all newt breeding sites.
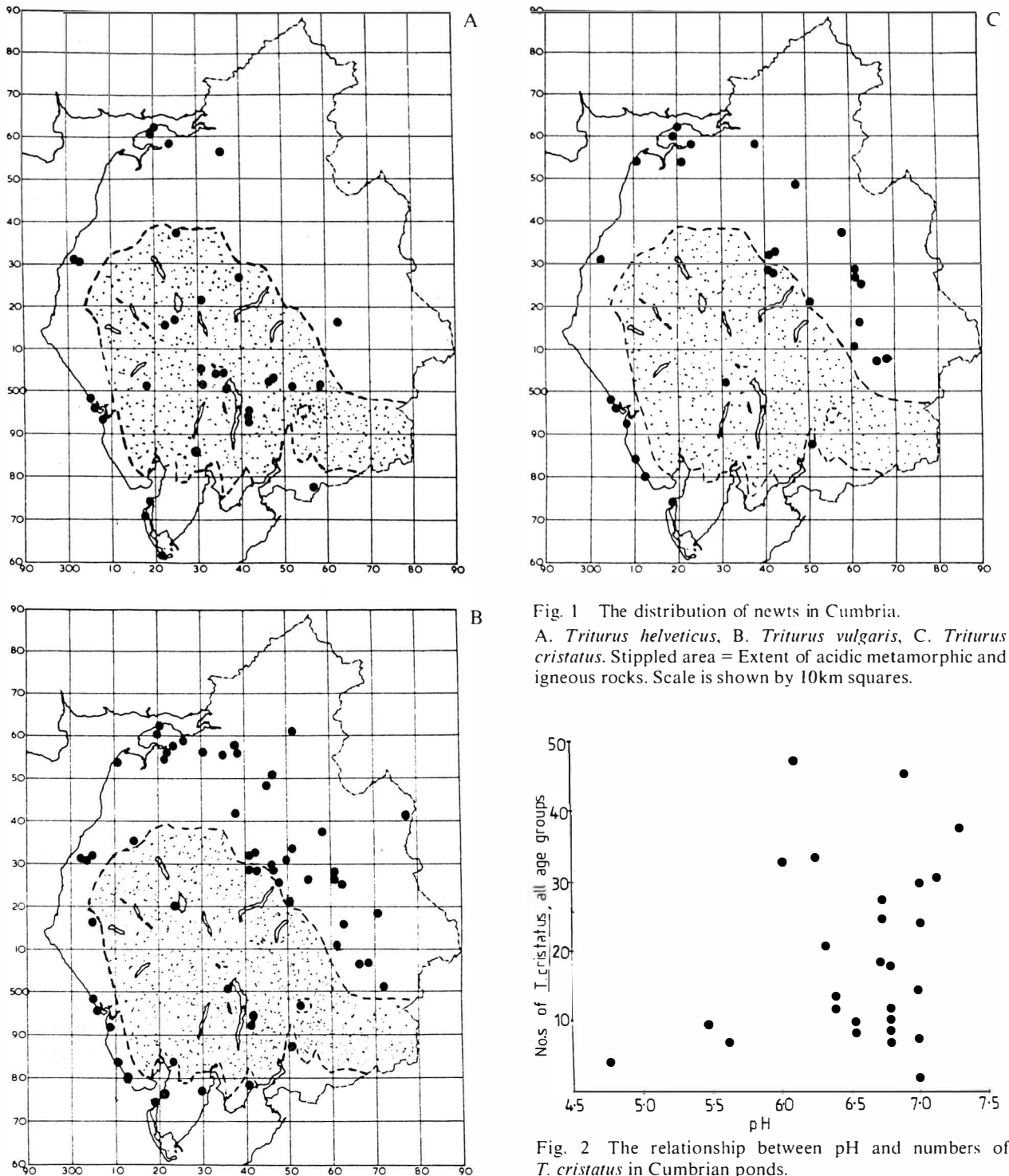
Fig. 1 The distribution of newts in Cumbria.
A. *Triturus helveticus*, B. *Triturus vulgaris*, C. *Triturus cristatus*. Stippled area = Extent of acidic metamorphic and igneous rocks. Scale is shown by 10km squares.
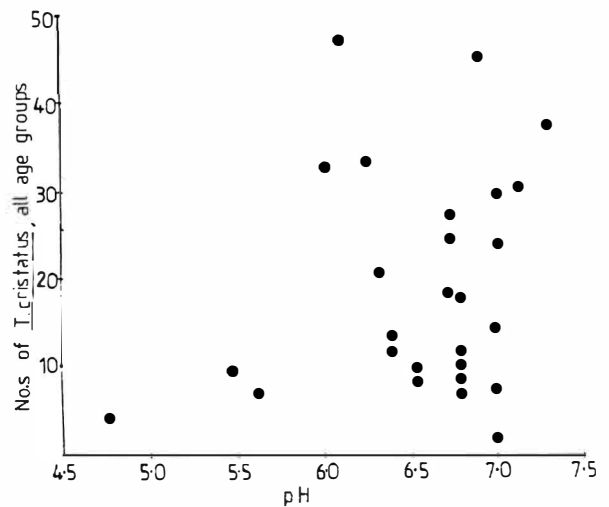
Fig. 2 The relationship between pH and numbers of *T. cristatus* in Cumbrian ponds.

The physical characteristics of the newt breeding sites is summarised in Table 2. There were no significant relationships between newts and elevation. *T. helveticus* had the highest mean for elevation and occurred in the highest site at 506m. The surface area and maximum depth of *T. cristatus* ponds was on average smaller than for *T. vulgaris* sites, but greater than *T. helveticus* ponds.

There was a significant negative correlation between the numbers of *T. cristatus* and *T. vulgaris* and the extent of open water, $r = -0.353$ and -0.421 respectively ($p < 0.05$ in both cases). There were no significant relationships between newts and maximum depths.

T. helveticus occurred in 20 ponds on the Skiddaw slates/Borrowdale volcanic groups. Only 4 of these sites contained other newts, three with *T. vulgaris* and one with *T. cristatus*. The opposite was the case on Carboniferous strata, where 18 ponds contained *T. vulgaris*, only one of which had *T. helveticus*.

Factor range	Sodium (mg/l)		Potassium (mg/l)		Calcium (mg/l)		pH		CaCO3 (mg/l)	
	<8.5	>8.5	<1	>1	<15	>15	<6.7	>6.7	<70	>70
No. of sites	24	25	24	25	25	24	24	25	25	24
T. helveticus sites	10	9	13	6	14	5	12	7	16	3
T. vulgaris sites	16	21	13	24	13	24	15	22	13	24
T. cristatus sites	12	15	9	18	12	15	11	16	10	17
T. helveticus only	8	4	11	1	10	2	8	4	11	1
T. vulgaris only	14	16	10	20	10	20	12	18	10	20

TABLE 3: Chemical characteristics of newt ponds

T. cristatus was found in 11 sites on Carboniferous limestone, all of which contained *T. vulgaris*. *T. helveticus* was not found on limestone, but did occur with *T. vulgaris* on sandstones, till and sand dunes.

Data from the 49 chemically-analysed sites are summarised in Table 3. In order to test for any site preferences, the chemical factors were studied one by one and the median value was taken so as to divide the sites into two groups of as near equal size as possible. Thus for sodium the median value was 8.5 mg/l, which divided the sites into two groups of 24 and 25.

There were no significant relationships between newts and sodium levels. However, the mean sodium level for *T. helveticus* was lower than that for the other species.

T. helveticus was associated with <15mg/l Calcium ($X^2 = 6.05$, d.f. = 1, $p < 0.05$), and Hardness ($X^2 = 10.1$, d.f. = 1, $p < 0.001$), and showed significant negative correlation with hardness ($r = -0.564$, $p < 0.05$) which accounted for 32 per cent of the variation in numbers of newts. *T. vulgaris* conversely was associated with >15mg/l Calcium ($X_2 = 6.63$, df = 1, $p > 0.05$).

Dominant habitat type	% of newt sites dominated by habitat type		
	T. cristatus	*T. helveticus*	*T. vulgaris*
Pasture farm land	28%	26%	33%
Arable farm land	0	0	0
Conifer woodland	6%	3%	0
Deciduous woodland	3%	0	6%
Mixed wood	0	0	0
Gardens and Buildings	3%	3%	7.4%
Scrub	16%	10%	7.4%
Marsh	13%	10%	17%
Moorland/Heath	9%	20%	11%
Sand dunes (grazed)	19%	23%	9.3%
Bare rock	3%	3%	5.5%

TABLE 4: Terrestrial habitats: dominant type around newt ponds

Habitat type	% of newt sites with habitat type		
	T. cristatus	*T. helveticus*	*T. vulgaris*
Pasture farm land	64%	41%	87%
Arable farm land	3.5%	0	8%
Coniferous woodland	14%	9%	13%
Deciduous woodland	14%	9%	21%
Mixed woodland	14%	0	15.3%
Gardens and buildings	15%	9%	31%
Scrub	39%	27%	51%
Marsh	36%	32%	39%
Moorland/Heath	46%	64%	51%
Sand dunes (grazed)	21%	23%	15%
Bare rock	7.1%	14%	15%

TABLE 5: Terrestrial habitats frequency around newt ponds.

T. *helveticus* was also associated with <1mg/l Potassium ($X^2 = 5.24$, d.f. = 1, p<0.05). T. *vulgaris* preferred >1mg/l Potassium, ($X^2 = 8.4$, d.f. = 1, p<0.05).

12 of the 19 T. *helveticus* sites had pH<6.7 while T. *vulgaris* was found in 15 sites with pH<6.7 and 22 with pH>6.7. The ponds containing only T. *helveticus* showed a greater tendency to have lower levels of metal concentrations and pH than sites with only T. *vulgaris*. Sites with both species had more intermediate levels of metals and pH. The mean pH for T. *helveticus* sites was 6.3, that for the other two species was 6.6. The relationship between pH and numbers of T. *cristatus* is shown in Fig. 2. The three sites with pH<6.0 had relatively small populations. Both T. *vulgaris* and T. *cristatus* were found much less often than expected by chance at pH<6 ($X^2 = 68.4$, and $X^2 = 69$ respectively, both df = 1, p<0.0001).

TERRESTRIAL HABITAT

A wide range of habitat types were encountered around newt breeding ponds. In all, 11 categories were represented, see Tables 4 and 5.

A scrub area was found around 43 per cent of all newt breeding sites and 39 per cent of T. *cristatus* sites had a scrub component. Woodland was found within 100m of 31 per cent of all newt sites, but was rarely the dominant habitat. Only one T. *helveticus* site and three T. *cristatus* sites were dominated by woodland. A marsh habitat was found around 33 per cent of all newt ponds, with a similar percentage for each species.

All three species were found in garden ponds. T. *cristatus* was found at one site with T. *vulgaris*, and T. *helveticus* occurred in a garden pool adjacent to open moorland. This species was not found in sites with an arable land component, and no newt sites were encountered where arable land was dominant. Conversely pasture farmland was the most common habitat type, being dominant around >25 per cent of all newt sites.

64 per cent of T. *helveticus* sites had some heath/moorland habitat and this was dominant around 6 ponds. Less than 11 per cent of the ponds containing the other species were dominated by moorland but ponds with large populations of T. *cristatus* and T. *vulgaris* were encountered on open moorland without any form of scrub or woodland within 1km.

DISCUSSION

The T. *cristatus* data do not support the view that the species prefers larger deeper ponds than does T. *vulgaris* (Cooke and Frazer, 1976). In fact T. *vulgaris* was more often found in larger sites, the largest of which also contained fish. Whether such sites would be suitable for T. *cristatus* if fish were absent is not known, but similar ponds in other studies contained large populations (Green, 1984). The mean surface area of T. *cristatus* ponds in this study was 910m^2. In Durham, Green (1984) found this species in sites up to 12,000m^2 in area, and only 7 of 46 sites were <100m^2. Beebee (1977) and Durkin and Cooke (1984) also thought the importance of deep sites for T. *cristatus* was overstated.

Newt breeding ponds occurred in a wide range of habitats, including gardens. Scrub and woodland components seemed to be important. Beebee (1977) found that T. *cristatus* was only found in significant numbers on Downland in ponds with a large scrub area nearby. Nevertheless in this study, large newt populations were encountered on open moorland several kilometres away from any scrub or woodland. However, frogs and toads were often absent from such sites, possibly indicating a difference in habitat. Rough pasture seems to be more suitable for amphibans than arable fields (Beebee, 1981, Green, 1984) but newts can utilise arable land adjacent to other habitats (Cooke, 1986).

The distribution of newts on the various geological strata in the north of England indicate some preferences which are likely to be associated with water quality. T. *vulgaris* and T. *helveticus* rarely occurred together in Cumbria, but in Northumbria, Durkin and Cooke (1984) found them together in 27 of 31 sites. They suggested this was related to the water being of intermediate quality in terms of pH, hardness and metal content.

T. *helveticus* can survive in ponds low in nutrients, and such sites are common in the Lake District. This may explain why Smith (1964) thought T. *helveticus* was a montane species. However the absence of T. *helveticus* from the Pennines (an upland area with hard water) supports the view taken by Cooke and Ferguson (1975) that the association was chemical rather than physical.

As in this study, Cooke and Frazer (1976) and Beebee (1983) found that T. *vulgaris* and T. *cristatus* were less common in ponds with pH<6. Cooke and Frazer (1976) suggested that embryonic T. *vulgaris* may be unable to survive at pH<6. However Dolmen (1980) found T. *vulgaris* breeding ponds in Norway with pH values below 6 (down to 4.5) during the period of egg and larval development.

T. *vulgaris* occurred in ponds with low potassium (<1mg/l) only when calcium levels exceeded 6mg/l. T. *helveticus* occurred in 6 sites with potassium and calcium concentrations below these levels. Cooke and Frazer (1976) found only two T. *vulgaris*, and 14 T. *helveticus* ponds with <6mg/l calcium. T. *vulgaris* can survive in ponds if either calcium or potassium, or both are present in high concentrations. Conversely T. *helveticus* can breed in ponds deficient in both these metals, and rarely occurs if calcium levels exceed 20mg/l. Research into the effects of different concentrations of metal ions on immature stages of newt development may well reveal the reasons for the differences in survivorship, which ultimately influence species distribution.

REFERENCES

Arnold, H. R. (1973). Provisional atlas of the amphibians and reptiles of the British Isles. Abbots Ripton: Biological records centre.

Beebee, T. J. C. (1977). Habitats of the British amphibians, (1). Chalk uplands. *Biol. conserv.*, **12,** 279-93.

Beebee, T. J. C. (1980). Habitats of the British amphibians, (4). Agricultural lowlands, and a general discussion of requirements. *Biol. Conserv.*, **21,** 127-39.

Beebee, T. J. C. (1983). Habitat selection by amphibians across an agricultural land-heathland transect in Britain. *Biol. Conserv.*, **27,** 111-24.

Cooke, A. S. (1986). The Warty newt *Triturus cristatus* at Shillow Hill: Ranging onto arable land. Report of the Huntingdon fauna and Flora Soc. 38th: 40-44.

Cooke, A. S. and Frazer, J. F. D. (1976). Characteristics of newt breeding sites. *J. Zool. (Lond.)*, **178,** 223-36.

Cooke, A. S. and Ferguson, P. F. (1975). Is the palmate newt a montane species? *Br. J. Herpet.*, **5,** 460-463.

Dolmen, D. (1980). Distribution and habitat of the smooth newt, *T. vulgaris(L.)* and the warty newt, *T. cristatus(L.)*, in Norway. *Proc. Euro. Herp. Symp.*, p. 127-139.

Durkin, J. and Cooke, J. (1984). A study of *T. cristatus* and other amphibians in Northumberland. *The Vasculum*, vol. 69, No. 3, 46-50.

Green, D. (1984). A study of great crested newts in Durham and Tyne & Wear, South Durham County Conservation Trust.

Smith, M. A. (1964). *The British Amphibians and Reptiles* (3rd edn.). Collins, London.

Yalden, D. W. (1986). The distribution of newts, *Triturus* spp., in the Peak District of England. *Herpetological Journal*, **1,** 97-101.

PARTITIONING OF WATER WITHIN THE ALLIGATOR (*ALLIGATOR MISSISSIPPIENSIS*) EGG AFTER 60 DAYS OF INCUBATION

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ABSTRACT

Eggs of *Alligator mississippiensis* were incubated up to day 60 of incubation under either dry conditions (on metal shelves, without a substrate) or wet conditions (on vermiculite). Incubation temperatures were 30°C and 33°C. Eggs on the shelves lost water during incubation; water loss from eggs on vermiculite was small, and in some cases, negligible. On day 60, after incubation at 30°C, eggs incubated on shelves had significantly less amniotic fluid and yolk sac than eggs incubated on vermiculite. In eggs incubated at 33°C, on day 60 amniotic fluid was absent and the mass of the yolk sac was smaller in eggs incubated under dry conditions. Embryo mass and the amount of allantoic fluid were unaffected by the extent of water loss from the eggs at both temperatures. The mass of allantoic fluid was correlated with the mass of the egg on day 60. Yolk sac mass at both temperatures was not correlated with egg mass on day 60 but was correlated with the water lost from the egg. These results suggest that (1) in alligator eggs, loss of water is borne primarily by the yolk sac; and (2) that retention of water in the allantois may be associated with a need to prevent a deleterious build-up of waste metabolites. This contrasts with the situation in avian eggs where water loss is borne primarily by the allantois and embryonic tissues.

INTRODUCTION

Water loss from avian eggs is a normal part of incubation (Ar and Rahn, 1980). This progressive dessication affects differentially the water content of individual compartments within the egg as incubation proceeds. The allantoic fluid shows the first signs of dehydration. When this compartment is exhausted the volume of amniotic fluid declines (Hoyt, 1979; Simkiss, 1980; Tullett and Burton, 1982). When all of these fluid reserves are exhausted, near the end of incubation, it is the embryonic tissues which become dehydrated (Hoyt, 1979; Tullett and Burton, 1982; Davis and Ackerman, 1987; Davis, Shen and Ackerman, 1988). The yolk sac, by contrast, is unaffected by dehydration (Hoyt, 1979; Tullett and Burton, 1982).

The water relations of reptilian eggs are highly variable and are dependent upon species, eggshell structure and hydration of the incubation substrate (Packard and Packard, 1980, 1984; Packard, Packard and Boardman, 1982; Packard, 1991). Soft-shelled eggs of squamates absorb large amounts of water during incubation but where the shell structure is more complex, as in pliable-shelled turtle eggs, the exchange of water with the nesting substrate is reduced. Eggs of other turtles and crocodilians which have rigid eggshells often exhibit no net water exchange during natural incubation (Ferguson, 1985; Packard, 1991). In addition, all reptilian eggs incubated on substrates with low water potentials, which still have humidities greater than 99 per cent (Tracy, Packard and Packard, 1978), can lose water during incubation when compared with substrates with higher water potentials.

Hence, the rigid-shelled eggs of the turtle *Trionyx triungis* can lose up to 20 per cent of their initial mass during natural incubation. This has little effect upon hatchability, although higher rates of water loss are lethal (Lesham and Dmi'el, 1986). Similarly, eggs of *Crocodylus porosus* can lose or gain up to 25 per cent of their initial mass without significantly affecting hatchability (Manolis, Webb and Dempsey, 1987; Grigg, 1987).

These different water relations have significant effects on the pattern of embryonic growth and hatchling mass reptiles (reviewed by Packard, 1991). However, unlike the situation concerning avian embryos, the effects of different patterns of water exchange on the dynamic water balance of reptilian embryos and their extra-embryonic compartments during incubation are unknown. Investigations to date have revealed, however, that there are both similarities and differences in the pattern of development of birds and reptiles, particularly crocodilians (Manolis *et al.*, 1987; Deeming and Ferguson, 1989, 1991a). In particular, unlike in the fowl, large amounts of allantoic fluid are present in crocodilian eggs at hatching (Manolis *et al.*, 1987; Deeming and Ferguson, 1989). In addition, unlike in bird eggs albumen proteins do not enter the amniotic fluid during development of *Alligator mississippiensis* (Deeming and Ferguson, 1991a).

This report describes an investigation of the effects of dehydration on the fluid compartments within eggs of *A. mississippiensis* on day 60 of incubation. This artificial treatment, will allow us to compare the effects of water loss in avian and crocodilian eggs. Alligator eggs incubated under dry conditions (without a substrate) were compared with eggs incubated on wet (on vermiculite) conditions.

