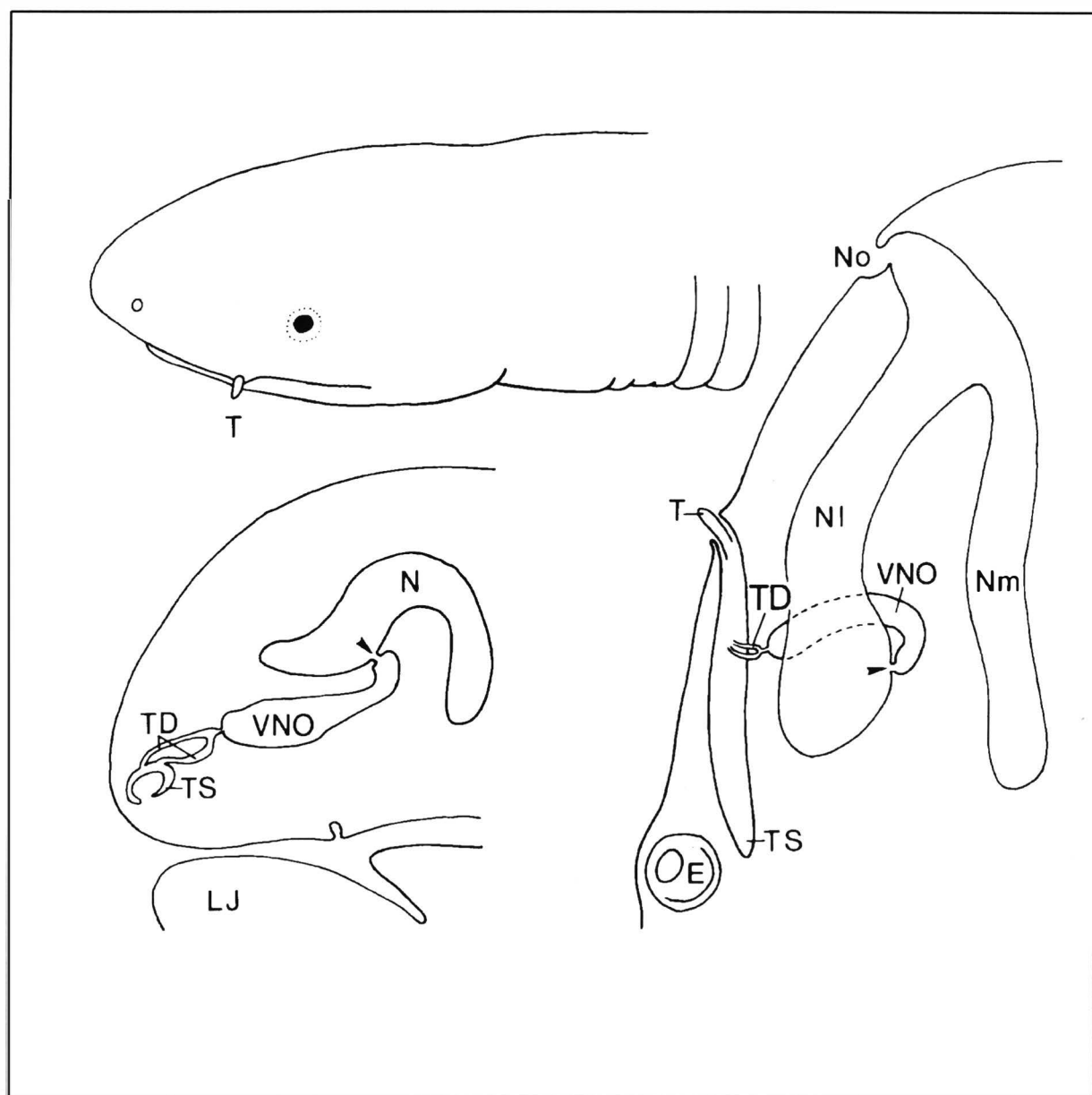


Volume 5, Number 3

July 1995
ISSN 0268-0130

THE HERPETOLOGICAL JOURNAL



Published by
THE BRITISH HERPETOLOGICAL SOCIETY

Indexed in
Current Contents

The Herpetological Journal is published quarterly by the British Herpetological Society and is issued free to members. Articles are listed in *Biological Abstracts*, *Current Awareness in Biological Sciences*, *Current Contents*, *Science Citation Index*, and *Zoological Record*.