MATERIALS AND METHODS

Eggs of *Alligator mississippiensis* were collected immediately after laying from wild nests in Louisiana, USA, and transported by air to Manchester as described in Deeming and Ferguson (1989). On arrival in the laboratory (day 3) the eggs were weighed and set in incubators at 30°C and 33°C, accurate to 0.01°C (Vinden Scientific Ltd.), and with approximately 100 per cent air humidity. In each incubator, 10 eggs randomly were placed on the metal shelves in the incubator and 10 eggs were placed on moist vermiculite (100g of water/100g of vermiculite).

On day 60 of post-oviposition incubation (the incubation period of alligator eggs at 30°C is 75 days and at 33°C, 65 days) the eggs were removed from the incubators, weighed and candled to assess embryonic viability. Viable eggs were placed on ice for an hour prior to opening. The allantoic and amniotic fluids were than sequentially decanted from the egg and weighed; the embryo, yolk sac and albumen were then removed from the shell and all components were weighed as described by Deeming and Ferguson (1989). Data were analysed using a Minitab statistical package (Ryan, Joiner and Ryan, 1985).

RESULTS

The incubation conditions affected the water loss from the egg. Despite the high humidity, eggs placed on shelves, without any substrate, lost considerable masses during incubation (Table 1). Air spaces, formed between the shell membrane and the calcite shell, were present in almost all of the eggs at both temperatures. By contrast, those eggs on vermiculite lost much less weight (Table 1) and air spaces were very small or absent.

At 30°C, significant differences between the two groups of eggs were observed in the mass of the yolk sac and the mass of amniotic fluid which were significantly larger, and the mass of the embryo was significantly smaller in eggs incubated on vermiculite (Table 1). In eggs incubated at 33°C, only the mass of the yolk sac was significantly affected by the increased rate of weight loss (Table 1).

The mass of the yolk sac at both incubation temperatures was inversely correlated with the weight

| | 30°C | | | | | 33°C | | | | |
	Shelf		Vermiculite		F¹	Shelf		Vermiculite		F²
Number of eggs	10		10			10		9		
Initial egg mass (g)	77.94	7.66	77.79	8.55	0.00	78.05	3.78	75.23	8.81	0.85
Egg mass at 60 days (g)	73.40	7.98	77.03	8.39	0.98	72.74	4.24	72.91	8.79	0.00
% Water loss	5.90	1.75	0.96	0.64	70.52	6.83	2.10	3.10	1.44	23.15
Shell mass (g)	10.13	0.90	10.09	0.95	0.01	9.74	0.53	9.91	1.10	2.65
Albumen mass (g)	2.02	0.39	2.37	0.70	1.92	0.55	1.34	0.00	0.00	2.12
Yolk sac mass (g)	21.83	3.05	26.54	2.00	16.53	10.37	2.03	13.22	1.65	11.08
Amniotic fluid mass (g)	1.63	0.56	2.61	0.64	13.39	—	—	—	—	—
Allantoic fluid mass (g)	10.66	3.29	11.02	3.49	0.06	8.38	2.63	9.00	3.85	0.17
Residues³ mass (g)	8.76	1.18	7.61	1.90	2.66	3.93	1.83	3.37	0.58	0.77
Embryo mass (g)	18.38	1.39	16.80	0.49	11.49	39.76	4.12	38.21	3.53	0.76

TABLE 1: Mass of *Alligator mississippiensis* eggs and their different fluid compartments on day 60 of incubation at 30°C and 33°C. Values are means and standard deviations and the results of the analysis of variance, as F-ratios (Ryan, Joiner and Ryan, 1985).

[1]F = 4.38 at the 5% level and 8.18 at the 1% level with degrees of freedom of 1,19. [2]F = 4.41 at the 5% level and 8.29 at the 1% level with degrees of freedom of 1,18. [3]Calculated by difference.
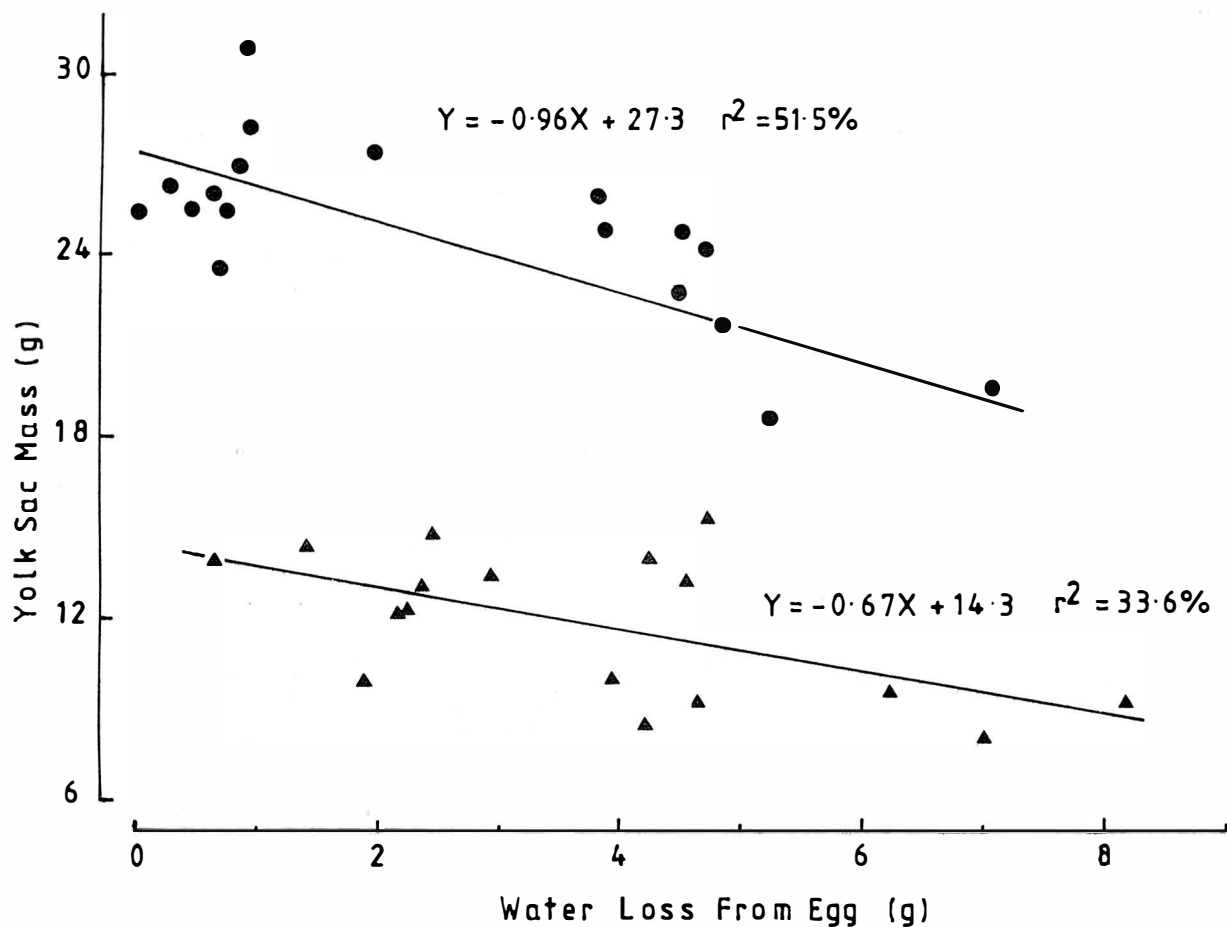
Fig. 1   The relationships between water loss from alligator (*Alligator mississippiensis*) eggs and the mass of the yolk sac by day 60 of incubation at 30°C (circles) and 33°C (triangles).
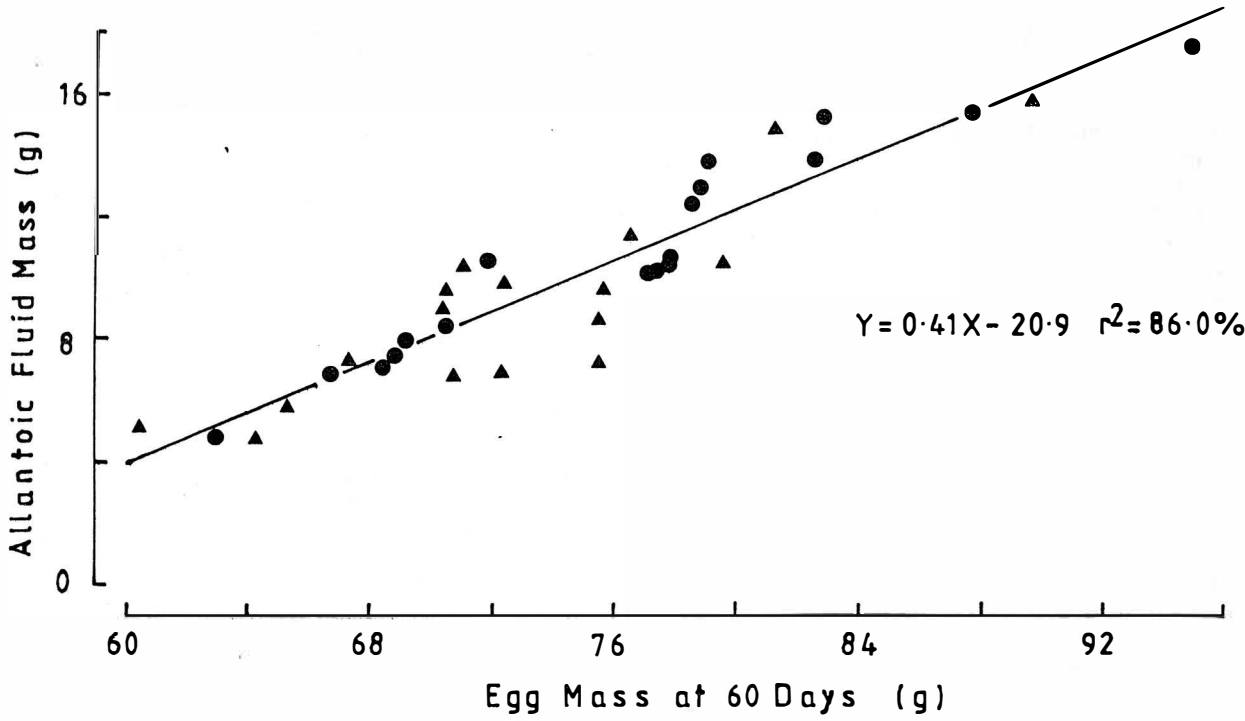
Fig. 2   The relationship between egg mass on day 60 of incubation and the mass of the allantoic fluid for alligator eggs incubated at 30°C (circles) and 33°C (triangles). Regression analysis (Ryan, Joiner and Ryan, 1985) revealed that the relationship was very similar at both temperatures and the line is a regression estimate for the combined data.

lost from the egg during incubation (Fig. 1). There was no significant correlation between mass of the yolk sac and egg mass on day 60 at either or both temperatures (not illustrated). The mass of allantoic fluid in eggs incubated at both 30°C and 33°C was not correlated with the rate of water loss from the egg at both incubation temperatures (not illustrated). By contrast, the mass of the egg on day 60 of incubation, irrespective of temperature, was correlated with the mass of allantoic fluid: larger eggs had more allantoic fluid (Fig. 2).

DISCUSSION

Embryos from eggs incubated at 30°C are at an earlier stage of development and are smaller than those at 33°C; the patterns of yolk and albumen utilisation and fluid formation are sufficiently similar at the two temperatures (Deeming and Ferguson, 1989). Therefore, in this analysis the data for embryos at 30°C were considered to be equivalent to embryos some 8-10 days earlier in incubation at 33°C. Hence, comparisons could be made both between embryos at different temperatures, and embryos at different stages of development.

Loss of water from alligator eggs affected the water relations of the different fluid compartments of the egg: the effects of dehydration were borne first by the amniotic fluid and then by the yolk sac. The allantoic fluid and embryo remained unaffected. This contrasts with eggs of the fowl: normal dehydration of the egg is borne by the allantois, amniotic fluid and by embryonic tissues whereas the yolk sac is unaffected (Hoyt, 1979; Tullett and Burton, 1982; Davis and Ackerman, 1987; Davis et al., 1988). The high water content of the yolk sac is considered to be important in the process of yolk-sac retraction (Tullett and Burton, 1982). In dehydrated alligator eggs, the effects of a reduced water content of the yolk sac upon yolk sac retraction are unclear.

These differences between the alligator and the fowl may be related to differences in the pattern of nitrogen excretion: urea in the alligator (Clark, Shannon and Sisken, 1957; Manolis et al., 1987; Deeming and Ferguson, unpublished observations) and uric acid in the fowl (Romanoff, 1967). During normal incubation as the fowl egg becomes dehydrated, water is lost from the allantois causing uric acid to crystalise and precipitate out of solution (Romanoff, 1967). By contrast, crocodilian embryos, in common with all other reptilian embryos (Vleck, 1991), produce urea as their major nitrogenous waste product. Alligator embryos in this study showed that during the later stages of development (stages 25-28) progressive dehydration of the egg leads to loss of water from the amniotic fluid and then the yolk sac; the volume of the allantoic fluid is maintained. Presumably, this prevents a deleterious increase in the concentration of urea within allantoic fluid. Although turtle embryos are tolerant of high concentrations of urea in their plasma (Packard and Packard, 1989) a threshold of toxicity must exist. If alligator embryos possess similar levels of tolerance to urea, loss of water from embryonic tissues, as is the case in the chick embryo

(Davis and Ackerman, 1987; Davis et al., 1988), may lead to a deleterious build-up of this toxic metabolite which would inhibit normal metabolism and threaten survival to hatching.

In eggs of the snake Elaphe obseleta, the amount of residual allantoic fluid is affected by the amount of water absorbed during incubation whereas live hatchling mass is unaffected (Deeming, 1989). Yolk sac mass was not determined in the above study but other reports show that dehydration of eggs during incubation appears not to affect the mass of the yolk sac in other reptiles. In pliable-shelled eggs of turtles, substrate water potential affects the rates of embryonic growth and yolk utilisation (Packard, Packard, Boardman, Morris and Shuman, 1983; Morris, Packard, Boardman, Paukstis, and Packard, 1983) but not the degree of hydration of the hatchling or residual yolk. For example, eggs of the turtle Terrapene ornata (initial mass of 10.5g) gain 0.6g of water on a wet substrate (−150kPa) but lose 1.8g of water on a dry substrate (−800kPa) (Packard, Packard and Gutzke, 1985). Both yolk-free hatchling, and residual yolk sac masses are reduced in eggs from the dry substrate but the percentage water content of the hatchling and yolk are unaffected by substrate water potential (Packard et al., 1985). Similarly, in parchment-shelled eggs of squamates, hatchling mass is unaffected by substrate water potential (Gutzke and Packard, 1987; Packard and Packard, 1987; Plummer and Snell, 1988) but in these reptiles, egg size is important. Small lizard eggs (<1g) normally produce hatchlings that are larger than the initial mass of the egg (Deeming and Ferguson, 1991b).

Water loss from crocodilian eggs from natural nests has been considered to be abnormal (Ferguson, 1985) but under artificial incubation conditions it is common and, within limits, does not appear to compromise embryonic survival (Manolis et al., 1987; Webb, Beal, Manolis and Dempsey, 1987; Whitehead, 1987). Hence, air spaces are, in all probability, experimental artifacts but they have proved useful in assessing the gaseous environment within the egg (Whitehead, 1987).

The percentage of water lost during incubation at 30°C was smaller than incubation at 33°C. This may be an experimental artifact but it may indicate more profound effects of temperature on water loss from these eggs. Temperature has direct effects upon the water exchange of turtle and snake eggs: as incubation temperature increases less water is exchanged between the egg and its environment (Gutzke and Packard, 1987; Packard, Packard, Miller and Boardman, 1987; Gutzke, Packard, Packard and Boardman, 1987). In addition, incubation temperature significantly affects the rate of development of alligator embryos and formation of sub-embryonic fluid is more rapid in alligator eggs incubated at 33°C, compared with eggs at 30°C (Deeming and Ferguson, 1989). It may be possible, therefore, that the pattern of water exchange of the eggs is dependent upon the stage of development of the embryo, and by association, upon incubation temperature. For example, at 33°C removal of water from the albumen by the embryo to form sub-embryonic fluid may sequester water and prevent its

loss across the shell during the first few days of incubation, thereby reducing the overall loss of water during incubation.

REFERENCES

Ar, A. and Rahn, H. (1980). Water in the avian egg: overall budget of incubation. *American Zoologist* **20**, 373-384.

Clark, H., Sisken, B. and Shannon, J. E. (1957). Excretion of nitrogen by the alligator embryo. *Journal of Cellular and Comparative Physiology* **50**, 129-134.

Davies, T. A. and Ackerman, R. A. (1987). Effects of increased water loss on growth and water content of the chick embryo. *The Journal of Experimental Zoology* Supplement 1, 144-156.

Davis, T. A., Shen, S. S. and Ackerman, R. A. (1988). Embryonic osmoregulation: consequences of high and low water loss during incubation of the chicken egg. *The Journal of Experimental Zoology* **245**, 144-156.

Deeming, D. C. (1989). The residues in the eggs of squamate reptiles at hatching. *The Herpetological Journal* **1**, 381-385.

Deeming, D. C. and Ferguson, M. W. J. (1989). Effects of incubation temperature on the growth and development of embryos of *Alligator mississippiensis*. *Journal of Comparative Physiology* **159B**, 183-193.

Deeming, D. C. and Ferguson, M. W. J. (1991a). Egg turning has no effect on growth and development of embryos of *Alligator mississippiensis*. *Acta Zoologica*, **72**, in press.

Deeming, D. C. and Ferguson, M. W. J. (1991b). Incubation and embryonic development in reptiles and birds. In *Avian Incubation*, pp. 3-37. Tullett, S. G. (ed.). Butterworths, London.

Ferguson, M. W. J. (1985). The reproductive biology and embryology of crocodilians. In *Biology Of The Reptilia. Vol. 14. Development A*, pp. 329-491. Gans, C., Billet, F. and Maderson, P. F. A. (eds.). John Wiley & Sons, New York.

Gutzke, W. H. N. and Packard, G. C. (1987). Influence of the hydric and thermal environments on eggs and hatchlings of bull snakes *Pituophis melanoleucus*. *Physiological Zoology* **60**, 9-17.

Hoyt, D. F. (1979). Osmoregulation by avian embryos: the allantois functions like a toad's bladder. *Physiological Zoology* **52**, 354-362.

Lesham, A. and Dmi'el, R. (1986). Water loss from *Trionyx triungis* eggs incubating in natural nests. *The Herpetological Journal* **1**, 115-117.

Manolis, S. C., Webb, G. J. W. and Dempsey, K. E. (1987). Crocodile egg chemistry. In: *Wildlife And Management: Crocodiles And Alligators*. pp. 445-472. Webb, G. J. W., Manolis, S. C. and Whitehead, P. J. (eds.), Surrey Beatty Pty Ltd, Sydney.

Morris, K. A., Packard, G. C., Boardman, T. J., Paukstis, G. L. and Packard, M. J. (1983). Effect of hydric

environment on growth of embryonic snapping turtles (*Chelydra serpentina*). *Herpetologica* **39**, 272-285.

Packard, G. C. (1991). The physiological and ecological importance of water to the embryos of oviparous reptiles. In: *Egg Incubation: Its Effects on Embryonic Development in Birds and Reptiles*, pp. 213-228. Deeming, D. C. and Ferguson, M. W. J. (eds.). Cambridge University Press, Cambridge, U.K.

Packard, G. C. and Packard, M. J. (1980). Evolution of the cleidoic egg among reptilian antedescents of birds. *American Zoologist* **20**, 351-362.

Packard, G. C. and Packard, M. J. (1984). Coupling of physiology of embryonic turtles to the hydric environment. In: *Respiration and Metabolism of Embryonic Vertebrates*. pp. 99-119. Seymour, R. S. (ed.). Dr. W. Junk, Dordrecht.

Packard, G. C. and Packard, M. J. (1987). Water relations and nitrogen excretion in embryos of the oviparous snake *Coluber constrictor*. *Copeia* **1987**, 395-406.

Packard, G. C. and Packard, M. J. (1989). Control of metabolism and growth in embryonic turtles: a test of urea hypothesis. *Journal of experimental Biology* **147**, 203-216.

Packard, M. J., Packard, G. C. and Boardman, T. J. (1982). Structure of eggshells and water relations of reptilian eggs. *Herpetologica* **38**, 136-155.

Packard, G. C., Packard, M. J. and Gutzke, W. H. N. (1985). Influence of hydration of the environment on eggs and embryos of the terrestrial turtle *Terrapene ornata*. *Physiological Zoology* **58**, 564-575.

Packard, G. C., Packard, M. J., Boardman, T. J., Morris, K. A. and Shuman, R. D. (1983). Influence of water exchanges by flexible-shelled eggs of painted turtles *Chrysemys picta* on metabolism and growth of embryos. *Physiological Zoology* **56**, 217-230.

Plummer, M. V. and Snell, H. L. (1988). Nest site selection and water relations of eggs in the snake. *Oepheodrys aestivus*. *Copeia* **1988**, 58-64.

Romanoff, A. L. (1967). *Biochemistry of the Avian Embryo*. John Wiley-Interscience, New York.

Ryan, B. F., Joiner, B. L. and Ryan, T. A. (1985). *Minitab Handbook*. 2nd edition, Duxbury Press, Boston.

Simkiss, K. (1980). Water and ionic fluxes inside the egg. *American Zoologist* **20**, 385-393.

Tracy, C. R., Packard, G. C. and Packard, M. J. (1978). Water relations of chelonian eggs. *Physiological Zoology* **51**, 378-387.

Tullett, S. G. and Burton, F. G. (1982). Factors affecting the weight and water status of the chick at hatch. *British Poultry Science* **23**, 361-369.

Vleck, D. (1990). Water economy and solute regulation of reptilian and avian embryos. In: *Egg Incubation: Its Effects on Embryonic Development in Birds and Reptiles*, pp. 245-259. Deeming, D. C. and Ferguson, M. W. J. (eds.). Cambridge University Press, Cambridge, U.K.

Webb, G. J. W., Beal, A. M., Manolis, S. C. and Dempsey, K. E. (1987). The effects of incubation temperature on sex determination and embryonic development rate in *Crocodylus johnstoni* and *C. porosus*. In: *Wildlife And Management: Crocodiles And Alligators*. pp. 507-531. Webb, G. J. W., Manolis, S. C. and Whitehead, P. J. (eds.), Surrey Beatty Pty Ltd, Sydney.

Whitehead, P. J. (1987). Respiration of *Crocodylus johnstoni* embryos. In: *Wildlife And Management: Crocodiles And Alligators*. pp. 473-497. Webb, G. J. W., Manolis, S. C. and Whitehead, P. J. (eds.), Surrey Beatty Pty Ltd, Sydney.

DIFFERENCES IN THERMOREGULATION BETWEEN *TESTUDO HERMANNI* AND *TESTUDO MARGINATA* AND THEIR ECOLOGICAL SIGNIFICANCE

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ABSTRACT

The activity patterns and body temperatures of *T. hermanni* and *T. marginta* were studied in the Peloponnese (southern Greece) during May, June, August and October 1984.

T. hermanni

In May the daily activity patterns of *T. hermanni* were unimodal, in June and August they were bimodal. In August during the afternoon the activity increased significantly, in October the activity was very low.

In August basking decreased significantly and mating increased significantly.

During these four months no significant differences in body temperatures were found. In May a maximum body temperature of 35°C was found; in feeding tortoises a maximum temperature of 34°C. After May no temperatures over 32°C were found.

T. marginata

In May and June the activity patterns of *T. marginata* were bimodal with the highest activity during the afternoon. In August an unimodal low activity pattern was found during the afternoon. In October the activity of *T. marginata* was unimodal and shifted towards the middle of the day. Sexual activity was seen in October only.

Body temperatures in all *T. marginata* samples were significantly higher than those in *T. hermanni*. During May a maximum body temperature of 36°C was found in basking tortoises, a maximum of 37°C in feeding tortoises.

The trend towards lower body temperatures in summer was greater in *T. marginata* than in *T. hermanni*. Body temperatures found in feeding tortoises in October equalled those found in May.

Ecological Consequences

In southern Greece the habitat separation between *T. hermanni* and *T. marginata* can be explained by morphological differences and a higher body temperature tolerance in *T. marginata*. Differences in the annual cycle of activities might also be of importance as regards the habitat separation between both species.

INTRODUCTION

Testudo hermanni belongs to the most widespread species of tortoises in Greece, found in almost every habitat and all over the mainland as well as on some islands (Werner, 1938; Willemsen and Hailey, 1989).

The distribution of *T. marginata* was limited to the mainland south of 40° 20′ and to some of the Greek islands (Werner, 1938; Stemmler, 1957; Watson, 1962; Clark, 1963, 1967; Willemsen and Hailey, 1989). *T. hermanni* is limited to certain kinds of habitats in southern Greece; outside these habitats *T. hermanni* is almost completely replaced by *T. marginata* (Willemsen and Hailey, 1989).

Morphologically *T. marginata* is better adapted to heavy terrain and dense vegetation but differences in morphology alone cannot explain the habitat separation between these two species. In northern Greece near the edge of the distribution area of *T. marginata*, *T. hermanni* is found in a high density sympatric with a *T. marginata* population of a low density, whereas in a similar habitat in southern Greece *T. hermanni* have been completely replaced by *T. marginata*.

In northern Greece there is a similar but possibly even more complicated situation with regard to *T. hermanni* and *T. graeca*. At some sites there is a clear habitat separation between *T. hermanni* and *T. graeca* while at other sites *T. hermanni* lives sympatrically with *T. graeca*, different species predominating at different sites. Stubbs (1981) and Wright *et al.* (1988) found that in coastal areas *T. graeca* was more abundant than *T. hermanni* in hotter and drier kinds of vegetation. They also found significantly higher body temperatures in *T. graeca*. Willemsen (unpublished) also found differences in thermoregulation in sympatric living populations of *T. hermanni* and *T. graeca* which could produce ecological separation and which would enable the two species to live sympatrically.

It is possible that differences in thermoregulation are also significant in the habitat separation between *T. hermanni* and *T. marginata* in southern Greece. *T. hermanni* prefers cooler and less dry habitats. Cherchi (1956) gives for normal activity a body temperature which ranges from 16°C to 32°C in *T. hermanni*. They will not voluntarily accept body temperatures over 34°C; juveniles have even lower body temperatures. A number of field studied have

also shown that *T. hermanni* will almost never accept body temperatures over 34°C (Meek, 1981, 1984, 1988). In literature no data about body temperatures of *T. marginata* were available.

SITES

Nowhere in Greece were sufficient tortoises of both species found for simultaneous comparison of their body temperatures. The only suitable *T. marginata* population was found near Gytheion, the nearest suitable populations of *T. hermanni* were found near Sparta and Kalamata. These sites are described by Willemsen and Hailey (1989).

METHODS

The activity of each tortoise was recorded, new tortoises were marked and recaptures were remarked with waterproof blue ink on the carapace to avoid wasting time with future recaptures. The use of red ink would have been more practical but there is some evidence that red ink makes juveniles more vulnerable to predators, mostly birds of the *Corvus* group.

All first captures were weighed, measured, sexed and, if possible, age was determined according to growth lines in the carapace scutes. Of recaptures only activity, weight and body temperatures were noted. The body temperature was measured with a mercury bulb thermometer in the cloaca to the nearest 0.5°C. In this study only *T. hermanni* over 10cm Straight Carapace Length (SCL) were used because the regulation in juveniles might be different (Cherchi, 1956), and the frequency of juveniles was very different in the two *T. hermanni* populations (Willemsen and Hailey, 1989). Unsexable *T. marginata* were not used.

RESULTS

MAY

The daily activity pattern of *T. hermanni* was unimodal from 9.30h to 17.49h, no observations were made from 13.00h to 14.00h (Fig. 1 and Table 1). The activity of *T. marginata* was almost bimodal (Fig. 2 and Table 2). There was little activity between 14.00h and 17.00h.

						Time						
May (Sparta)	0800	0900	1000	1100	1200	1400	1500	1600	1700	1800	1900	2000
Basking		24.8-4.1	26.4-4.0	30.0-3.7	31.0-1.6	31.6-1.1	30.1-0.0					
		19-29 (14)	27-32 (15)	27-35 (7)	28-33 (9)	30-33 (6)	30-30 (1)					
Feeding					30.0-1.4	32.5-0.7	31.6-1.1	29.2-1.2	30.0-0.0			
					29-31 (2)	32-33 (2)	31-34 (9)	31-34 (6)	30-30 (1)			
Other		25.0-0.0	29.5-2.6	31.2-5.2	28.3-2.1	31.5-1.3	29.5-0.7	30.0-2.8	30.0-0.0			
		25-25 (2)	26-32 (4)	22-34 (5)	26-30 (3)	30-33 (4)	29-30 (2)	28-30 (2)	30-30 (3)			
June (Kalamata)												
Basking	25.8-3.4	25.2-3.2	27.3-3.9									
	20-30 (8)	20-30 (9)	23-31 (4)									
Feeding		29.5-6.3	30.1-1.0	30.0-0.0						34.0-0.0	32.0-1.4	
		25-34 (2)	29-31 (3)	30-30 (1)						34-34 (1)	31-33 (2)	
Other	27.0-0.0	30.0-1.0	28.7-3.5	31.5-2.1								32.0-0.0
	27-27 (1)	29-31 (3)	25-32 (3)	30-33 (2)								32-32 (1)
August (Sparta)												
Basking	24.0-0.0	25.0-2.5	27.7-2.9	30.0-0.0							30.0-0.0	
	24-24 (1)	22-28 (8)	26-31 (3)	30-30 (1)							30-30 (1)	
Feeding			30.0-0.0	32.0-0.0					32.0-0.0	31.0-0.0		
			30-30 (1)	32-32 (1)					32-32 (1)	31-31 (1)		
Other		22.5-1.6	32.5-0.7	32.0-0.0					31.0-0.0	32.0-1.0	28.8-1.6	28.7-1.2
		21-25 (6)	32-33 (2)	32-32 (1)					31-31 (1)	31-33 (3)	26-31 (9)	28-30 (3)
October (Kalamata)												
Basking					20.0-0.0	30.0-0.0		29.0-0.0				
					20-20 (1)	30-30 (1)		29-29 (1)				
Feeding					30.0-0.0		31.0-0.0					
					30-30 (1)		31-31 (1)					
Other								31.7-0.6				
								31-32 (3)				

TABLE 1: Diural variation of body temperature in *T. hermanni* in different months. Basking, feeding and other activities (includes moving, mating and stationary animals) shown separately. Times are East European summer time. Data are shown as mean –1 S.D., range and sample size.
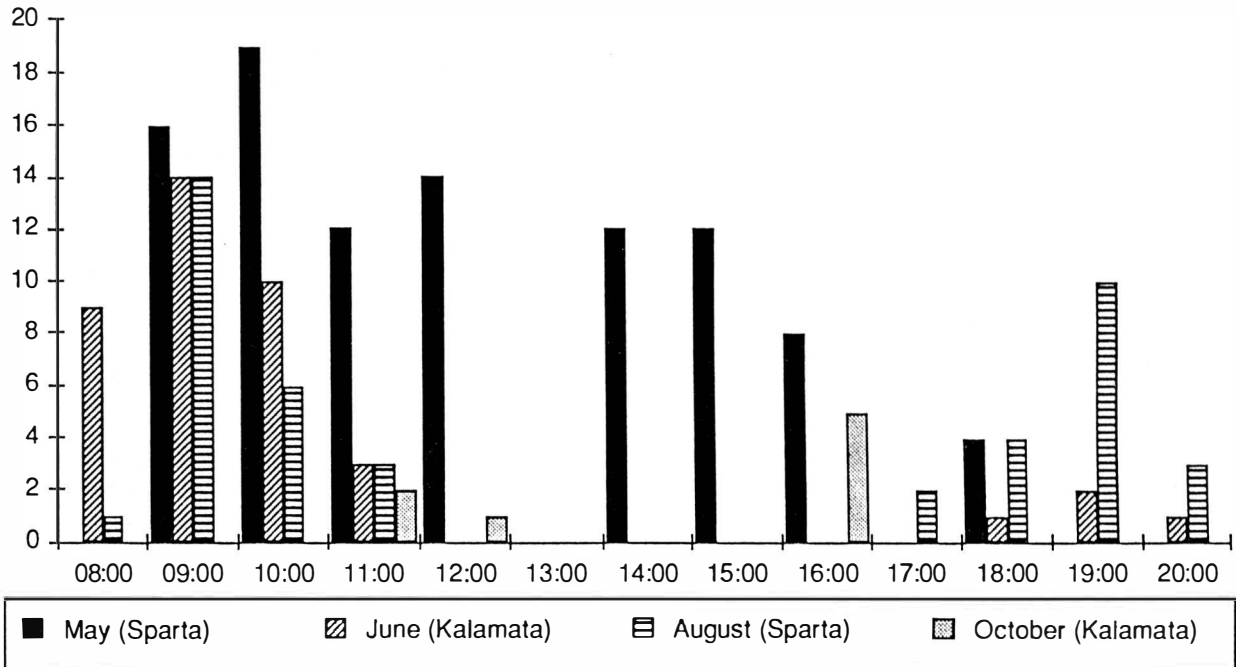
Fig. 1   Activity pattern of *T. hermanni* in the different months at the two sites. Each bar shows the number of tortoises found in 1-hour period. Times are East European summer time.
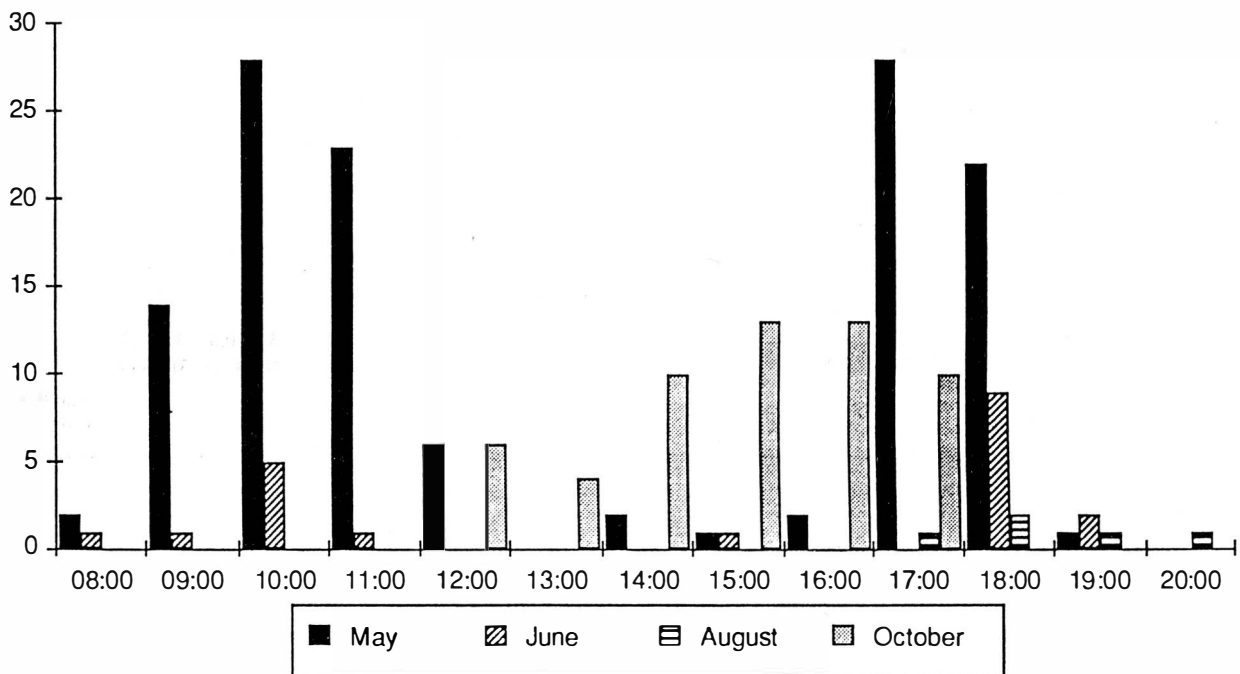

Fig. 2   Activity pattern of *T. marginata* in the different months. Each bar shows the number of tortoises found in 1-hour period. Times are East European summer time.

The first tortoises were seen at 8.56h and the last ones at 19.31h. The morning activity period was similarly important in both species; 63 per cent of *T. hermanni* and 57 per cent of *T. marginata* were found before 13.00h ($X^2 = 1.00$, p>0.01). However *T. marginata* were active longer in the evening. Only 4 per cent of *T. hermanni* were found after 17.00h compared to 39 per cent of *T. marginata* ($X^2 = 37.70$, p<0.0001).

ACTIVITIES

Most tortoises of both species were seen in the morning; 86 per cent of basking *T. hermanni* and 83 per cent of basking *T. marginata* were seen before 13.00h. Basking accounted for a higher proportion of observations of *T. hermanni* (54 per cent) than *T. marginata* (23 per cent) ($X^2 = 22.00$, p <0.0001). The reverse was found for feeding tortoises which made up 21 per cent of the observations in *T. hermanni*

		Time												
May		0800	0900	1000	1100	1200	1300	1400	1500	1600	1700	1800	1900	2000
	Basking	28.0-0 28-28 (1)	28.3-1.9 27-32 (8)	30.4-3.5 22-35 (11)	34.2-0.8 33-35 (5)						35.5-0.8 34-36 (4)	33.00-0.0 33-33 (1)		
	Feeding			30.0-2.8 28-32 (2)	31.6-1.7 29-34 (7)	34.1-2.1 30-37 (9)	35.0-1.0 34-36 (3)			35.0-0.0 35-35 (1)	34.2-1.3 32-36 (20)	33.5-1.6 30-36 (18)	32.0-0.0 32-32 (1)	
	Other	28.0-0.0 28-28 (1)	28.5-5.1 21-31 (4)	33.3-2.1 30-36 (10)	30.4-3.3 28-35 (9)	34.0-1.7 32-35 (3)		36.5-2.1 35-38 (2)	32.0-0.0 32-32 (1)	30.0-0.0 30-30 (1)	34.5-0.5 34-35 (4)	32.0-1.0 31-33 (3)		
June														
	Basking	32.0-0.0 23-23 (1)		26.5-0.7 26-27 (2)								33.0-0.0 33-33 (1)		
	Feeding			27.0-0.0 27-27 (1)								32.7-1.2 32-35 (6)	34.0-0.0 34-34 (1)	
	Other		34.0-0.0 34-34 (1)	26.0-1.4 25-27 (2)	36.0-0.0 36-36				26.0-0.0 26-26 (1)			33.0-1.4 32-34 (2)	33.00-0.0 33-33 (1)	
August														
	Basking												33.00-0.0 33-33 (1)	
	Feeding											32.5-2.1 31-34 (2)		
	Other										37.0-0.0 37-37 (1)			35-0-0.0 35-35 (1)
October														
	Basking							33.5-0.7 33-34 (2)	33.0-0.0 33-33 (1)	30.5-2.1 29-32 (2)				
	Feeding						31.0-0.0 31-31 (1)	32.5-0.7 32-33 (2)	33.3-1.0 32-34 (4)	33.5-1.6 32-37 (8)	31.1-1.2 29-33 (8)	29.3-0.6 29-30 (3)		
	Other						32.2-1.3 31-34 (5)	32.5-2.1 31-34 (2)	34.0-1.8 32-36 (4)	32.3-1.5 30-33 (4)	31.0-2.0 29-33 (3)	30.0-1.2 28-31 (7)		

TABLE 2: Diurnal variation of body temperature in *T. marginata* in different months. All observations were made at Gytheion. Times are East European summer time. Data are shown as mean –1 S.D., range and sample size.

compared to 47 per cent of *T. marginata* ($X^2 = 17.20$, $p < 0.0001$).

Most (90 per cent) of the feeding *T. hermanni* were found after 13.00h compared to 65 per cent of feeding *T. marginata* ($X^2 = 4.46$, $p < 0.05$).

11 per cent of *T. hermanni* were found inactive, significantly more than the 2 per cent of *T. marginata* ($X^2 = 12.10$, $p < 0.001$). Six *T. hermanni* were involved in sexual activity; only one male *T. marginata* was found attempting to mate with a feeding female.