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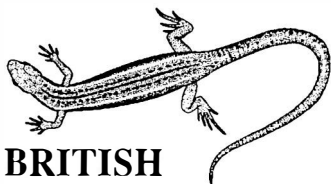
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FRONT COVER: Head and nasal cavities of *Ichthyophis kohtaoensis* (W. Himstedt & D. Simon)

PROCEEDINGS OF THE SECOND WORLD CONGRESS OF HERPETOLOGY:

FORAGING AND FOOD CHOICE SYMPOSIUM

The following four papers were presented at a symposium held at the Second World Congress of Herpetology, Adelaide, South Australia, on Monday 3 January 1994. The symposium was organized by Dirk Bauwens and Richard Griffiths. The papers have been reviewed and edited by the symposium organizers with the assistance of referees.

HERPETOLOGICAL JOURNAL, Vol. 5, pp. 245-251 (1995)

PREY SELECTION BY LACERTID LIZARDS: A SHORT REVIEW

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The vast majority of papers on optimal foraging have dealt with small, endothermic birds and mammals. Lacertid lizards are insectivorous ectotherms whose energy requirements and food consumption rates are relatively much lower. Maximizing the net rate of energy intake (profitability) may, therefore, be just an optional strategy for these small ectotherms. Nevertheless, lacertids exhibit precisely defined patterns of prey selection. They are selective in the sizes of the prey they capture, and mean prey size (but not profitability, counterbalanced by the longer times required for handling the larger prey) is a good predictor of prey selection in most of the species examined. The foraging choices of lacertid lizards represent complex behavioural responses, in which at least the following factors may be involved: (1) time constraints, related to reproductive cycles, that seem to favour time minimization in the breeding season; (2) movement minimization in the postbreeding season; (3) nutrient optimization; (4) predation risk that may force lizards to balance between the conflicting demands of feeding and avoiding danger; and (5) body temperature, whose effects on lizard performance may cause temperature dependent shifts in prey choice and feeding behaviour.

INTRODUCTION

Members of the family Lacertidae are small to medium-sized insectivorous lizards that feed on a wide variety of mainly arthropod prey but lack obvious dietary specializations (Greene, 1982). In addition, the energy requirements and food consumption rates of such lizards are an order of magnitude lower than those of similarly-sized birds and mammals (Pough, 1980; Nagy, 1983). This has favoured the opinion that lacertids are opportunistic predators and that variations in the composition of their diets reflect little more than body size constraints and differences in prey availability (Avery, 1966; Arnold, 1987; Mou, 1987). However, it is noteworthy that even lizards require food, that foraging lacertids can "decide" to eat a given food item and not another, and that such decisions can be shaped by natural selection, to allow lizards to perform as efficiently as possible in order to maximize the fitness associated with their pattern of food choice (Pyke, Pulliam & Charnov, 1977; Pyke, 1984; Stephens & Krebs, 1986).

Despite these theoretical considerations, few researchers have attempted to test the predictions of these alternative views, particularly in the case of lacertids (for studies dealing with optimal foraging in other lizard families, see e.g. Stamps, Tanaka & Krishnan, 1981; Munger, 1984; Paulissen, 1987;

Dearing & Schall, 1992). In fact, there are relatively few empirical studies that have measured prey availability in the field (but see Heulin, 1986; Pollo & Pérez-Mellado, 1988; Díaz & Carrascal, 1990, 1993; Domínguez & Salvador, 1990; Pérez-Mellado *et al.*, 1991; Martín & Salvador, 1993; Gil, Pérez-Mellado & Guerrero, 1993), and without such basic information no food selection patterns can be detected and evaluated. On the other hand, no method of measuring prey availability is free of problems (Cooper & Whitmore, 1990). Direct counts of arthropods are probably closer to the availability of prey as experienced by predators, but do not allow for quantitative estimates of prey size or energy contents (e.g. Díaz & Díaz, 1990); trapping methods yield results that depend not only on the abundance of prey but also on their behaviour (e.g. pitfall traps yield high numbers of ground-dwelling arthropods, whereas flying taxa are more easily caught in adhesive traps).