THERMOREGULATION

The mean in the body temperature of *T. hermanni* was lower than the temperature of *T. marginata* (Tables 3 and 4; $t = 8.46$, $p < 0.0001$). The body temperatures of *T. marginata* were also significantly higher when basking ($t = 3.88$, $p < 0.0001$), when moving ($t = 2.24$, $p < 0.025$) and when feeding ($t = 6.00$, $p < 0.0001$).

JUNE

The daily pattern of *T. hermanni* was bimodal, in the morning from 8.40h to 11.16h, in the afternoon from 18.58h to 19.52h. (Fig. 1 and Table 1). During the afternoon the activity was low, only 10 per cent of *T. hermanni* were found after 12.00h. The daily activity pattern of *T. marginata* was also bimodal between 8.40h and 11.09h and again between 15.30 and 19.52h (Fig. 2 and Table 2).

During the afternoon *T. marginata* were significantly more active than *T. hermanni* ($X^2 = 17.25$, $p < 0.001$).

ACTIVITIES

In *T. hermanni* most tortoises were found basking (53 per cent) compared to only 20 per cent in *T. marginata* ($X^2 = 5.71$, $p < 0.05$).

There were no significant differences in the frequency of activities of each species compared to those in May.

THERMOREGULATION

The mean in the body temperature of *T. hermanni* was lower than the mean in the body temperature of *T. marginata* (Tables 3 and 4; $t = 3.02$, $p < 0.001$). Though the average June body temperature of *T. hermanni* was lower ($1.1°C$) than the May temperature, the difference was not significant ($t = 1.66$, $p < 0.05$).

	Basking	Moving	Feeding	Mating	Fighting	Stationary	Total
May	27.8-4.3 19-35 (52)	29.5-3.4 22-33 (8)	30.7-1.5 28-34 (20)	27.8-2.8 25-31 (6)		31.0-2.5 29-34 (11)	29.0-3.7 19-35 (97)
June	25.8-3.4 20-31 (21)	30.0-2.2 27-33 (6)	30.8-2.8 25-34 (9)	29.5-3.1 25-32 (4)			27.9-3.1 20-34 (40)
August	26.2-2.9 21-31 (14)	33.0-0.0 33-33 (1)	31.4-1.0 30-32 (4)	30.1-3.4 21-33 (20)	23.0-1.4 22-24 (2)	31.5-0.7 31-32 (2)	28.7-3.6 21-33 (43)
October	26.3-5.5 20-30 (3)	31.0-0.0 31-31 (1)	30.5-0.7 30-31 (2)		32.0-0.0 32-32 (2)		29.4-3.9 20-32 (8)

TABLE 3: Variation of body temperature of *T. hermanni* with activity type in every month. Data are shown as mean, S.D., range and sample size.

	Basking	Moving	Feeding	Mating	Stationary	Total
May	31.3-3.2 22-36 (30)	32.0-2.7 21-38 (34)	33.5-1.9 28-37 (61)	30.0-0.0 30-30 (1)	32.7-4.0 28-35 (3)	32.6-2.7 21-28 (129)
June	27.3-4.3 23-33 (4)	32.2-3.8 26-36 (5)	32.3-2.5 27-35 (8)		28.7-4.7 25-34 (3)	30.7-3.9 23-36 (20)
August	33.00-0.0 33-33 (1)	36.0-1.4 35-37 (2)	32.5-2.1 31-34 (2)			34.0-2.1 31-37 (5)
October	32.2-1.9 29.34 (5)	32.0-1.6 29-35 (15)	32.1-1.9 29-37 (26)	30.9-1.8 28-33 (9)	36.0-0.0 36-36 (1)	31.9-1.9 28-37 (56)

TABLE 4: Variation of body temperature of *T. marginata* with activity type in every month. Data are shown as mean, S. D., range and sample size.

In *T. marginata* however, the mean in the June body temperature was significantly lower than the May body temperature (t = 2.74, p < 0.005).

Basking tortoises of both species showed significantly lower body temperatures in June (*T. hermanni*: t = 1.90, p < 0.05; *T. marginata*: t = 2.27, p < 0.025).

In *T. hermanni* the maximum body temperature found in basking tortoises was 4°C lower than in May, in *T. marginata* 3°C lower than in May (Tables 3 and 4).

In June the body temperature of basking, feeding and moving *T. hermanni* was not significantly different from that one found in *T. marginata* (t = 0.78, p < 0.01; t = 1.16, p > 0.05; t = 1.20 p > 0.05).

AUGUST

The activity of *T. hermanni* was bimodal. In the morning tortoises were found from 8.23h to 11.23h, in the afternoon from 17.32h to 20.07h (Fig. 1 and Table 1).

The activity of *T. marginata* was unimodal and low, only five tortoises were found after 17.00h (Fig. 2 and Table 2). During the afternoon *T. hermanni* were significantly more active than registered in June (44 per cent against 10 per cent; $X^2 = 12.14$, p < 0.001).

ACTIVITIES

In August the frequency of basking *T. hermanni* was significantly lower than in May (33 per cent against 54 per cent; $X^2 = 5.32$, p < 0.025). Although the frequency of basking *T. hermanni* was almost the same in May and in June (43 and 53 per cent), there was not a significant difference in the frequency of basking *T. hermanni* in June and August ($X^2 = 3.33$, p > 0.05). Probably the number of the animals in the samples was too small. In May and August no significant differences were found in the frequency of feeding *T. hermanni* ($X^2 = 2.73$, p > 0.05). In August 47 per cent of *T. hermanni* were found in a sexual act, this was significantly more than in June ($X^2 = 31.52$, p < 0.0001; $X^2 = 13.56$, p < 0.001).

THERMOREGULATION

In May, June and August no significant differences were found in the means of the body temperatures of *T. hermanni* (T = 0.45, p < 0.25; t = 1.08, p > 0.10; Table 3). Although the basking *T. hermanni* the maximal body temperature was 4°C lower than in May, there was no significant difference from the mean of May (t = 1.31, p > 0.05; Table 3). No significant differences in the means of the body temperatures of the other activities were found between *T. hermanni* samples in May, June and August either though no body temperatures over 33°C were found.

In August the mean of the body temperatures of *T. marginata* was significantly higher than the one in June but not significantly higher than in May (t = 1.81, p <0.05; t = 1.15, p >0.010). The mean of the body temperatures in *T. hermanni* was significantly lower than in *T. marginata* (t = 3.21, p >0.025).

OCTOBER

In October the activity of *T. hermanni* was low in southern Greece. Near Sparta only three tortoises were found in two days. The activity was little higher near Kalamata; eight tortoises were found in two days. Tortoises were found from 11.39h to 12.39h and from 16.28h to 16.43h (Fig. 1 and Table 1). The number of animals in the samples was too small to be sure whether the activity pattern was still unimodal or not. The activity of *T. marginata* was high and unimodal. Tortoises were found from 12.30h to 17.32h (Fig. 2 and Table 2).

ACTIVITIES

The frequency of basking *T. marginata* was 9 per cent, significantly lower than in May; there was no significant difference from June (X^2 = 5.23, p <0.025; X^2 = 1.60, p > 0.10). Except for two fighting males, no sexual activity was seen in *T. hermanni*; in *T. marginata* a high sexual activity was seen (17 per cent; Table 4). In samples from May, June and October almost no differences were found in the frequency of moving *T. marginata* (26, 20 and 27 per cent). The frequency of feeding in *T. marginata* was almost the same as in May: 47 per cent; June 40 per cent and October: 46 per cent).

THERMOREGULATION

In the means of the body temperatures of *T. hermanni* no significant differences were found in October compared to the samples of May, June and August (May: t = 0.29, p >0.40; June: t = 1.20, p >0.10; August: t = 0.50, p >0.025). The mean of the body temperature in *T. marginata* was significantly lower in October than in May and August (t = 1.76, p <0.05; t = 2.35, p <0.025) but was significantly higher in June (t = 1.80, p <0.05). Although the mean of the body temperature in basking *T. marginata* was higher in May, this difference was not significant (t = 0.61, p <0.25) but in October the body temperatures in *T. marginata* were not significantly higher than in June (t = 2.36, p <0.05). No differences were found in the body temperature of moving *T. marginata* in the samples of May, June and October (May: 32.0°C; June: 32.2°C and October: 32.0°C). In feeding *T. marginata* the body temperatures were significantly lower than in May (t = 3.15, p <0.001), but not significant from June to October (t = 0.24, p >0.40). In feeding *T. marginata* the maximum body temperature (37°C) was as high as in May and higher than in June and August. In basking *T. marginata* the maximum body temperature was 34°C and also lower than in May. In October the mean in the body temperature of *T. hermanni* was significant lower than in *T. marginata* (t = 2.98, p <0.0025) as well in all other samples.

DISCUSSION

ACTIVITY

The activity patterns found during this study are similar to those found in other Greek *T. hermanni* populations. A trend for unimodal activity pattern in spring to a bimodal activity pattern in summer was found between 1975 and 1986 in a great number of Greek *T. hermanni* populations. When an unimodal activity pattern changed into a bimodal one, the activity during the afternoon was always low, exactly as in the pattern found near Kalamata in June. Later in summer the activity was clearly bimodal, sometimes higher in the morning, something in the evening. In autumn the activity was again unimodal but the period of activity was shorter than in spring; daily activity started late and ended early. In southern Yugoslavia the activity of *T. hermanni* was unimodal throughout the year (Meek and Inskeep, 1981; Meek, 1988). In France the daily activity pattern was unimodal, the activity strongly decreased during the hot hours in summer (Cheylan, 1981). In summer in northern Greece the daily activity pattern of *T. hermanni* was bimodal (Stubbs *et al.*, 1981; Wright *et al.*, 1988). In the early dry and hot year 1985 the activity pattern of *T. hermanni* was unimodal already in May (Willemsen unpublished).

During relatively cool, cloudy days in summer the activity pattern of *T. hermanni* can again be unimodal, also in an environment with much shade *T. hermanni* were found still active during the hot hours in summer. It seems the daily activity pattern of *T. hermanni* is determined by air temperature and probably by the intensity of the sun. In the cooler part of its distribution area the activity pattern remains unimodal, in the hotter part the activity is limited to the cooler hours of the day.

The activity of *T. hermanni* is the highest in spring and decreases during summer (Hailey, 1988). This trend was found in all Greek populations although in spring the activity was probably equal, after spring the activity can differ much in the different populations and also from year to year. The activity pattern of *T. hermanni* in a great number of populations over several years will be described in another paper.

The daily activity pattern of *T. marginata* was similar to that of *T. hermanni*, unimodal in spring although in this study the pattern had already become bimodal in May; in April 1983 the activity pattern still was unimodal. After spring the activity pattern became bimodal and was unimodal again in autumn, shifting towards the middle of the day.

However, there were also some differences in the activity pattern of *T. marginata*. Though *T. hermanni* is something almost totally inactive during summer, in general *T. hermanni* can still be found in fair numbers in southern Greece during summer. The low activity in *T. marginata* in August 1984 was not exceptional. Stemmler (1957) could not find any *T. marginata* in summer during his stay in southern Greece but he did find a large number of *T. hermanni* at different sites. Near the border of the distribution area of *T. marginata* in northern Greece, he found several

T. marginata together with *T. hermanni.* Probably *T. marginata* will aestivate more than *T. hermanni.*

Much research on tortoises have been done during the summer months in Greece by many investigators. All authors describe *T. marginata* as a tortoise seldom to be found. Without any doubt all *T. marginata* populations are less dense than the average *T. hermanni* population but the very low densities which have been found in *T. marginata* populations might be caused by sampling at the wrong time.

The high activity in October is not exceptional; Clark (1963) found a high activity in *T. marginata* during autumn but he gives no exact data. Local people found *T. marginata* still active during autumn and even during early winter while *T. hermanni* were only seen during summer. Although *T. hermanni* can again become active on sunny days in winter (Swingland and Stubbs. 1985) it is unlikely that *T. hermanni* would be active in large numbers in southern Greece after the visits in October.

IMPORTANCE OF ACTIVITY PATTERNS

The daily and seasonal activity patterns of tortoises have more than theoretical value, for the number of active tortoises can be used for density calculations (Hailey, 1988). Density calculations are important for conservation purposes, however, without sufficient knowledge on activity patterns errors in these calculations can be disastrous. At this moment only the high activity in spring of *T. hermanni* up to the middle of May, in probably all Greek populations, is a certain fact. Much more detailed knowledge is needed to be sure about the activity pattern after spring. In southern Greece the activity of *T. marginata* is high and probably also takes place in late autumn, but nothing is known about differences between different populations and differences in different years.

DIFFERENCES IN ACTIVITIES

Differences in basking, moving and inactive *T. hermanni* and *T. marginata* can be easily explained by differences in vegetation of the site near Gytheion. Near Gytheion, except for the animals found in the heath, all tortoises were found on the open patches, for the macchie was inaccessible. This may cause an undersampling of basking and stationary tortoises, and possible an oversampling of feeding tortoises.

The trend of the decreasing number of basking *T. hermanni* in summer was also found by Meek (1988). The relatively large number of basking *T. hermanni* in June could be due to the kind of vegetation as this site had much more shade than Sparta.

In this study no differences in frequency of feeding *T. hermanni* and *T. marginata* were found between the different visits. Meek (1988) found an increasing frequency of feeding *T. hermanni* in summer, but in the present study this was not found.

In France *T. hermanni* was sexually active during its entire active period, but the highest activity was found in April and August (Swingland and Stubbs, 1985). They found the same trend in Greece, but the sexual activity in spring was lower than in France. The results found in 1984 near Kalamata and Sparta match those

found in France and in Greece. Meek did not find sexual activity in *T. hermanni* in autumn, but in Greece sexual activity was seen in October (Willemsen), so there could be some differences in behaviour between Greek and Yugoslavian *T. hermanni* populations. Except for one male no sexual activity was seen in *T. marginata* before autumn 1984. Clark (1963) gives a high sexual activity in *T. marginata* in autumn. In Greek *T. marginata* populations no sexual activity was seen after April and before October (Willemsen), so it is likely that the sexual cycle of *T. marginata* differs from that of *T. hermanni.*

BODY TEMPERATURES

No significant differences in body temperature of *T. hermanni* were found during four months of research, though it is possible that differences would be significant in larger samples. Cherchi (1956) gives 32°C as maximum body temperature for normal activities and 34°C as maximum voluntary body temperature. In the field basking *T. hermanni* accept body temperatures to 35°C and feeding tortoises to 34°C (Meek, 1988). The body temperature of basking and feeding tortoises is of special interest, for these activities are completely voluntary. Basking tortoises are mostly found close to cover, so that in case of overheating they can go directly into cover. Feeding tortoises are mostly found on open patches, often rather far from the nearest cover, so they have to watch their body temperatures more closely than the basking tortoises. Activity such as moving, mating and especially nesting can not be stopped at once, so in these tortoises the body temperature can easily exceed the maximum voluntary value and sometimes even the critical value.

Near Meteora every year in June, in the nesting season, several mostly old females were found dead on the open patches, which were used as nesting sites. Overheating could be possible cause of death. In moving and stationary tortoises often rather low and rather high temperatures were found, because many of these animals were either at the beginning of their activities and still had a low body temperature, or were at the end of their activities and often had a body temperature over the maximum normal body temperature.

In all studies about thermoregulation of *T. hermanni* the maximum voluntary body temperature remains under 35°C in active tortoises, but the limit which Cherchi gives (32°C) is too low. In the field 34°C is the maximum body temperature for normal activities. Although the mean in SCL in *T. hermanni* populations in Greece and Yugoslavia differs widely (Willemsen and Hailey, 1989), no difference in body temperature tolerance was found in larger and smaller tortoises with a SCL over 10cm (Willemsen).

In June and August there was a trend towards lower body temperatures. Meek (1982, 1988) also found this trend. After May no body temperatures over 31°C were found in basking tortoises. In August the maximum body temperature in feeding *T. hermanni* was 32°C, but in June it was still the same as in May. This relatively high body temperature was probably caused by environmental differences of the site near

Kalamata. It seems *T. hermanni* keep their body temperatures lower in summer than in spring, thus keeping on the safe side in summer. The sample of October was too small to say much about the body temperatures during that month.

In all samples the body temperatures of *T. marginata* was significantly higher than in *T. hermanni*. In basking and in feeding *T. marginata* maximum body temperatures of 36°C and 37°C were found. In contrast to *T. hermanni* the body temperatures of *T. marginata* in feeding tortoises were higher than in basking animals. It is possible that tortoises with a maximum body temperature after basking never left the macchie and so were never found. In *T. marginata* the body temperatures had decreased significantly in June, and the trend towards lower body temperatures was stronger than in *T. hermanni*. Although the mean in the body temperature in *T. marginata* was still higher than in *T. hermanni* in June, the differences in body temperatures of different activities were no longer significantly different. The habitat near Gytheion is much hotter in summer than the relatively cool habitat of Kalamata and also that of Sparta, so in summer *T. marginata* maintains a lower body temperature, to be on the safe side. In August only five *T. marginata* were found during a six day visit, so the activity of *T. marginata* was very low. All tortoises were found during the afternoon. Except in moving tortoises no body temperatures over 34°C were found, so the maximum voluntary body temperature is probably lower than in May.

The unimodal activity during the evening could be explained by the high risk of overheating during the morning hours, when air temperature and heliothermic energy were increasing fast. However, at other cooler sites in southern Greece *T. marginata* was seen in the morning in August, so the unimodal evening activity could be characteristic for the hotter habitats in southern Greece during summer. In October the body temperatures of *T. marginata* were higher than in June but lower than in May and in August. It is possible that if the number of animals in the sample in August had been larger the results would have been the reverse. In October the same maximum body temperature in feeding *T. marginata* were found as in May. The unimodal activity pattern of *T. marginata* found in the middle of the day and the significant lower body temperatures in feeding animals as compared to those in May may indicate that in October overheating was unlikely, so the tortoises could safely use the hottest hours of the day. However, under these circumstances *T. marginata* is still able to reach the same maximum body temperature in feeding tortoises. Pigmentation and shape of *T. marginata* will make it easier to absorb heat, compared to *T. hermanni* of equal size.

The relatively low body temperatures found in *T. hermanni* in October (no body temperature was over 32°C) were possibly caused by the kind of habitat of Kalamata; but we must not rule out the possibility that *T. hermanni* will not be able, under the circumstances of October, to reach the same maximum body temperatures as in May.

In all samples the maximum body temperatures in *T. marginata* were significantly higher than in *T. hermanni*. The maximum voluntary body temperatues of *T. hermanni* tallied with the values which were found in a number of other studies, so the values found in this study can be considered representative of the species *T. hermanni*.

In feeding *T. marginata* the body temperatures were 3°C higher than in *T. hermanni*. In dry and hot habitats this will give an ecological advantage over *T. hermanni*. This partly explains the habitat separation between these two species, but some difficulties remain. If *T. marginata* heats up faster than *T. hermanni*, as suggested by the body temperatures found in October, the ecological advantage of a higher body temperature tolerance in *T. marginata* would be reduced. In this study no lower temperatures than 25°C in feeding *T. hermanni* and no lower than 28°C in feeding *T. marginata* were found.

Cherchi (1956) gives 16°C as the minimum body temperature for normal activity in *T. hermanni*. In spring, especially in northern Greece, the climate is rather cool and wet with a lower heating rate of the sun than in southern Greece. Under these circumstances a lower body temperature minimum in *T. hermanni* could give an ecological advantage over *T. marginata*. In early April 1982 during a period of cool weather only *T. hermanni* were found near Litochoron. On this site *T. marginata* lives sympatrically in low density with *T. hermanni* (Willemsen and Hailey, 1989). In northern Greece the soil vegetation dies in early summer and does not regenerate in autumn, at least not under circumstances which make activities of tortoises still possible, so *T. marginata* will miss its autumnal activity there; sexual activity in autumn could be an indication of importance of an autumnal activity of this species. Thus the climatical circumstances in spring and in autumn could make northern Greece unsuitable for *T. marginata*.

The fact that *T. hermanni* is still active with a lower body temperature could make *T. hermanni* able to complete with *T. marginata* in those kinds of habitats, namely on the border of the distribution area of *T. marginata*, where in southern Greece *T. marginata* has replaced *T. hermanni* completely. In fact *T. hermanni* is found only in relatively wet and cool habitats in southern Greece, often sympatric with a sparse *T. marginata* population, and the reverse is found in dry and hot habitats (Willemsen and Hailey, 1989). This is an indication that the higher body temperature tolerance of *T. marginata* supplies an ecological advantage in those habitats, in spite of a probably faster heating rate. It also seems that aestivation is more common in *T. marginata* than in *T. hermanni* in southern Greece, so if the physiological ability of *T. marginata* to escape the difficult hot summer months by aestivation is greater than in *T. hermanni*, then this will also give *T. marginata* an ecological advantage in hot habitats. Also morphological differences could make *T. marginata* less suitable for habitats in which *T. marginata* lives in southern Greece.

ACKNOWLEDGEMENTS

REFERENCES

Cherchi, M. A. (1956). Termoregolazione in *Testudo hermanni. Boll. Mus. Inst.* Univ. Genova. **26**, 5-46.

Cheylan, M. (1981). Biologie et Ecologie de la Tortue D'HERMANN, *Testudo hermanni*, GMELIN, 1789. *Mémoires et Traveaux de l'Institut de Montepellier*, No. 13.

Clark, R. J. (1963). On the possibility of an autumnal mating in the tortoise (*Testudo graeca ibera*) *Brit. J. of Herpetology* **3**, 85-86.

Clark, R. J. (1967). Herpetofauna of the islands of the Agro-Saronic Gulf, Greece. *Proceedings of the California Academy of Sciences.* Vol. XXXV, No. 2, 23-36.

Hailey, A. (1988). Length of routine movements in a tortoise. In press.

Hailey, A. (1988). Population ecology and conservation of tortoises: the estimation of density and dynamics of a small population. *Herpetological Journal*, 263-271.

Hailey, A., Wright, J. and Steer, A. (1988). Population ecology and conservation of tortoises: the effects of disturbance. *Herpetological Journal*, 294-301.

Hardin, G. (1960). The competitve exclusion principle. *Science* **131**, 1292-1298.

Lambert, M. R. K. (1981). Temperature, activity and field sighting in the Mediterranean spur-thighed or common garden tortoise *Testudo graeca L. Biol. Cons.* **21**, 39-54.

Meek, R. (1984). Thermoregulatory behaviour in a population of Hermann's tortoise (*Testudo hermanni*) in southern Yugoslavia. *Brit. J. of Herpetology* **6**, 437-445.

Meek, R. (1988). The thermal ecology of Hermann's tortoise (*Testudo hermanni*) in summer and autumn in Yugoslavia. *J. Zool Lond.* **214**.

Meek, R. and Inskeep, R. (1981). Aspects of field biology of a population of Hermann's tortoise (*Testudo hermanni*) in southern Yugoslavia. *Brit. J. of Herpetology* **6**, 159-164.

Stemmler, O. (1957). Schildkröten Griechenlands *Vivaristik* **3**, 159-164.

Stubbs, D., Hailey, A., Tyler, W. and Pulford, E. (1981). *Expedition to Greece* 1980. University of London Natural Society.

Stubbs, D. and Swingland, I. R. (1985). The ecology of a Mediterranean tortoise (*Testudo hermanni*): a declining population.

Thornton, I. (1972). *Darwin's Islands.* A Natural History of the Galapagos. History press Garden City, New York.

Watson, G. E. (1962). Notes on copulation and distribution of Aegean land tortoises. *Copeia* **1962**, 317-321.

Wermuth, H. (1952). *Testudo hermanni robertmertensi* n.subsp. und ihr Vorkommen im Spanien. *Senckenbergiana*, Band 33, Nummer 1/3, Seite 157-164.

Werner, F. (1938). Die Amphibien un Reptilien Griechenlands. *Zoologica* **94**, 1-117.

Willemsen, R. E. and Hailey, A. (1989). Status and conservation of tortoises in Greece. *Herpetological Journal*, 315-330.

Wright, J., Steer, E. and Hailey, A. (1988). Habitat separation in tortoises, and the consequences for activity and thermoregulation. *Can. J. of Zool.*, **66**, 1537-1544.

AMPHIBIANS OF THE WHITEMOOR CHANNEL EARLY FLANDRIAN SITE NEAR BOSLEY, EAST CHESHIRE; WITH REMARKS ON THE FOSSIL DISTRIBUTION OF *BUFO CALAMITA* IN BRITAIN

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ABSTRACT

A lacustrine *Chara* marl (ca. 10,000-8,800 radiocarbon years BP) at the Whitemoor Channel Site near Bosley, East Cheshire, yielded fossil amphibian remains, including palmate newt *Triturus helveticus*, smooth newt *Triturus vulgaris*, natterjack toad *Bufo calamita*, common toad *Bufo bufo*, common frog *Rana temporaria* and material belonging to these genera which probably represent the same five species. All of these species are extant and occur naturally in Britain today, although for the past two hundred years the natterjack toad *Bufo calamita* has occurred only locally in Britain, being essentially restricted to coastal dunes and inland heaths. The well-dated Flandrian (early Holocene) finds from Whitemoor Channel are an important addition to previous, poorly stratified, records from Cow Cave, Chudleigh, Devon, and Ightham Fissures, Sevenoaks, Kent. Taken together, these records demonstrate early colonisation of England by *B. calamita* after the last Cold Stage and suggest a wider geographical occurrence of the natterjack than in Britain today.

INTRODUCTION

In their account of the sediments infilling a former glacial meltwater channel cut into Upper Carboniferous sandstones and shales at Whitemoor near Bosley, Cheshire, (SJ917678) Johnson, Franks and Pollard (1970) described a fossiliferous shell marl or *Chara* marl ('white calcareous marl') containing amphibian remains. The occurrence of this highly calcareous sediment in an area of generally acidic bedrock reflects leaching of carbonate early in the Flandrian from freshly laid down glacial deposits. In an addendum to the above report, A. J. Stuart listed fishes: brown trout *Salmo trutta* and rudd *Scardinius erythropthalmus*; and amphibians: newt *Triturus* sp.; common frog *Rana temporaria*; and common toad *Bufo bufo*. We now present the results of a detailed study of the amphibian material.

Johnson *et al.* (1970) recorded the following section at the centre of the channel:

> Fen peat (flooring valley) 1.70m
>
> *Chara* marl 1.00m
>
> blue-grey calcareous mud 0.10m
>
> blue-grey silty clay (base not seen)

Toward the margin, the *Chara* marl was only 0.30m thick, and was absent altogether in borings only 20m from the centre of the depression. The marl comprised unconsolidated, fine, granular calcium carbonate of biogenic origin, principally the characteristic oogonia and ribbed stem components of stonewort *Chara*. Shells of freshwater Mollusca were abundant, comprising mainly *Lymnaea peregra, Planorbis albus,* and the rarer *Sphaerium corneum*. Ostracoda were also recorded.

The pollen diagram indicates open habitats with grasses and sedges during the deposition of the calcareous mud in pollen assemblage zone III at the end of the Devensian Lateglacial (Johnson *et al.*, 1970). Pollen assemblages from the overlying marl record the development of birch *Betula* woodland, with alder *Alnus*, hazel *Corylus* and willow *Salix*. Grasses, sedges and aquatic plants are also represented. These assemblages are characteristic of the very early part of the Flandrian or Holocene, representing pollen substages Fl Ia and Fl Ib of West (e.g. 1977), equivalent to zones IV and V of Godwin (e.g. 1975). Comparison with the radiocarbon-calibrated sequence at Red Moss, Lancashire, 53km to the northwest, (Hibbert, Switsur and West, 1971) suggests that the fossiliferous marl at Whitemoor spans the period from approximately 10,000 to 8,800 radiocarbon years before the present (BP). At the beginning of substage FlII (zone VI), marked by the expansion of pine *Pinus*, oak *Quercus* and elm *Ulmus*, deposition of peat began, indicating drying out of the lake and colonisation by fen vegetation.

The small auger used in the original survey by Johnson *et al.* (1970), while satisfactory for obtaining a series of pollen samples, produced only sparse vertebrate remains. Two larger samples of shell marl, totalling about 0.06 cubic metres, were recovered from beneath waterlogged fen peat by A. J. Stuart, using a purpose-built hand auger 20cm in diameter. Abundant amphibian remains and shells were readily obtained by washing the unconsolidated sediment through a millimetre sieve. The high concentration of bones probably reflects slow accumulation, averaging about 1mm of sediment per year.
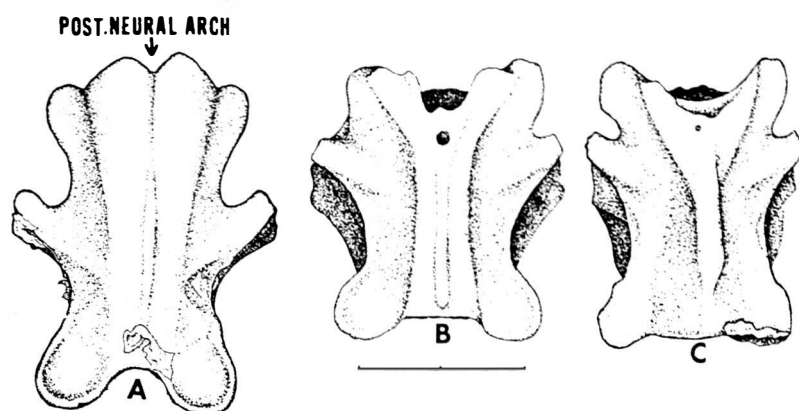
Fig. 1 Trunk vertebrae of modern *Triturus*. A, *T. cristatus*; B, *T. vulgaris*; C, *T. helveticus*. The line equals 2mm and applies to all figures.

SYSTEMATIC PALAEONTOLOGY

The fossil material discussed herein is preserved in the collections of the Castle Museum, Norwich, under the accession number NCM 143.989. Numbers of individual specimens are shown in parentheses, e.g. NCM 143.989 (1).

Class Amphibia Linnaeus, 1758
Order Caudata Oppel, 1811
Family Salamandridae Gray, 1825
Genus *Triturus* Rafinesque, 1815

On the basis of the modern skeletons that were studied, the British species of *Triturus* may be distinguished from one another on the basis of several isolated postcranial elements, including vertebrate, humeri and femora. *Triturus cristatus* is much more osteologically distinct from *T. helveticus* and *T. vulgaris* than are the latter two species from each other. This corresponds with Arnold and Burton (1978) where *T. cristatus* is the nominate form of the *T. cristatus* group and *T. helveticus* and *T. vulgaris* are placed in the *T. vulgaris* group. Estes (1981) considers *T. cristatus* to be a primitive species of the genus *Triturus*. Arnold and Burton (1978) have shown that the fronto-squamosal arch is absent in *T. cristatus*, present but incomplete in *T. vulgaris* and complete in *T. helveticus*.

Trunk Vertebrae. — Based on modern skeletons examined: *T. cristatus* (2), *T. vulgaris* (6) and *T. helveticus* (1), the trunk vertebrae of all three species may be distinguished from each other (Fig. 1). The trunk vertebrae of *T. cristatus* are larger and have a lower neural spine than in *T. vulgaris* and *T. helveticus*. Moreover, in *T. cristatus* they have the posterior neural arch extending posterior to the postzygapophyses and a narrow, V-shaped notch; the posterior neural arch ends anterior to the postzygapophyses and has a U-shaped notch in *T. vulgaris* and *T. helveticus*.

The trunk vertebrae of *T. vulgaris* may be separated from those of *T. helveticus* on the basis of the narrowly U-shaped notch in the posterior neural arch of the former species and the broadly U-shaped notch in the latter species. None of the Whitemoor Channel vertebrae represents *T. cristatus*, but may vertebrae with the posterior neural arches complete could be assigned to either *T. vulgaris* or *T. helveticus*.

Humeri. — The humeri of *T. cristatus* have a more elongate crista ventralis (terminology of Duellman and

Trueb, 1987) and a thicker shaft than in *T. vulgaris* and *T. helveticus* (Fig. 2), but we have been unable to separate the humeri of the latter two species satisfactorily from one another. The single humerus from the Whitemoor Channel Site represents either *T. vulgaris* or *T. helveticus*.

Femora. — The femora of *T. cristatus* have the tibial end more widely flared, the medial part of the shaft wider, and the area between the trochanter and the femoral end more elongate than in *T. vulgaris* and *T. helveticus* (Fig. 3), but we cannot distinguish the femora of the latter two species. The three femora from the Whitemoor Channel Site represent either *T. vulgaris* or *T. helveticus* or both, but none represent *T. cristatus*.

Triturus vulgaris (Linnaeus, 1758) Smooth Newt

Material. — Ten vertebrae NCM 143.989 (1-10).

Remarks. — The smooth newt occurs in the area today (Yalden, 1986). This species is said to be more terrestrial than many species of the genus and occurs in a wide variety of damp habitats (Arnold and Burton, 1978).

Triturus helveticus (Razoumowsky, 1789) Palmate Newt

Material. — Twenty vertebrae NCM 143.989 (11-30).

Remarks. — The palmate newt occurs in the area today (Frazer, 1983). This species is said to be more aquatic than *T. vulgaris*. It breeds in a wide variety of aquatic habitats, sometimes lentic ones, and sometimes even in brackish water near the sea (Arnold and
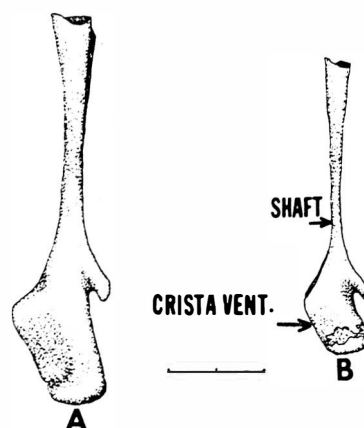

Fig. 2 Right humeri of modern *Triturus*. A, *T. cristatus*; B, *T. helveticus*. The line equals 2mm and applies to all figures.
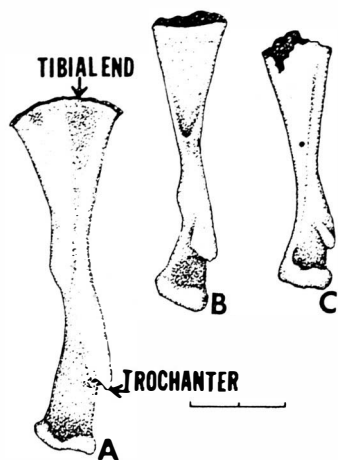
Fig. 3 Right femora of modern *Triturus*. A, *T. cristatus*; B, *T. vulgaris*; C, *T. helveticus*. The line equals 2mm and applies to both figures.
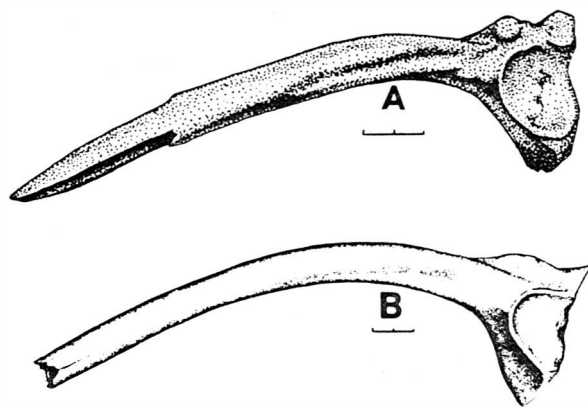

Fig. 4 Left ilia of fossil *Bufo* from the Whitemoor Channel site. A, *B. calamita* NCM 143.989 (97); B, *B. bufo* NCM 143.989 (104). Each line equals 2mm.

Burton, 1978), but tends to prefer more acidic waters than *T. vulgaris* (Yalden, 1986).

Triturus sp. indet.

Material. — Left dentary NCM 143.989 (31); nine atlantes NCM 143.989 (32-40); 51 vertebrae NCM 143.989 (41-91); right humerus NCM 143.989 (92); two right and one left femora NCM 143.989 (93-95).

Remarks. — We were unable to assign the non-vertebral elements to species, although we feel that *T. vulgaris* and *T. helveticus* are those represented. The above vertebrae were not assigned to species because diagnostic parts were missing.

Order Anura Rafinesque, 1815

Family Bufonidae Gray, 1825

Genus *Bufo* Laurenti, 1768

Holman (1989) discussed the identification of *Bufo bufo*, *Bufo calamita* and *Bufo viridis* on the basis of isolated ilia. Two ilial characters in combination enable one to identify fossil specimens as *B. bufo* or *B. calamita* with a high degree of confidence. (1) *B. bufo* has a low, roughened or rounded ilial prominence, whereas *B. calamita* has a relatively high and triangular one (Fig. 4a). An 'unusual' morph occasionally occurs in the ilium of *B. bufo*, however, where the ilial prominance arises from the shaft as a low, irregularly shaped crest (Holman, 1989a, p. 10, Fig. 1). (2) *B. bufo* lacks the elongate ventral ridge ('*calamita* ridge' of Holman, 1989b) that occurs on the posterior part of the ilial shaft and that is separated from the upper part of the shaft by an indented area in *B. calamita*. It appears likely that the differences in ilial structure between the two species reflect the differences in locomotion, as *B. calamita* makes 'mouse-like' dashes that *B. bufo* does not show. Böhme (1977) has provided a means for distinguishing the sphenethomoids and sacra of *B. bufo* and *B. calamita*, but these elements appear to be more variable than the ilia (Holman, 1989b).

Bufo calamita Laurenti, 1768 Natterjack Toad

Material. — Sacrum NCM 143.989 (96) and two left ilia NCM 143.989 (97-98) (Fig. 4a).

Remarks. — This record as well as other fossil records of *B. calamita* in England will be addressed in the discussion section of the present paper.

Bufo bufo (Linnaeus, 1758) Common Toad

Material. — Three left sphenethmoids (one with a supraoccipital attached) NCM 143.989 (99-101); two sacra (one partial) NCM 143.989 (102-103); and one left ilium NCM 143.989 (104) (Fig. 4b).

Remarks. — This toad occurs in the area today (Frazer, 1983). The common toad has a wide range of habitats, but it needs shallow, standing water to be able to reproduce.

Bufo sp. indet.

Material. — Four left exoccipitals NCM 143.989 (105-108); two parasphenoids NCM 143.989 (109-110); one left and one right dentaries NCM 143.989 (111-112); two left and two right angulosplenials NCM 143.989 (113-116); three atlantes NCM 143.989 (117-119); six left scapulae NCM 143.989 (120-125); four left and one right suprascapulae and two suprascapular fragments NCM 143.989 (126-132); two left humeri NCM 143.989 (133-134); one left and one right radioulnae NCM 143.989 (135-136).

Remarks. — These bones are easily distinguished from those of *Rana*, but we are unable to distinguish between *B. bufo* and *B. calamita* on the basis of these elements because of a lack of available comparative material of modern *B. calamita*.

Family Ranidae Gray, 1825

Genus *Rana* Linnaeus, 1758

Böhme (1977) has given characters that distinguish individual bones of certain species of *Rana* from each other. We have been able to identify *R. temporaria* on the basis of sphenethmoids, sacra and ilia using the characters pointed out by Böhme and by the examination of modern skeletal material.

Rana temporaria Linnaeus, 1758 Common Frog

Material. — Sacral vertebra NCM 143.989 (137); two right ilia NCM 143.989 (138-139); a partial associated skeleton NCM 143.989 (140).
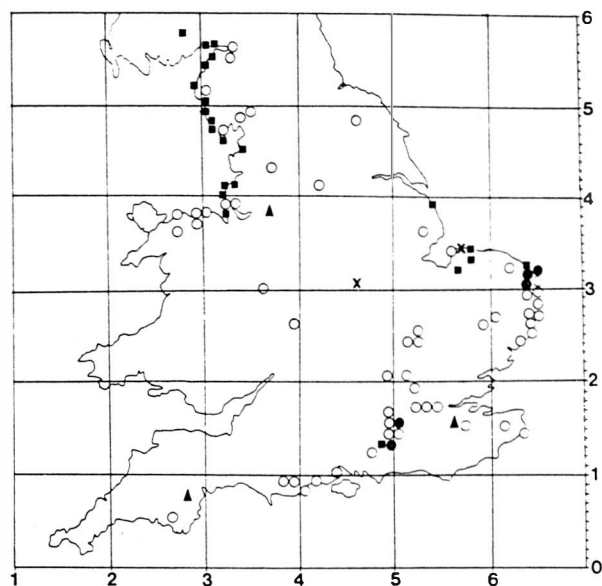
Fig. 5 Map of the distribution of fossil and modern *Bufo calamita* in England. Modified and redrawn from Frazer, 1983. Triangles indicate fossil records. Open circles indicate historic records up to and including 1959. Closed circles indicate records from 1960 through 1969. Squares indicate records from 1970 to 1983. X's indicate introduced individuals or populations.