In this review, I use and reanalyse the information available in the literature, with an emphasis on the Iberian species for which there are data on prey availability. I address the following questions related to the patterns of food choice shown by lacertid lizards: (1) Are the species and populations examined selective in their food choices, or do they capture prey in proportion to their relative abundance in the environment? (2) If lacertid lizards are actually selective when mak-

TABLE 1. Rank correlations between electivity (estimated by means of Ivlev's index in its original [1961] or In Q modified form [Jacobs, 1974]) and prey size classes (1 mm and 3 mm intervals; all prey taxa pooled). The first size class with electivity index (IE) greater than 0 (i.e., the first positively selected size class), the size class with highest IE, and the maximum snout-vent length reached by each lizard species (according to Barbadillo, 1986) are also shown. References: 1: Díaz & Carrascal, 1990; 2: Domínguez & Salvador, 1990; 3: Pérez-Mellado *et al.*, 1991.

Species	Rank correlation r_s	N	P	First size class with IE > 0	Size class with highest IE	Maximum SVL	Ref.
<i>Psammodromus</i>							
<i>algirus</i>	0.700	5	> 0.10	3 - 6 mm	9 - 12 mm	8.2 cm	1
<i>Podarcis</i>							
<i>bocagei</i>	0.750	7	0.06	3 - 4 mm	5 - 6 mm	7.0 cm	2
<i>Lacerta</i>							
<i>schreiberi</i>	0.674	12	< 0.05	3 - 4 mm	11 - 13 mm	12.0 cm	2
<i>L. monticola</i>							
males	0.727	12	< 0.02	3 - 4 mm	8 - 11 mm	8.0 cm	3
females	0.573	14	< 0.05	3 - 4 mm	5 - 6 mm	-	3

ing their foraging decisions, what cues do they employ? (e.g. do they try to maximize profitability, defined as the ratio of energy per attack to the handling time per attack?) (3) Are there predictable patterns of seasonal variation in their patterns of food selection? If so, what are the ecological correlates of such seasonal changes? (4) Are nutrient constraints important for these insectivorous predators? (5) How do conflicting demands, such as increased predation risk in good foraging sites, affect their patterns of prey choice? And (6) given the fact that body temperature interacts with prey characteristics in determining handling times (Avery, Bedford & Newcombe, 1982; Van Damme, Bauwens & Verheyen, 1991; Díaz, 1994) and hence prey profitability, are there any effects of changes in body temperature on the patterns of food choice shown by lacertid lizards?

EXTENT OF SELECTIVITY AND FORAGING CUES EMPLOYED

With respect to the question of whether insectivorous lacertids are selective or not in their foraging behaviour, I examined the correlations between the relative abundance in the environment and their relative contribution to the diet of the food types consumed by four species of lacertid lizards: the Algerian sand racer *Psammodromus algirus* (Díaz & Carrascal, 1990), Schreiber's green lizard *Lacerta schreiberi* (Domínguez and Salvador, 1990), Bocage's wall lizard *Podarcis bocagei* (Domínguez and Salvador, 1990), and the Iberian rock lizard *Lacerta monticola* (Pérez-Mellado *et al.*, 1991). In all these species, the correlations were non-significant, with an average coefficient of determination of 8.9 % (SD = 9.29). A similar result was obtained by Pollo & Pérez-Mellado (1988) in a study of the feeding ecology of *Acanthodactylus erythrurus*, *Psammodromus algirus*, and *Psammodromus hispanicus* in central Spain. This

means that lizards did not eat prey taxa in direct proportion to their availability, but showed patterns of food consumption that reflected an active choice of some food types and a rejection of others.

One factor that might be important for prey selection is prey size (Díaz & Carrascal, 1990; Pérez-Mellado *et al.*, 1991). In fact, and considering all prey types pooled, the four species listed above (*P. algirus*, *L. schreiberi*, *P. bocagei*, and *L. monticola*) showed positive correlations between electivity (defined as the relationship between the proportion of a given food type in the diet and the proportion of that same food type in the environment, with both proportions computed on the basis of number of prey) and prey size (Table 1). Thus, electivity tended to increase with increasing prey length, especially for the smaller size classes. This is because all availability samples were skewed towards the smaller sizes, following the general tendency of the arthropod faunas from temperate regions (Whittaker, 1952; Schoener & Janzen, 1968), whereas lizards seldom captured prey smaller than 3 mm in length. The size class with highest electivity varied among species in a way that was roughly consistent with differences in body size (Table 1). In two of the species studied, *Psammodromus algirus* (Díaz & Carrascal, 1990) and *Lacerta monticola* (Pérez-Mellado *et al.*, 1991), lizards were more size-selective when feeding from the smaller-sized prey taxa, whereas the difference between the mean size of the prey available and consumed was not significant for the larger prey taxa. All this evidence suggests that prey size is an important cue for prey selection by lacertid lizards. As a matter of fact, the electivity scores for individual prey taxa (ants, coleopterans, etc.) were positively rank-correlated with their mean size in three of the four species: *Psammodromus algirus* ($r_s = 0.857$, $n = 7$, $P < 0.05$), *Lacerta schreiberi* ($r_s = 0.745$, $n = 12$, $P < 0.05$) and *Lacerta monticola* (males: $r_s =$

TABLE 2. Seasonal patterns of prey choice in *Psammodromus algirus*, according to data in Díaz & Carrascal (1990, 1993). Values shown are mean \pm 1 SE. e/t: profitability (net rate of energy intake).