Remarks. — The sacra of *R. temporaria* have their diapophyses more posteriorly directed than those of other British and European *Rana* and the ilial crest (vexillum of Böhme, 1977) of the ilium is quite reduced anteriorly compared with other British and European *Rana* (Böhme, 1977). The associated frog skeleton is identified as *R. temporaria* on the basis of the structure of the right sphenethmoid (Böhme, 1977, p. 291, Fig. 5). This fossil skeleton lacks both ilia as well as the sacrum.

The common frog is found in the area today (Frazer, 1983). This species may be found quite far from permanent water, but needs shallow, still water to be able to reproduce.

Rana sp. indet.

Material. — Right premaxilla NCM 143.989 (141); right maxilla NCM 143.989 (142); left angulosplenial NCM 143.989 (143); two atlantes NCM 143.989 (144-146); two left and two right humeri NCM 143.989 (146-149); four left radioulnae NCM 143.989 (150-153); one urostyle NCM 143.989 (154).

Remarks. — These skeletal elements are distinguishable from those of *Bufo bufo* and other European genera, but we are unable to determine what species of *Rana* they represent.

DISCUSSION

The Whitemoor Channel site, East Cheshire has yielded at least two species of newt and three species of anuran, all of which represent forms living in Britain today. Moreover, with the exception of a record of *Emys orbicularis* from the Flandrian of East Wretham near Thetford, Norfolk (A. Newton, 1862; Stuart, 1982)

assemblages from Flandrian sites in Britain have thus far yielded only extant British species (E. Newton, 1894; Holman, 1985, 1987a, 1988). This is in contrast to Cromerian, Hoxnian and Ispwichian interglacial herpetofaunas which have yielded exotic anurans and reptiles found on the European Continent today, but not occurring naturally in Britain (Holman, 1987b, 1987c; Holman, Clayden and Stuart, 1988; Holman, Stuart and Clayden, 1990, Stuart, 1982).

Beebee (1978) spurred an interesting exchange of ideas in the 1980's (Beebee, 1980, 1988/89; Walters, 1981; Wilkinson, 1988; Yalden, 1980a, 1980b, 1981) on the explanation for the restricted distribution of Britain's rare amphibians and reptiles (natterjack toad *B. calamita*, sand lizard *Lacerta agilis* and smooth snake *Coronella austriaca*).

In essence Beebee (1978) postulated that the present distribution of rare herpetological species resulted from human activities in the Neolithic which created heathland corridors in the dominant regional deciduous forst, connecting the West Midlands and northwest England with East Anglia. Yalden (1980a) drew attention to the climatic warming at the onset of the Flandrian (Holocene) from a little before 10,000 BP, which was so rapid that there was considerable delay before the arrival of forest trees, and suggested that the resulting open conditions would have allowed the rare species to colonise Britain extensively. The subsequent development of dense forest then restricted them to coastal dunes and heaths. Walters (1981) suggested that warmer climates in the past would have allowed the rare species to occupy a wider diversity of habitats in Britain as they do further south in mainland Europe, and agreed with Yalden that it was unnecessary to search for previous existing heaths and dunes when plotting dispersal routes. Wilkinson (1988) and Beebee (1988/89) further commented on *Bufo calamita* history in Britain, in short notes, based in part on poorly stratified (? Flandrian) records (Holman, 1985, 1988).

Since its first mention as a British species by Pennant in 1776 (Smith, 1973) *B. calamita* has occurred widely, but locally, in England and southwest Scotland, mostly confined to coastal dune and inland heath sites. It is also found in southwest Ireland. In recent decades it has become extinct at many localities where it was formerly present (Fig. 5) and its survival in Britain is now largely dependant on careful management of the remaining sites.

The natterjack is distributed from Iberia across to north-central Europe, reaching as far north as about 55° N in Britain and 58° N in south Sweden and Estonia (Arnold and Burton, 1978). The species exploits a wider range of habitats in southwest Europe, where it is also more abundant. Northward and eastward it becomes associated with sandy soils that provide warmer microclimates (Beebee, 1983). According to Beebee, all habitats outside the warm Iberian Peninsula share the same features; well-drained soils and low vegetation allowing high amounts of sunshine to reach ground level, so that summer temperatures can be much higher than typical for that latitude. Beebee regards *B. calamita* as primarily a species of southwest Europe, able to extend

its range elsewhere, including Britain, by exploiting locally warm habitats.

The fossil records of *B. calamita* are from: 1. ?Flandrian cave deposits from Cow Cave, Chudleigh, Devon (Holman, 1988); 2. ?Flandrian fissure deposits from Ightham Fissures, near Sevenoaks, Kent (Holman, 1985); and 3. early Flandrian (approximately 10,000 to 8,800 BP) from the present site at Whitemoor Channel, Cheshire.

The Cow Cave and Ightham sites lack precise stratigraphic information. They probably date from sometime within the Flandrian, within the time range of 10,000 BP to a few hundred years ago. The Ightham fissures also yielded *C. austriaca* (Holman, 1985). Today, *B. calamita* is apparently extinct in Devon, but there is a pre-1960 coastal record for the species (Frazer, 1983). The Chudleigh site is about 9km from the coast. In relation to the Ightham fossils, there are two pre-1960 records from Kent, one from the Dover-Deal area and the other from a more inland locality near Canterbury (Frazer, 1983).

The only well-dated fossils (those from the Whitemoor Channel) are of importance because they date from early in the Flandrian when most of the modern fauna and flora was immigrating from the Continent in response to climatic amelioration following the much more severe climates of the Last Cold Stage. Britain was then broadly connected to Continental Europe across the eastern Channel and the southern North Sea (e.g. Stuart, 1982). Substages Fl Ia and Fl Ib at Whitemoor (Johnson *et al.*, 1970), Red Moss (Hibbert *et al.*, 1971) and other sites in Cheshire and Lancashire cover the period of development of birch woodland in a landscape previously dominated by grasses and sedges. Since birch casts relatively light shade, it is probable that open, sunny environments would have been widespread throughout this period. The rapid temperature rise very early in the Flandrian is well shown in analyses of radiocarbon-dated beetle faunas from Britain by Atkinson *et al.* (1987). Their curve indicates that mean annual temperatures were already as high as today by about 9,500 BP. But values rather higher than those of today were not reached until much later in the Flandrian ('Climatic Optimum') about 5-7,000 BP.

In the early Flandrian, as today, Whitemoor was neither a coastal dune site nor heathland. There is no indication of heaths (Ericaceae) in the pollen diagram from the site (Johnson *et al.*, 1970). Given the nature of the bedrock and presence of glacial till ('boulder clay'), both sandy and clay soils would have been available locally. *Bufo calamita* in Britain and Ireland lives in coastal dunes or heathland. Reports from Cambridgeshire (Jenyns, 1830) and the Furness region (Frazer, 1983) actually reflect typical habitats (T. J. C. Beebee, personal communication to J.A.H.). Throughout its range today the natterjack breeds in shallow, often ephemeral, and preferably non-acid pools, unshaded by vegetation (Beebee, 1983). The Whitemoor pool, some 30 metres in diameter, shallow, highly calcareous and unshaded (there was no terrestrial plant material other than pollen in the sediment) would have met these criteria.

The natterjack occurs today in northern England only along coastal dunes, extending from Cheshire to Cumbria and the Scottish shore of the Solway Firth (Frazer, 1983; Beebee, 1983). There are a few pre-1960 records from inland sites in northern England (Fig. 5), although there are considered probably incorrect by Beebee (1983, Fig. 4).

The fossil evidence from the Whitemoor Channel therefore favours Yalden's view (1980a, 1980b, 1981) that the natterjack was spread more widely in Britain in the early Flandrian before the arrival of dense forest restricted it to local open sites. Coastal dune habitats were present throughout the Flandrian, and numerous pollen diagrams provide evidence of the Flandrian history of heathland in Britain. Pollen of Ericaceae, presumably mostly *Erica* and *Calluna*, pollen and plant macrofossils specially identified as heather *Calluna vulgaris*, and plant macrofossils only of crossed-leaved heath *Erica tetralix* occur throughout the Devensian Lateglacial and early Flandrian in moderate frequencies, becoming much more abundant from the beginning of substage Fl Id (zone VIIa, about 7,000 BP; Godwin, 1975). At first, heath communities probably existed locally on acid soils, and after about 7,000 BP greatly expanded with increased podsolisation (Godwin, 1975). From about 5,000 BP, with the arrival of Neolithic farmers, human activities — forest clearance, burning and grazing livestock — appear to have enhanced this natural succession. No doubt, as suggested by Beebee, the natterjack and other rare herpetological species would have expanded their ranges with the spread of heathland at this time.

The evidence from Whitemoor emphasises the potential for recovering fossil herpetological material from other well-stratified and dated late Quaternary sites, with the promise of telling us more about the origins of our present herpetofauna.

ACKNOWLEDGEMENTS

REFERENCES

Arnold, E. E. and Burton, J. A. (1978). *A Field Guide to the Reptiles and Amphibians of Britain and Europe.* London: Collins.

Atkinson, T. C., Briffa, K. R. and Coope, G. R. (1987). Seasonal temperatures in Britain during the past 22,000 years, reconstructed using beetle remains. *Nature* 325 (6105), 587-592.

Beebee, T. J. C. (1978). An attempt to explain the distribution of rare herptiles *Bufo calamita*, *Lacerta agilis* and *Coronella austriaca* in Britain. *British Journal of Herpetology* 5, 763-770.

Beebee, T. J. C. (1980). Historical aspects of British herpeto-fauna distribution. *British Journal of Herpetology* **6**, 105.

Beebee, T. J. C. (1983). *The Natterjack Toad*. Oxford: University Press.

Beebee, T. J. C. (1988/89). Just a bit more about herp history in Britain. *British Herpetological Society Bulletin*, **26**, 28.

Böhme, G. (1977). Zur bestimmung quartärer Anuran Europas an Hand von Skelettelementen. *Wissen-schaftliche Zeitschrift der Humboldt-Universität zu Berlin, Mathematik-Naturwissenschaft* **26**, 283-300.

Duellman, W. E. and Trueb, L. (1987). *Biology of Amphibians* New York: McGraw-Hill.

Estes, R. (1981). *Gymnophiona, Caudata: In, Handbuch der Paläoherpetologie*. Stuttgart and New York: Fischer Verlag.

Frazer, D. (1983). *Reptiles and Amphibians in Britain*. London: Collins.

Godwin, H. (1975). *The History of the British Flora (2nd Edition)*. Cambridge: University Press.

Hibbert, F. A., Switsur, V. R. and West, R. G. (1971). Radiocarbon dating of Flandrian pollen zones at Red Moss, Lancashire. *Proceedings of the Royal Society of London B* **177**, 161-171.

Holman, J. A. (1985). Herpetofauna of the Pleistocene fissures near Ightham. Kent. *Herpetological Journal* **1**, 26-32.

Holman, J. A. (1987a). Additional records of British Pleisto-cene amphibians and reptiles. *British Herpetological Society Bulletin* **19**, 18-20.

Holman, J. A. (1987b). Herpetofauna of the Swanton Morley site (Pleistocene: Ipswichian). Norfolk. *Herpetological Journal* **1**, 199-201.

Holman, J. A. (1987c). Middle Pleistocene herpetological records from interglacial deposits at Sugworth, near Oxford. *British Herpetological Society Bulletin* **21**, 5-7.

Holman, J. A. (1988). Herpetofauna of the Late Devensian/Early Flandrian Cow Cave site, Chudleigh, Devon. *Herpetological Journal* **1**, 214-218.

Holman, J. A. (1989a). Additional herpetological records from the Middle Pleistocene (Cromerian Interglacial) freshwater bed, West Runton, Norfolk. *British Herpeto-logical Society Bulletin* **27**, 9-12.

Holman, J. A. (1989b). Identification of *Bufo calamita* and *Bufo bufo* on the basis of skeletel elements. *British Herpetological Society Bulletin* **29**, 54-55.

Holman, J. A., Clayden, J. D. and Stuart, A. J. (1988). Herpetofauna of the West Runton Freshwater Bed (Middle Pleistocene: Cromerian Interglacial). West Runcton. Norfolk. *Bulletin of the Geological Society of Norfolk* **38**, 121-136.

Holman, J. A., Stuart, A. J. and Clayden, J. D. (1990). A Middle Pleistocene herpetofauna from Cudmore Grove, Essex, England, and its paleogeographic and paleo-climatic implications. *Journal of Vertebrate Paleontology* **10**, 86-94

Jenyns, L. (1830). Some observations on the habits and character of the natterjack (*Bufo rubeta*). *Transactions of the Cambridge Philosophical Society* **3**, 373-377.

Johnson, R. H., Franks, J. W. and Pollard, J. E. (1970). Some Holocene faunal and floral remains in the Whitemoor meltwater channel at Bosley, East Cheshire. *North Staffordshire Journal of Field Studies* **10**, 65-74.

Newton, A. (1862). On the discovery of ancient remains of *Emys lutaria* in Norfolk. *Annual Magazine of Natural History* **3**, 224-228.

Newton, E. T. (1894). The vertebrate fauna collected by Mr. Lewis Abbott from the fissure near Ightham, Kent. *Quarterly Journal of the Geological Society of London* **50**, 183-204.

Sanchiz, F. B. (1977). La Familia Bufonidae (Amphibia, Anura) en el Tertiario Europea. *Trajabos sobre Neogene-Cuatanario* **8**, 75-111.

Smith, M. A. (1973). *British Amphibians and Reptiles (5th Edition)* London: Collins.

Stuart, A. J. (1982). *Pleistocene Vertebrates in the British Isles*. London and New York: Longman.

Walters, G. J. (1981). Historical aspects of the British herpeto-fauna distribution. *British Journal of Herpetology* **6**, 177.

West, R. G. (1977). *Pleistocene Geology and Biology: with Especial Reference to the British Isles*. London: Longman.

Wilkinson, D. M. (1988). The Flandrian history of rare herptiles in Britain: A consideration of the hypotheses of Beebee and Yalden. *Herpetological Society Bulletin* **25**, 39-41.

Yalden, D. W. (1980a). An alternative explanation of the distribution of the rare herptiles in Britain. *British Journal of Herpetology* **6**, 37-40.

Yalden, D. W. (1980b). Reply to T. J. C. Beebee. *British Journal of Herpetology* **6**, 105-106.

Yalden, D. W. (1981). Reply to G. J. Walters. *British Journal of Herpetology* **6**, 178.

Yalden, D. W. (1986). The distribution of newts, *Triturus* spp. in the Peak District, England. *Herpetological Journal* **1**, 97-101.

PRELIMINARY STUDY ON THE BREEDING PATTERN OF THE EGYPTIAN TORTOISE, *TESTUDO KLEINMANNI*, IN ISRAEL

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ABSTRACT

Egyptian tortoises were collected in the field and X-rayed at 2-4 week intervals during two breeding seasons. Females laid 2-3 clutches per year, each consisting of 1-3 large eggs. The internesting period was estimated to be 20-30 days. The nest was a shallow pit at a base of a bush. The breeding biology of *Testudo kleinmanni* is similar to that of other small highly specialised tortoises.

INTRODUCTION

The Egyptian tortoise, *Testudo kleinmanni*, is a small terrestrial tortoise which inhabits sandy areas and dunes throughout northeastern Libya (Schleich, 1989), northern Egypt, Sinai and eastwards to the northern Negev in Israel (Flower, 1933; Iverson, 1986; Mendelssohn, 1982). The Egyptian tortoise is an endangered species threatened by habitat destruction (Mendelssohn, 1982) and commercial collecting (Buskirk, 1985).

The limited information on its breeding biology has originated from captive individuals in Egypt and Israel. Data on wild populations are not available. Lortet (1887) observed mating during March-April and nesting during May. Flower's (1933) observations on a large number of individuals in Giza Zoo indicated that peaks in copulation frequency occurred in September-October while eggs were laid mainly in June. Egg length and width ranged from 29-30mm and 22-23mm, respectively. Sixty-nine individuals hatched in Giza Zoo, 53 per cent in October, 24 per cent in November, 9 per cent both in September and February and 5 per cent in January (Flower, 1933). These young were totally yellow in colour and their carapace length, width and height was 33mm, 28mm and 18mm, respectively. In Israel, captive tortoises mated during October-November and February-April, while eggs were laid between April and July. Hatching started in August and ended in October, except for a single case in December. The incubation period, at constant 30°C, was 97-119 days (Mendelssohn, 1982). Half of these clutches (*n* = 12) consisted of one egg, two clutches consisted of two eggs, three other clutches of three eggs and one of four eggs (Mendelssohn, 1982).

This paper describes preliminary observations on the breeding pattern of a wild population of the Egyptian tortoise in Israel.

METHODS

Study site — The study was carried out at Holot Agur, about 15km north of Beer-Milka (34° 24′ E, 31°C 00′ N), in the northwestern Negev desert. The area is characterised by east-west trending sand ridges separated by deep valleys. Mean annual air temperature is 20°C (Israel Meteorological Service, unpubl. data), with mean maximum 30°C in the hottest month (July) and mean minimum 12°C in the coldest month (January). Subzero temperatures are rare. Large fluctuations in air temperature (10-15°C) are common during the day. Most precipitation (100-200mm) occurs between October and March. Vegetation cover averages 20-30 per cent and consists primarily of *Artemisia monosperma* plant association (Waisel, Pollak and Cohen, 1982).

Field methods — Adult females were randomly collected, mainly by following fresh tracks on the sand, and X-rayed (Gibbons and Green, 1979; Turner, Medica and Lyons, 1984) using a portable X-ray generator (Softex K-2; 3mA; 50kV; individuals were placed 50cm away from the generator and were exposed for 10 seconds). Four females were fitted with radio-transmitters (15-17g) that were glued with dental acrylic to the posterior carapace (Geffen and Mendelssohn, 1988, 1989). These females were X-rayed every 2-4 weeks during their daily inactivity period (evening, Geffen and Mendelssohn, 1989), between January and July, and were returned to the location of collection a few hours later.

In May 1984 two females, that were previously X-rayed and were known to carry eggs, were each placed in a small enclosure (1m²) for 2-3 weeks. Each enclosure was built around a large bush with a complex system of rodent burrows. The females were released after the eggs were laid. The aim of this procedure was to enable us to locate nests and monitor the incubation period in the wild. We used only two females, largely because very few females were located daily.

Every 2-4 weeks daily air (50cm above ground) and surface (1 and 5cm deep) temperatures were taken, using a digital thermometer (Wescor TH-65, accurate to ±0.1°C), from a bush base near each nest. At each visit, temperature measurements were taken at equal intervals four times daily. In addition, sand samples were collected twice a day (at 0500 and 1400) from the

	SCL	Age	1983					1984					
			15.4	29.4	6.5	20.5	24.6	18.2	16.3	13.4	4.5	18.5	8.6
#1	111.3	9							0				
#2	113.6	8	0							0			
#3	116.5	9			2	2	0						
#4	106.4	6		2	2	2	1			0		0	
#5	113.4	7						0	2	1	3	3	0
#6	113.0	9	2					0		1	2	2	0
#7	112.6	6							1	2	2	0	0
#8	120.7	8										2	
#9	114.3	7										1	2
#10	107.3	7						0					
$\overline{X}$	112.9	7.6	1.0	2.0	2.0	2.0	0.5	0	1.0	0.8	2.3	1.3	0.5

TABLE 1: Number of eggs, determined by X-ray, in nine Egyptian tortoise females during two breeding seasons. Dates of X-raying are presented for each year, with the mean number of eggs per tortoise for each date shown at the bottom line. SCL = Straight Carapace Length (mm). Age represented as number of growth rings counted on carapace plates.