	Breeding season (early spring)	Postbreeding season (midsummer)
Availability of prey (no. of prey/trap/week)	Low 11.8 ± 1.0	High 28.3 ± 4.2
Size of prey captured (mean dry mass, in mg)	Small 4.6 ± 0.5	Large 25.8 ± 8.1
Effect of size on prey taxa selection (r_s , n , P)	NS -0.314, 6, $P > 0.4$	significant 0.857, 7, $P < 0.05$
Effect of e/t on prey taxa selection (r_s , n , P)	significant 0.886, 6, $P < 0.05$	NS 0.607, 7, $P > 0.1$
Cue employed	profitability (ratio of energy to handling time, e/t)	prey size (gross energy intake)
Hypothesized strategy	time minimization	movement minimization
Selective pressure	save time for non-foraging activities (reproduction)	reduce no. of capture movements and hence predation risk

0.516, $n = 18$, $P < 0.05$; females: $r_s = 0.533$, $n = 18$, $P < 0.05$).

Why are large prey selected by lacertid lizards? It has been argued that the time required for handling a given item increases disproportionately with prey size, thus making profitability decline with increasing prey size (Pough & Andrews, 1985). However, the data obtained in a series of feeding experiments with *Psammodromus algirus* (Díaz & Carrascal, 1993) indicate that this is true only for prey length, but not for prey dry mass, which is a more realistic measure of energy intake. Handling time increased exponentially with prey length and linearly with prey mass, and there was no correlation between mass and profitability, either within (see Table 1 in Díaz & Carrascal, 1993) or among prey types (rank-correlation between mean dry mass and mean profitability for Araneae, Heteroptera, Orthoptera, Coleoptera, Diptera, Formicidae, and insect larvae: $r_s = 0.143$, $n = 7$, $P > 0.7$). Instead, the average profitability of a prey type was determined by the slope of the regression line relating handling time to prey mass. Controlling for size effects, soft and round-shaped arthropods were easier to handle, and hence more profitable, than hard and elongated ones (Díaz & Carrascal, 1993). It is noteworthy that Pollo & Pérez-Mellado (1988) found an active selection of the larval forms of several insect orders by *Acanthodactylus*

erythrurus, *Psammodromus algirus*, and *P. hispanicus*, and they hypothesized that these preferences could be due to the low chitin contents, large size and low mobility of such insect larvae. Nevertheless, the lack of correlation between prey size and profitability implies that the selection of the larger prey types by *P. algirus* (and, presumably, by other lacertid lizards) cannot be explained in terms of maximizing the net rate of energy intake per unit of time spent foraging.

SEASONAL VARIATION OF PATTERNS OF PREY CHOICE

Patterns of prey choice, and hence diet composition, should be regarded within the context of seasonal changes in the ecology of lizards, because both prey availability and the time budget of lizards, show seasonal variation in temperate environments. Thus, prey profitability could be important as a foraging cue, not throughout the whole activity season but at some particular times of year. An analysis that combined diet samples of *Psammodromus algirus* with pitfall-trap censuses (Díaz & Carrascal, 1993) showed that the effect of profitability on size selection within prey types was most marked in late April, decreased in mid-June and disappeared in late July. If the importance of profitability in the early breeding season was due to a time minimization strategy (Schoener, 1971; see be-

low), one would expect a pronounced effect of profitability not only on size selection *within* prey types, but also on food selection *among* prey types. A reanalysis of the data in Díaz & Carrascal (1990, 1993), which is summarized in Table 2, shows that this happened to be the case (even considering the potential biases introduced by the pitfall-based method of measuring prey availability). It should be noted that at the beginning of the breeding season the abundance of prey was low and that large prey were particularly scarce, so that the prey eaten were on average relatively small. Within this context, prey profitability had a pronounced effect on prey taxa selection, accounting for more than two thirds of its observed variance ($R^2 = 66.7\%$). Conversely, in midsummer, when reproduction was over, the absolute abundance of arthropods in the environment increased, the mean size of the prey eaten increased and the importance of profitability as a foraging cue decreased. Instead, prey size seemed to be the main cue employed in foraging decisions (Table 2; see Díaz & Carrascal, 1990).