	Intercept	Slope	r^2	F	P	d.f.
Clutch size	−2.50	0.04	0.05	0.59	>0.4	1.13
Egg width	8.92	0.14	0.20	5.60	<0.05	1.23
Widest egg per clutch	1.75	0.21	0.37	7.01	<0.05	1.13

TABLE 2: Linear relationships of reproductive variables to body size (straight carapace length) in *Testudo kleinmanni.*

surface (1 and 5cm deep) and stored in sealed containers. The sand samples were later weighed, dried in a oven (100°C) and in a desiccator. Water content in the sand was calculated as the difference in weight of samples before and after drying.

Data analysis — Clutch size and measurements of eggs were calculated from X-ray negatives. Correction for egg positions in the tortoise body ($\approx$ 2cm above the X-ray film) were made by reducing measurements by 2 per cent. Linear regression and one way ANOVA were used in the statistical analysis.

RESULTS

During this study we observed only two mating pairs, both during March. On one occasion a male was observed to attempt copulating 28 times within one hour. This behaviour consisted of series of knocks on the posterior part of the female's carapace, causing the female to stop, followed by the male climbing on the female's back, pushing his tail beneath hers and simultaneously uttering a series of high pitched, rasping calls (described by Flower, 1933 and Loveridge and Williams, 1957).

Table 1 summarises the number of eggs observed in nine females during two nesting seasons. During no other period of the year did females carry eggs. Eggs were first observed in the oviduct during March-April and last observed during the end of June. Most clutches (8) consisted of two eggs (total number of clutches = 14), five consisted of one egg and one consisted of three eggs (mean $\pm$ SD = 1.71 $\pm$ 0.61).

Two nests were found in July (6.7.84), one in each enclosure. The nests, that contained two and three eggs, were located in a shady spot at a base of a bush, facing south. The eggs in each nest were laid in a shallow pit (3-4cm deep) and covered with sand. The sand around the eggs was clumped as if it was previously wetted. Mean ($\pm$SD) length and width of the eggs was 31.6mm $\pm$1.1 and 21.4mm $\pm$0.5, respectively. The eggs were not moved from their original position when measurements were taken. Sand temperature at a depth of 5cm ranged between 24.3-38.2°C in July, 23.5-35.3°C in August and 23.9-34.5°C in September. Sand water content at the surface during the summer ranged between 0.13-0.30 per cent and at depth of 5cm between 0.16-0.27 per cent.

In one nest two young hatched after 70-90 days. On 14.9.84 we observed one individual hatching, the other hatched one or two days later. Hatchling body length was 25.7 and 30mm and their weight was 3-4g. No hatching occurred in the other nest, but an egg from this nest contained a live embryo (10mm) and a large yolk sac 10 months after the eggs were laid.

Egg width and number were measured from X-ray negatives. Mean egg width was 24.3mm $\pm$1.1, and varied significantly between females (F = 4.6, d.f. = 6.23, P<0.01). Egg width significantly correlated with body size (Table 2).

DISCUSSION

The period of mating appeared to be limited to the spring (March). Although copulations were reported to occur in captivity during autumn (September-October, Flower, 1933; Mendelssohn, 1982), there were no indications that they occur in autumn in the wild. Furthermore, Geffen and Mendelssohn (1989)

reported that captive individuals showed a different annual activity cycle due to availability of food round the year. This phenomenon might have implications on the breeding behaviour of tortoises in captivity. Copulation attempts during autumn were observed in the wild in *Gopherus polyphemus* but females were not receptive during that time (Landers, Garner and McRae, 1980).

Sperm storage is a well documented phenomenon with terrestrial tortoises (Moll, 1979). Fitting four females with transmitters prevented them from copulating due to the location and size of the transmitter, however they produced 2-3 egg clutches annually. Sperm storage appears to be an especially important mechanism in species with relatively low density populations (e.g. Egyptian tortoise, 27 individuals per km²; Geffen, 1985), ensuring reproduction when males are not encountered.

Ovulation of similar sized ova in the ovaries occurs simultaneously (Moll, 1979), so presence of different numbers of eggs in a female's oviduct at different times within one season is indicative of several different clutches. Differences in shell thickness are easily observed by X-ray, where thin shelled eggs indicate the formation of a new clutch. We concluded from Table 1 that:

1) The nesting period lasted from March to the end of June.

2) Within the nesting period each female produces 4-6 eggs in two-three cycles.

3) The internesting period is estimated to be between 20 and 30 days.

Egg size in nature was similar to that measured in captivity by Flower (1933). Congdon and Gibbons (1983, 1985) studied the relationships between reproductive characters and body size in a variety of turtle species, and concluded that among species clutch size increases with body size. In many species, egg width increases with body size (Congdon and Gibbons, 1985; Hailey and Loumbourdis, 1988) probably reflecting the width of the pelvic canal. Hailey and Loumbourdis (1988) argued that small individuals can overcome this constraint by modifying egg shape, thus smaller individuals are expected to carry more elongated eggs. This could not be investigated here as egg length can not be accurately measured from X-ray photographs. It appears that production of multiple clutches per year is a common phenomenon in the *Testudo* species and it may reflect the morphological constraint of packing shelled eggs within the body (Swingland and Stubbs, 1985; Andreu and Villamor, 1986; Hailey and Loumbourdis, 1988).

The nest construction, as well as the indication for urination during oviposition are typical for terrestrial tortoises (Ehrenfeld, 1979). Urination in the nest may camouflage the eggs' smell, thus decreasing detection by potential predators (Patterson, 1981). Urination may also increase the humidity in the nest, thus decreasing water loss by evaporation from the eggs. Incubation time in the wild was lower than in captivity (Mendelssohn, 1982) but this may be due to the difference in temperature regime during incubation. Fluctuations in nest temperature and low rates of

humidity have also been observed in *Testudo hermanni* (Cheylan, 1981). Data from Giza Zoo showed that hatching takes place mainly during autumn and early winter. In this period food (annual plants) is likely to be most abundant and potential predators are either hibernating (desert monitor, *Varanus griseus*) or elsewhere (birds of prey, Geffen and Mendelssohn, 1988, 1989), thus hatching during autumn and early winter may increase survival of the young. The extended and unsynchronised hatching period reflects the annual nesting cycles, but it also provides a mechanism to ensure that at least some of the young will emerge when conditions are more favourable, especially in years with low rain fall. The case of the egg, that after 10 months had not yet hatched, but contained a live embryo, may indicate that under the same ambient conditions changes in incubation time can occur. Such, probably mutative, changes may have selective survival value if hatching occurs in winter, when food is most abundant, instead of during early autumn.

The Egyptian tortoise breeding strategy can be categorised as type II (Moll, 1979), characterised by a small number of relatively large-size eggs, a prolonged nesting period and solitary nesting site that does not require specific location or structure. Tortoises that are included in this category are highly specialised small species like *Homopus*, *Kinixys* and *Malacochersus*. The small body size limits the number of eggs in each clutch because egg size cannot be reduced beyond a certain point and still contain the necessary amount of water and energy reserves needed for the embryo to develop and survive the incubation period. Evolution led these species to develop fewer but larger eggs yielding fewer offspring but increasing their survival. Small numbers of eggs and the lack of need for a specific nesting location decreases egg predation in these species (Moll, 1979).

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REFERENCES

Andreu, A. C. and M. D. Villamor (1986). Reproduction of *Testudo graeca graeca* in Donana, S.W. Spain. 589-592. In: Studies in Herpetology. Rocek, Z. (ed.). Charles University, Prague.

Buskirk, J. R. (1985). The endangered Egyptian tortoise, *Testudo kleinmanni*: status in Egypt and Israel. In: Proceedings of the Ninth International Herpetological Symposium on captive propagation and husbandry. 35-51. McKeown, S., Caporaso, F. and K. H. Peterson (eds.). Thurmont: Zoological Consortium Inc.

Cheylan, M. (1981). Biologie et ecologie de la tortue d'Hermann *Testudo hermanni*, Gmelin, 1789. Contribution de l'espece a la connaissance des climats quaternaires de la France. *Mem. Trav. E. P. H. E. Ins. Montpellier* 13.

Congdon, J. D. and J. W. Gibbons (1983). Relationships of reproductive characteristics to body size in *Pseudemys scripta*. Herpetologica 39(2), 147-151.

Congdon, J. D. and J. W. Gibbons (1985). Egg components reproductive characteristics of turtles: relationships to body size. Herpetologica 41(2), 194-205.

Ehrenfeld, D. W. (1979). Behaviour associated with nesting. In: Turtles perspectives and research, 417-434. Harless, M. and H. Morlock (eds.). Willey-Interscience.

Flower, S. S. (1933). Note on the recent reptiles and amphibians of Egypt. *Proc. Zool. Soc. Lond.* 745-749.

Geffen, E. (1985). On the biology of the Egyptian tortoise (*Testudo kleinmanni*) in Holot Agur. Israel. M.Sc. thesis. Tel Aviv Univ. (in Hebrew with English summary).

Geffen, E. and H. Mendelssohn (1988). Home range use and seasonal movements in the Egyptian tortoise (*Testudo kleinmanni*) in the northwestern Negev, Israel. Herpetologica 44(5), 354-359.

Geffen, E. and H. Mendelssohn (1989). Activity patterns and thermoregulatory behaviour of the Egyptian tortoise *Testudo kleinmanni* in Israel. *J. Herpetol.* 23(4), 404-409.

Gibbons, J. W. and J. L. Green (1979). X-ray photography: a technique to determine reproductive patterns of freshwater turtles. Herpetologica 35, 86-89.

Hailey, A. and N. S. Loumbourdis (1988). Egg size and shape, clutch dynamics, and reproductive effort in European tortoises. *Can. J. Zool.* 66(8), 1527-1536.

Iverson, J. B. (1986). A check list with distribution maps of the turtles of the world. Indiana: Paust Printing.

Landers, L. J., J. A. Garner and W. A. McRae (1980). Reproduction of the Gopher tortoise (*Gopherus polyphemus*), in southwestern Georgia. Herpetologica 36, 353-361.

Lortet, L. (1987). Observations sur les tortues et paludines du bassin de la Mediterranée. *Archiv. Mus. Natur. Lyon.* 4, 1-26.

Loveridge, A. and E. E. Williams (1957). Revision on the African tortoises and turtles of the suborder Cryptodira. *Bull. Mus. Comp. Zool.* 115, 276-283.

Mendelssohn, H. (1982). Egyptian tortoise. In: The IUCN Amphihibia-Reptilia red data book, 1, 133-136. Groombridge, B. (ed.). Switzerland, Gland: IUCN.

Moll, E. O. (1979). Reproductive cycles and adaptations. In: Turtles perspectives and research, 305-331. Harless, M. and H. Morlock (eds.). Willey-Interscience.

Patterson, R. (1971). The role of urination in egg predator defense in the desert tortoise (*Gopherus agassizii*). Herpetologica 27, 197-199.

Schleich, H. H. (1989). Merkwalsausbildungen an Landschildkröten in Nordost-Libyen. Herpetozoa 1, 97-108.

Swingland, I. R. and D. Stubbs (1985). The ecology of the Mediterranean tortoise (*Testudo hermanni*): reproduction. *J. Zool.* 205, 595-610.

Turner, F. B., P. A. Medica and C. L. Lyons (1984). Reproduction and survival of the desert tortoise (*Scaptochyles agassizii*) in Ivanpah valley, California. *Copeia* 4, 811-820.

Waisel, Y., G. Pollak and Y. Cohen (1982). The ecology of vegetation of Israel. Tel Aviv Univ. Tel Aviv: Sifriat Poalim L.T.D. Publ. House (in Hebrew).

SHORT NOTE:
VISUAL STIMULI AND SPONTANEOUS LOCOMOTOR PATTERNS OF COMMON LIZARDS, *LACERTA VIVIPARA*

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ABSTRACT

The movement pattern of adult male *Lacerta vivipara* travelling spontaneously along a wooden-walled channel was similar to the previously measured pattern of animals moving across an open space, comprising an alternation of short ($\sim$1 s) bursts of locomotion with even shorter ($\sim$0.1 s) pauses. Changing the structure and appearance of the walls of the channel altered the locomotor pattern. Grass turf separated from the lizards by glass had the greatest effect, causing a decrease in mean burst speed and an increase in mean pause duration. This persisted for 25 trials, suggesting that the response to the visual stimulus presented by turf was investigatory and not merely due to its novelty, whereas the smaller effect seen when the walls were of white card waned with time and so may have been primarily a response to change.

INTRODUCTION AND METHODS

Many species of lizards move in a characteristically discontinuous way, alternating short periods of locomotor activity with short pauses when their limbs are immobile. It was shown by Avery, Mueller, Smith and Bond (1987) that in adult *Lacerta vivipara* at their active body temperature travelling spontaneously across an open space between two tungsten bulbs used for thermoregulation, the bursts of locomotion had a mean duration of 0.30 s and a mean speed of 14.6 cm s^{-1} (equivalent to 2.9 snout-vent lengths (SVL) s^{-1}), and that the intervening pauses had a mean duration of 0.12 s. These values were consistent in any set of experimental conditions — the coefficients of variation for mean burst speed and mean pause duration, for example, were 52 per cent and 77 per cent respectively.

The functions of the pauses which give the locomotor pattern its appearance of jerkiness are not known. It has been suggested that they might result from physiological constraints, or that they might be an adaptation to increase the probability of perception of potential prey or predators. The experiment reported in this paper investigates the suggestion by Avery *et al.* (1987) that prey detection is important by investigating the effects of a number of novel visual stimuli, some of which are indirectly related to food and others not, on locomotor variables.

The experimental animals were three adult male *L. vivipara* with intact tails weighing 2.5-3.0g and with snout-vent lengths of approximately 50mm. They were housed under conditions described by Avery *et al.* (1987) in an arena measuring 180 x 55cm with a 60W tungsten bulb beneath which they could bask at each end. The space between the bulbs at the centre of the arena contained a trackway, 45cm long and 10cm high, initially constructed of wooden blocks. Although the lizards could climb over the wooden blocks and so escape sideways out of the trackway, they rarely did so. In the first experiment the trackway was 20cm in width, in subsequent experiments 10cm in width. The lizards were video filmed whilst running along the trackway, and the tapes analysed, by the methods described in Avery *et al.* (1987).

Subsequently the wooden blocks were removed and replaced with glass. Grass turf was placed behind the glass and encased in further glass so that the lizards

had no access to it; this also ensured that the stimulus was visual and not olfactory. As a control experiment the glass was retained, but the grass turf replaced by wooden blocks. In a further experiment the wooden blocks were replaced by plain white cardboard, providing minimal visual stimulus, in an attempt to separate the effects of stimulus complexity and novelty. Twenty-five sequences of movement were analysed in each of these five sets of conditions: the variables recorded were (a) distance moved during locomotor bursts (b) duration of locomotor bursts and (c) duration of pauses. From these the derived variables burst speed (a/b), overall speed ($\Sigma a/\Sigma b+\Sigma c$)) and pause frequency could be calculated. All speeds are expressed in units SVL s^{-1}.

RESULTS AND DISCUSSION

Locomotor variables for lizards under the two standardising sets of conditions, i.e. when moving along wooden-walled channels 20cm or 10cm in width, are shown in the first two lines of Table 1. None of the variables differed significantly between the two widths; mean burst speed and mean pause duration did not differ significantly from those observed in adult lizards of the same species moving spontaneously across an open space in the laboratory (Avery *et al.*, 1987; *t*-tests, $P > 0.1$ in all cases), although the mean duration of bursts was higher ($t = 2.41$, $P < 0.05$). This was probably because the wooden walls constrained the movement of the animals so that they had less opportunity to change direction, and so travelled in straighter lines, than when crossing an open space.

Replacing the wooden walls with turf (separated from the lizards by panes of glass) resulted in a marked change in the locomotor pattern (third line of Table 1). Mean pause duration and pause frequency increased, mean burst speed and mean duration of bursts decreased (all except mean pause duration significant at $P = 0.05$, one-way ANOVA with Student-Neuman-Keuls (SNK) tests).

Values for locomotor variables in lizards moving between walls of glass-fronted wood or plain white card were intermediate between the 'standardising' and the 'turf' conditions (lines 4 and 5 of Table 1). Mean burst speeds were higher, but not significantly different from, the 'turf' condition; mean burst durations and pause frequencies were not significantly

	Mean burst speed (SVL s^{-1})		Overall speed (SVL s^{-1})		Mean burst duration (s)		Mean pause duration (s)		Mean pause frequency (s^{-1})		Pause duration as a percentage of total time
Wood, 20cm width	2.90	41	2.62	48	0.96	73	0.13	115	0.70	93	10.6
Wood, 10cm width	2.78	29	2.53	34	1.14	57	0.15	133	0.63	95	10.2
Turf with glass	1.49 A	45	1.14 B	101	0.64 C	61	0.22	71	1.10 E	68	24.3
Wood with glass	1.83 A	19	1.61 B	31	0.97	52	0.35 D	143	0.71	87	20.2
White card with glass	1.79 A	37	1.76 B	45	0.99	70	0.14	45	0.82	51	14.0

TABLE 1: Variables relating to locomotion of *Lacerta vivipara* under defined experimental conditions. Figures in each column show means followed by their coefficients of variation. Means marked A-E differ significantly from those in the 'wood' condition (one-way ANOVA with SNK tests, $P < 0.05$).

different from those under 'standardising' conditions (one-way ANOVA with SNK tests). Mean pause duration with walls of glass-fronted wood was higher than under any of the other four conditions, however (SNK test, $P<0.05$), with a very high coefficient of variation (Table 1). This was probably because lizards were able to see their own reflection in the glass from some angles, and paused for longer to observe it! (Reflected images were clearer when the glass was backed by wood than by turf or white card).

Short pauses in lizard locomotion might have a physiological explanation, for example they might be due to rapid depletion of the high energy molecule phosphagen or arginine phosphate (AP, see Prestwich, 1988); or they might be functional, relating to the ability of the animal to more successfully perceive prey when it is immobile (as in many birds, see for example Tye, 1989). The relative likelihoods of these different kinds of explanations were discussed by Avery *et al.* (1987): circumstantial evidence favoured the second class of hypotheses, because mean pause duration increased in the presence of crickets (*Acheta domestica*), on which the lizards feed avidly. The results shown in Table 1 provide further circumstantial support for such an explanation; they show that a relatively simple visual stimulus (turf) alone can elicit a change in locomotor pattern. It is suggested that this stimulus is associated with potential prey because the invertebrates on which *L. vivipara* feed (see Avery, 1966) tend to be more abundant in dense vegetation than in open spaces; it therefore elicits an investigatory response, resulting in slower speeds and longer pauses.

It might be argued that the responses shown in Table 1 were due to the novelty of the stimuli. This was tested by comparing mean burst speeds and mean pause durations during the first eight trials and the last eight trials within each condition. The only significant difference was in mean pause duration in trials with white card ($0.19 \pm 0.02, 0.09 \pm 0.02$ s; $t = 3.06$, $P<0.01$). This suggests that the lizards initially responded to the white card because of its novelty, but habituated to it and hence reduced mean pause frequency; whereas in all other conditions they were responding to visual complexity as well as novelty, and the response remained. It is perhaps significant in this context that the mean pause duration in the last eight trials in the 'white card' condition was the lowest recorded in any of the present experiments (c.f. Table 1) — white card provides minimal visual stimulus.

Experiments examining the responses of *L. vivipara* to a potential predator (the snake *Vipera berus*) have shown that olfactory stimuli can also alter locomotor behaviour. Changes in the proportion of the behaviour category 'no move' occurred in response to both the physical presence of the snake (primarily a visual stimulus) and to a cage in which the snake had recently been housed (an olfactory stimulus). Some of the pauses were of extremely long duration, however, and were interpreted as attempts to avoid detection (Vanderstighelen, 1987).

The experiment reported here does not investigate the possibility of individual differences in behaviour — the data from the three lizards have been pooled in compiling Table 1. A more detailed investigation should consider the possibility of such variation, however, since it is known to occur in both locomotor patterns (e.g. Garland, 1985; Huey and Dunham, 1987) and foraging behaviour (e.g. Ehlinger, 1989) of many kinds of animals.

REFERENCES

Avery, R. A. (1966). Food and feeding habits of the common lizard (*Lacerta vivipara*) in the west of England. *J. Zool., Lond.* **149**, 115-121.

Avery, R. A., Mueller, C. F., Smith, J. A. and Bond, D. J. (1987). The movement patterns of lacertid lizards: speed, gait and pauses in *Lacerta vivipara. J. Zool., Lond.* **211**, 47-63.

Ehlinger, T. J. (1989). Learning and individual variation in bluegill foraging: habitat-specific techniques. *Anim. Behav.* **38**, 643-658.

Garland, T. J. (1985). Ontogenetic and individual variation in size, shape and speed in the Australian agamid lizard *Amphibolurus nuchalis. J. Zool., Lond.* **207**, 425-439.

Huey, R. B. and Dunham, A. E. (1987). Repeatability of locomotor performance in natural populations of the lizard *Sceloporus merriami. Evolution* **41**, 1116-1120.

Prestwich, K. N. (1988). The constraints on maximal activity in spiders. II. Limitations imposed by phosphagen depletion and anaerobic metabolism. *J. Comp. Physiol. B* **158**, 449-456.

Tye, A. (1989). A model of search behaviour for the northern wheatear *Oenanthe oenanthe* (Aves, Turdidae) and other pause-travel predators. *Ethology* **83**, 1-18.

Vanderstighelen, D. (1987). Responses of the common lizard (*Lacerta vivipara*) to visual and chemical stimuli of the viper (*Vipera berus*). In *Proceedings of the 4th Ordinary General Meeting, Societas Europaea Herpetologica,* 425-428. Van Gelder, J. J., Bergers, P. J. M. and Strijbosch, H. (Eds.). University of Nijmegen: Faculty of Science.

BOOK REVIEWS:

(1) Wörterbuch der Herpetologie (Dictionary of Herpetology). Klaus Kabisch. (477 pp. (1990). Gustav Fischer Verlag, Jena. ISBN 3-334-00307-8). 48.-DM (hardcover).

This dictionary (in German language) is a source of concise information on about 2,000 head-words to morphology, taxonomy, physiology, ethology and ecology of amphibians and reptiles. The depth of information varies considerably among the fields treated. The largest number of head-words pertain to the complex morphology/anatomy due to the cooperation of the author with Johannes Klapperstück. This goes to the extreme that almost every vena and arteria makes a separate head-word. Taxonomy follows with the complete account of the European herpetofauna and a selected number of exotic species. The criterion for including a non-European species is apparently not of scientific nature but oriented mainly on the interest of amateur keepers of herps. Species names are given in German and in Latin, subspecies are not mentioned. The features of the higher taxa are mentioned up to the level of families. Ethology, ecology and physiology are treated in less head-words and rather superficially due to the complex interactions in these fields and the enormous differences among species.

Despite of the large number of head-words and the broad area treated, typographical errors or unreliable information are amazingly few. However, the definition of uricotely (i.e. nitrogen excretion in form of uric acid) as a kind of parental care (irrigation of spawn with urinary bladder fluid) is certainly a serious error. There are also some minor mistakes in the geographical distribution and the behaviour of species, e.g. *Gastrotheca marsupiata.* This Peruvian marsupial frog has often been confounded with the Ecuadorian *G. riobambae* in literature, so that the information given below this head-word is a mixture of the biology of both species. This kind of error simply reflects that we still know very little about the vast majority of tropical herps. Finally, a surely personal view on the practice of naming every species treated in German. I do not feel that it makes any sense to create trivial names for widely unknown exotic species.

What is the intended readership for the dictionary of herpetology? The publishers aim at a broad range from amateur herpetologists through biology students to professional zoologists. However, only the complex morphology/anatomy reaches a level of scientific interest, whereas the treatment of the other fields often remains superficial. Considering the selection of head-words I suspect that the author himself aims at the large number of German-speaking amateur herpetologists, and I think that he is right. This book compiles a lot of information useful for people who like to know more about the exotic herps which they keep in their aquaria. Furthermore, it is of interest for the increasing number of people concerned with the destruction of habitats threatening our local herpetofaunas. Its relatively low price makes this dictionary accessible for all these people. I recommend it for those who want to learn more about amphibians and reptiles than compiled in pure field guides but do not like to read scientific text books.

Ulrich Sinsch

(2) Life History and Ecology of the Slider Turtle. J. Whitfield Gibbons — Smithsonian Institute.

Initiated by the United States Atomic Energy Commission, this book is the result of research to examine the impact on natural environments of a nuclear facility which was later expanded to include studies on the local populations of plants and animals. In particular, the influence of thermal pollution on the environment and its life forms were to be examined. Chelonians have apparently been a major study group here, particularly the slider turtle *Trachemys (=Pseudemys) scripta.* This book is about the research carried out on the animal and is based on a series of studies that can be traced back more than 20 years.

Although the book's main author is J. Whitfield Gibbons, there are in fact additional contributions from 31 other workers who, between them, have produced 368 pages of text comprised of 24 chapters covering a range of subject matter which deals, after three introductory papers, with Taxonomic Status and Genetics (4 papers), Reproduction and Growth (6 papers), Structure, Demography and Interaction amongst Populations (6 papers), Bioenergetics (4 papers) and a final concluding paper which discusses the 'Significance of Long Term Research on Long-Lived Turtles'.

In general the papers are derived from research carried out on the Savannah River Plant in the Upper Coastal Plain of South Carolina. However, included are particularly interesting discussions such as in the paper by J. D. Congdon and J. Whitfield Gibbons on 'The Evolution of Turtle Life Histories' which traces the origin of delayed maturity, relatively low mortalities and hence long life spans in chelonians to the evolution of the protective bony shell which appeared sometime in the Triassic.

A further paper on the theme of evolutionary biology is the discussion concerning 'Turtle Eggs, their Ecology and Evolution' by J. D. Congdon and J. Whitfield Gibbons. The origins of the reptilian egg can be traced to the ancient Cotylosaurian reptiles, the romerid captorhinomorphs who apparently produced a relatively naked amniotic egg rather similar to the condition found in certain modern amphibians where the eggs are deposited in a terrestrial nest and a miniature adult eventually emerges instead of the normal amphibian larvae. The authors also discuss recent work on parental investment which indicates that reptile eggs provide significant amounts of energy-giving material for maintenance and growth in the young reptile after hatching. Thus the earlier view that reptiles provide little post-natal care must now be modified; they would appear to provide such care but in a more indirect way than mammals and birds.

Probably because it is a subject that particularly interests me, I found the paper on 'Thermoregulation and Climate Space of the Slider Turtle' by J. R. Spotila, R. E. Foley and E. H. Standora very useful. In part it is a review of previous works on the subject, but they have additionally produced a climatic space diagram for *T. scripta* (a rather complex model determining the relationship between heat exchange rates of the animal and its environment). They then tested the predictions of the model with a series of experiments on *T. scripta* inhabiting ponds whose water is heated artificially as a result of being used as a coolant for plutonium reactors. This results in a series of aquatic thermal gradients which become progressively warmer with proximity to the reactors. The results were of great interest and I am sure will be familiar to researchers who have observed reptile thermoregulation in the field.

These were the papers that caught my eye, other reviewers would no doubt have drawn attention to other papers in the book, but then this is one of the major strengths of the work, its subject diversity. However, it is valuable for other reasons, not the least being that it provides a wealth of information on that much maligned species, the red-eared slider, which passes through the pet trade in enormous numbers every year. The book does much to fill gaps in our knowledge of not only terrapin biology but also reptile biology in general. The authors are to be congratulated for their efforts because anyone who reads this book will, I am sure, benefit. I certainly did, but furthermore I enjoyed reading it.

R. Meek

(3) Atlas de Repartition des Amphibiens et Reptiles de France. Compiled by J. Castanet and R. Guyetant: Société Herpétologique de France (1989). £10.00; available from the SHF, Université Paris VII, Laboratoire d'Anatomie Comparée, 2 Place Jussieu, 75231 Paris Cedex 05, France.

This new Atlas describing the distributions of all French amphibians and reptiles is a welcome successor to the Preliminary Atlas published in 1978. A foreword by the project coordinators is followed by sections on presentation, methods of data collection, lists of contributors and of species, a brief background outlining how present-day distribution patterns may have arisen, and then the bulk of the work: distribution maps and a page of accompanying text for each of 70 animals. The list includes hybrid forms (e.g. *Triturus cristatus* x *T. marmoratus*, once incorrectly ascribed to a separate species '*T. blasii*') and species which occur in France more or less by accident (some of the marine turtles washed up on beaches). Each text is written by a herpetologist with experience of the species in question 'in the field' in France, and is thus brief but authoritative. Finally there is a bibliography including more than 250 citations.

It is a most impressive work and will be invaluable to all herpetologists with an interest in French herpetofauna, from professionals to casual visitors. Records, a total of 44,200 from 1,200 contributors, are separated into those from 1950-1970, and those post-1970; they are much more complete than those in the preliminary atlas, and for most species probably give an accurate picture of current distribution at the resolution of 25km x 15km squares (for convenience, the squares were chosen on the basis of France's 1/50,000-scale map coverage). It was interesting to see how widespread natterjacks are, and how sand lizards are absent from northern and western France; the latter species makes an interesting comparison with the green lizard, which is widespread in the west and northwest and must therefore tolerate a more 'Atlantic' climate than *Lacerta agilis*. So why haven't green lizards been able to establish themselves in England?

Altogether a most pleasing publication. It does, of course, require at least a basic competence in French (or perhaps, as in my case, a member of the family to do the translation for you). There are no English summaries.

Trevor Beebee

OBITUARY
PROFESSOR ANGUS D'ALBINI BELLAIRS, 1918-1990

Angus Bellairs, who was an Emeritus Professor of the University of London and a distinguished international herpetologist, died on 26th September 1990. His passing will be sadly mourned by a very wide community of herpetologists and zoologists around the world. His death marks the end of an era, where it was possible for one man to know virtually everything about all reptiles.

Angus D'Albini Bellairs was born on 11th January 1918 and educated at Stowe School, Queen's College, Cambridge and University College Hospital, London. Interested in natural history, especially in reptiles, for as long as he could remember, he was delighted to find that it was possible to read Zoology at Cambridge in combination with the traditional medical subjects. At Cambridge, his zoological interests became directed to comparative anatomy and he was lucky enough to meet several teachers who later became lifelong friends: in particular, Dixon Boyd, Frank Goldby, Hugh Cott and Rex Parrington who as Angus later wrote 'showed in his elegant and stimulating lectures on fossil reptiles the best that the formal discipline of a university course can offer'.

When Angus graduated from Cambridge in 1939, the clouds of World War II were looming. He had already decided to study medicine and qualified in 1942. In the same year, he was called up into the Royal Army Medical Corps and found the army surprisingly less unpleasant than he had expected, and in some ways, more democratic than University life! He was posted as Medical Officer to the Fourth Divisional Engineers and his unit went almost immediately to North Africa and took part in the final battles in Tunisia: it went briefly to Egypt and then to Italy, participating in the fighting around Cassino. Angus was then suddenly posted across the world to a branch of the Army Biological Directorate at the Headquarters of General Slim's, 14th ('forgotten') Army in Burma.

This transfer carried promotion to Major. Everywhere Angus went, he collected reptiles and there was a general rumour (which he may have encouraged) that anyone in his unit who reported sick with a reptile in a tin was bound to receive a day off duty! All this reptile material was carefully preserved and sent back to Dixon Boyd in England, who tended it until after the war: many of the specimens were utilised by Angus throughout his entire subsequent career. As would be expected, this posting to the Far East afforded further opportunities for collection and also fascinating human experiences in the course of duty. One of Angus' main projects in the 14th Army was a follow up of non-commissioned soldier patients in Indian Hospitals which took him into many weird and wonderful Medical Institutions throughout the length and breadth of the sub-continent. He told wonderful stories of the alcoholic Colonel commanding an Indian Hospital who carried out his ward rounds on a bicycle when he was not shooting imaginary tigers through the window of his hut. He also remembered the capricious medical documentation of the Indian Army: an aged sepoy diagnosed as suffering from senility might be temporarily down graded to Category B for further treatment! In 1945, Angus was attached to the British Army Staff in Washington and by the strangest of military chances, Victory Day found him in Times Square, New York where he participated in celebrations, possibly reminiscent of Mafeking night in London.

Angus had long decided that his career after the War was not to be in clinical medicine and it would have been logical for him to seek a post in a Zoology Department of one of the restructuring British Universities. However, J. D. Boyd, then Professor of Anatomy at the London Hospital Medical College persuaded him that Anatomy, which at that time contained a strong tradition of comparative work, might be a suitable milieu in which to combine his zoological interests with his medical experience, and offered him a Lectureship in his Department. During his time at The London Hospital Medical College, Angus naturally paid his respects to Professor G. R. (later Sir Gavin) De Beer, the doyen of cranial morphologists in the Anatomy Department of University College London. There he met a research student, Ruth Morgan, whom he subsequently married and who is now herself Professor of Embryology in the same Anatomy Department at University College London. Their daughter, Vivien, qualified in Medicine at Oxford and is now a GP in Colchester.

In 1951, J. D. Boyd moved to the Chair of Anatomy in Cambridge and managed to take Angus with him as a Lecturer in Anatomy. However, Angus missed being in the capital, and found the high teaching loads in Cambridge tiresome. He was therefore delighted in 1953 to obtain promotion to the Readership in Anatomy (later in Embryology) at St. Mary's Hospital, Medical School, London, where he remained happily until his retirement in 1982. In 1970, Angus Bellairs was awarded a personal Chair in Vertebrate

Morphology and became an Emeritus Professor of the University of London upon his retirement.

Angus Bellairs felt deeply attached to two other major scientific institutions in the capital: The British Museum of Natural History and the Zoological Society of London. His relationship with the Zoo was a particularly happy one and since 1957, he held an honorary appointment as Consulting Herpetologist to the Zoological Society of London. He was a member of the Zoological Society's Publications Committee for many years and was a founder member of the British Herpetological Society in 1947; and for some years, Editor of its Journal, the *British Journal of Herpetology*. Both this society and the American Society of Ichthyologists and Herpetologists elected him to Honorary Membership. Angus was also a member of the Anatomical Society of Great Britain and Ireland, the Linnean Society and a Fellow of the Institute of Biology. In the year of his retirement, I organised a scientific symposium at the Zoological Society of London in honour of the occasion. It was a joint symposium, co-sponsored by the Zoological Society of London, the Anatomical Society of Great Britain and Ireland and the British Herpetological Society and well attended by leading authorities from around the world. His Festschrift (The Structure Development and Evolution of Reptiles) was published as Symposia 52 in the Zoological Society of London series by Academic Press in 1984.

Angus Bellairs made a number of scientific travels in post-war years. In 1953, he studied and collected reptiles in Algeria, during the tenure of an award from King's College, Cambridge. Then, in 1955, he obtained a Royal Society and Nuffield Foundation Commonwealth Scholarship to visit Universities in South Africa. He enjoyed the zoology, especially the crocodile watching. In 1970, he was Visiting Professor of Zoology at the University of Kuwait and as a person of the highest reputed moral integrity was put in charge of the girl students' field excursions, teaching them to handle lizards and harmless snakes without fear. In 1973, he took part in an expedition to the Galapagos Islands to study the behaviour of giant tortoises. In the early 1970s, he was instrumental, (with others) in establishing the Crocodile Specialist Group of the International Union for the Conservation of Nature and Natural Resources on which he served for some years.

He remained active in retirement. In 1985, he was an invited speaker at a major International Crocodile Conference in Darwin, Australia hosted by the Conservation Commission of the Northern Territory. Despite his advancing years, he was interested in every adventure: I have fond memories of helicopter surveys of crocodile populations with Angus Bellairs, peering out of the doorless helicopter at the reptiles beneath, and of treks in tropical swamps with Angus up to his waist in mud. He established a lasting friendship with Dr Grahame Webb, an Australian Herpetologist whose novel-writing ability he much envied. It was always Angus' post retirement ambition to write a really good novel: a herpetological thriller. He achieved this ambition in 1989, when his novel 'The Isle of Sea Lizards' was published and launched at The

First World Congress of Herpetology held at the University of Kent (11th-19th September 1989), he personally signed all of the copies. Those who read the novel will recognise it as an unusual mixture of reptile biology and university politics, two subjects which fascinated Angus Bellairs. Indeed, some colleagues may even recognise themselves (or others) under a particular pseudonym! The First World Congress of Herpetology was also a highlight for Angus as he was the Honorary President of the largest gathering of reptile experts ever assembled from around the world.

Angus Bellairs authored about 80 scientific publications, mostly on reptiles, though he also studied birds and mammals. Many of the publications were concerned with the structure and development of the skull and its associated organs. His studies on cranial morphology are summarised and embodied in a substantial monograph in the important series, 'Biology of the Reptilia', in 1981. He studied reptilian teratology and discovered cleft palate in snakes and cyclopia in turtles. He also studied regeneration of the tail in lizards, in collaboration with Susan V. Bryant, a former graduate student, now a Professor in the University of California. Another former graduate student is Professor Paul Maderson of Brooklyn College, New York, renowned for his studies on the reptilian skin.

Although Angus enjoyed scientific collaboration with his friends, he liked to think of himself as something of a loner, pursuing a little known subject in his own way and relatively independent of the vagaries of biological fashion and of grant awards. Indeed, he often referred to himself as a 'scientific antique collector'. He prepared nearly all of his own material: typed his own papers, illustrated them with his own drawings. He liked writing and authored three books, two of which ('The Life of Reptiles, Volumes 1 and 2', Weidenfeld, 1969 and 'Reptiles' (with J. Attridge), Hutchinson's University Library 1975) have been translated into numerous foreign languages. In these books, he tried to provide a synthesis of the various kinds of knowledge available about reptiles, from physiology to behaviour and he liked to paraphrase Terence in saying 'Nothing reptilian is alien to me'.

Angus Bellairs had numerous other interests, including all natural history, especially of the domestic cat which he felt showed an admirable combination of friendliness and independence, antique collecting, military history and modern fiction.

Angus Bellairs' death is a serious loss to the international reptile community. It marks the passing of a friendly, gentle, man who was always knowledgeable on some aspect of reptilian biology, no matter how idiosyncratic and who was always delighted to talk about reptiles and their biology in his unique, happy style. Angus Bellairs always reminded me of the archetypal British Professor: intelligent, well read, fascinating raconteur, mildly eccentric, extremely embroiled in his own subject, and always happy to help and encourage others.

He is survived by his wife, Ruth and their daughter Vivien, to whom we extend our deepest sympathies.

Professor Mark W. J. Ferguson

ERRATUM: Corrected Table 1 from Bullock, D. J. and Jury, H. M., Vol. 1, No. 11, pages 532-534.

| | Pitfall | Stomach | | | |
| | Volume | Volume | | Number | |
Prey type	%	X	%	X	%
Annelida					
Oligochaeta	0.0	134.9	9.6	4.6	24.9
Arthropoda					
Araneae	1.0	24.8	1.8	0.2	0.9
Opiliones	41.1	0.0	0.0	0.0	0.0
Isopoda	0.0	1.1	0.1	0.7	3.6
Diplopoda	0.4	8.0	0.6	0.1	0.3
Chilopoda	1.2	0.0	0.0	0.0	0.0
Collembola	0.1	0.0	0.0	0.0	0.0
Dermaptera	4.0	21.1	1.5	1.3	7.2
Dictyoptera	22.0	0.0	0.0	0.0	0.0
Orthoptera	18.3	15.5	1.1	0.2	0.9
Psocoptera	tr	0.0	0.0	0.0	0.0
Hemiptera (nymph)	0.1	0.0	0.0	0.0	0.0
Thysanoptera	0.1	0.0	0.0	0.0	0.0
Lepidoptera	0.0	30.7	2.1	0.4	2.4
Diptera	2.0	0.1	tr	0.1	0.3
Hymenoptera (Ants)	1.7	2.2	0.2	0.7	3.6
(Others)	0.0	4.9	0.3	0.6	3.0
Coleoptera (Adults)	7.4	526.2	37.5	3.1	16.8
(Larvae)	0.0	15.9	1.1	1.4	7.8
Mollusca					
Gastropoda	0.0	3.1	0.2	0.8	4.5
Reptilia					
Anolis oculatus	—	555.6	39.6	0.1	0.3
Others	0.5	5.1	0.4	0.5	2.7
Seed and Vegetation	—	53.9	3.8	3.8	20.7

TABLE 1: Summary of the stomach contents of *Ameiva fuscata*. Volumes measured in mm^3. 'Others' includes empty Gastropoda shells, Myrmeleontidae, Acari and unidentified items.

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 I; 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. Contributions are therefore encouraged to justify killing or vivisection carefully in relation to their work.

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