This change of foraging cue can be explained, considering that in the breeding season the selection of the more profitable prey types, besides being consistent with the ecological context shown in Table 2, could also be related to a time minimization strategy. At this time of year, the time budget of lizards is more skewed towards reproductive activities (Díaz, Alonso-Gómez & Delgado, 1994), so that the selection of the more profitable types would allow lizards to save time for other, non-foraging activities (home-range patrolling, mate guarding, etc.). Alternatively, in the postbreeding season the selection of the larger prey, which implies maximizing the gross energy intake per capture unit, is consistent with a movement minimization strategy that would reduce predation risk. Eating large prey implies making less captures, which would be adaptive if the probability of lizards being detected by their own predators is more dependent on the number of capture movements, than on the time invested in handling the captured prey (Pough & Andrews, 1985; Díaz & Carrascal, 1993). Since lacertid lizards are easy prey for a wide variety of sympatric predators (Valverde,

1967; Martín & López, 1990), this could explain their observed general tendency towards selecting the larger prey available in the environment (Díaz & Carrascal, 1990).

NUTRIENT CONSTRAINTS AND PREDATION RISK

Most lacertids exhibit a highly diversified diet (e.g. Mellado *et al.*, 1975; Valakos, 1986; Arnold, 1987; Castilla, Bauwens & Llorente, 1991; Pollo & Pérez-Mellado, 1991; but see Pérez-Mellado, 1992; and Gil, Pérez-Mellado & Guerrero, 1993, for a discussion of the phylogenetic constraints that might explain the acute myrmecophagy of *Acanthodactylus*). This could indicate that these lizards attempt to maintain a balanced diet, as imposed by the demands of minimal amounts of certain nutrients. In the two species for which there were data on the seasonal variation of relative abundance of the prey consumed and available, *Psammodromus algirus* (see Table 3 for a reanalysis of the data presented in Díaz & Carrascal, 1993) and *Lacerta monticola* (Pérez-Mellado *et al.*, 1991), some of the major prey types had fairly constant seasonal contributions to the diet, despite considerable fluctuations in their relative abundance throughout the year. The fact that nutrient constraints may be more important than energy optimization for small insectivorous ectotherms has been invoked to explain the food selection patterns of insectivorous spiders (Miyashita, 1968; Greenstone, 1979), iguanids (Stamps, Tanaka & Krishnan, 1981; Vogel, Hettrich & Ricono, 1986), chamaeleons (Eason, 1990), and lacertids (Pérez-Mellado *et al.*, 1991). Nevertheless, the importance of nutrient constraints for lacertids remains speculative in the absence of detailed studies that should determine the nutrient contents of different arthropod groups (Pérez-Mellado *et al.*, 1991).

With respect to the effects of predation risk on the foraging tactics of lacertids, Martín & Salvador (1993) experimentally increased the vulnerability to predation of a number of Iberian rock-lizards (*Lacerta monticola*) by removing their tails (Dial & Fitzpatrick, 1981). Tailed (control) lizards foraged in grass and

TABLE 3. Seasonal variation of the relative abundance of some major prey taxa in the diet of *Psammodromus algirus* and in the corresponding samples of food availability in the environment (based on data presented in Díaz & Carrascal, 1993). It should be noted that a constant consumption of spiders and heteropterans was also found by Carretero & Llorente (1993) in a sandy coastal area of NE Spain.

	Late April	Mid June	Late July	G	P
Araneae					
% in diet	12.4	17.7	22.2	3.93	> 0.1
% in environment	17.0	18.3	5.9	63.14	< 0.001
Hemiptera					
% in diet	17.3	15.9	12.0	1.36	> 0.5
% in environment	1.9	6.6	1.3	37.19	< 0.001

shrub areas, whereas tailless animals shifted towards foraging in more protected, rocky microhabitats, with lower food availability (Martín & Salvador, 1992). Accordingly, the dietary diversity of tailless lizards decreased with respect to controls, as they specialized in the consumption of apparently suboptimal, but easy to capture, *Bibio* flies (Martín & Salvador, 1993). These findings indicate that the need to balance between the conflicting demands of feeding and avoiding danger, which has been classically illustrated in experiments with fish (Milinski & Heller, 1978; Gilliam, 1982; Werner *et al.*, 1983), may also be important for lacertid lizards.

EFFECTS OF BODY TEMPERATURE ON PATTERNS OF FOOD SELECTION

The role of body temperature in shaping the food selection patterns of lacertids has been investigated in experimental studies that have shown an exponential increase in handling times with decreasing body temperatures and an increased foraging efficiency at higher temperatures (Avery, Bedford & Newcombe, 1982; Avery & Mynott, 1990; Van Damme, Bauwens & Verheyen, 1991; Díaz, *in press*). With increasing temperature, *Lacerta vivipara* exhibited a dietary shift from small to large crickets (Van Damme, Bauwens & Verheyen, 1991) and from slow- (mealworms) to fast-moving prey (crickets) (Avery, Bedford & Newcombe, 1982). Similarly, the proportion of feeding trials in which the first prey captured by *Psammodromus algirus* was a winged (instead of a wingless) fly, tended to increase at higher body temperatures (Díaz, 1994). In the later study, the most remarkable finding was that the effects of body temperature on the predatory efficiency of lizards (capture success and distance at which successful attacks could be launched) were more clear-cut for winged prey than for wingless ones. Thus, high body temperatures might not only improve predatory efficiency, but also widen the range of prey types available under field conditions, because only at high temperatures would lizards be able to counterbalance the escape abilities of their faster fleeing prey (Díaz, 1994).

Although these studies found qualitative changes in food choice at higher temperatures, they were not specifically designed to test for the effects of temperature on food choice. For instance, it would be interesting to offer lizards a mixture of two prey "types" (large and small) in variable proportions at different temperatures and to compare the observed patterns of food selection with the results obtained in experiments using insectivorous passerines (Krebs *et al.*, 1977). At least two expectations, with important consequences from the viewpoint of foraging models, would be worth considering: at low temperatures, handling time would increase faster (and profitability would decrease faster) for the large than for the small prey, and food requirements would also vary with body temperature. Thus, lacertids (and actually most insectivorous lizards)

could help to widen the scope of foraging models by including a variable, temperature, which is of crucial importance for most (ectothermic) terrestrial animals.

In summary, the available evidence reviewed in this paper shows that insectivorous lacertid lizards have precisely defined patterns of food selection, that their foraging decisions are in no way simple, and that they provide excellent study subjects for expanding and testing all aspects of foraging theory, despite the scarcity of studies that have used them as the model predators (see review by Stephens & Krebs, 1986).

ACKNOWLEDGEMENTS

Dirk Bauwens and Richard Griffiths kindly invited me to participate in the Foraging and Food Choice Symposium held at the Second World Congress of Herpetology (Adelaide, Australia, December 1993 - January 1994). My gratitude is due to M. Díaz, L. M. Carrascal, T. Santos, and J. L. Tellería, for comments and suggestions on a previous draft, and to D. Bauwens and an anonymous reviewer for useful criticisms at the review stage.

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Accepted: 23.1.95

THE PROBLEM OF FOOD COMPETITION IN AMPHIBIANS

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Competition occurs when resources are limited and may be determined only by its effects on the component species. It must change the condition of resources and the fitness of competitors (or at least part of them) so that both are negatively affected. Original data and analysis of the literature revealed that food competition in amphibians is usually discussed in terms of (1) negative interactions between individuals; (2) density-dependent responses of individuals; (3) density-dependent responses without estimation of food resources; (4) differences in the biology of syntopic species; (5) feeding rate variability; (6) the impact of amphibians on their food resources; and (7) density-dependent responses with estimation of food resources. Food competition can only be identified in the last case, where depletion of food resources is demonstrated together with negative interactions between species. Such events have been demonstrated in some laboratory or microcosm experiments, but not in nature. Food competition appears to be rather rare in natural guilds of amphibians.

INTRODUCTION

According to Darwin, competition is regarded as one of the main forces of organic evolution. However, scientists vary in their interpretation of competition, its mechanisms and how it manifests itself in nature. Nowadays, Milne's (1961, p.67) definition of the term "competition" appears to be the most precise. According to Milne (1961), competition may be identified only by its effects in nature. These effects are reflected by both competitors and the resources upon which they rely. To become a potential subject of competition, the usable part of the resource spectrum must be limited in abundance and in its availability to consumers. In addition, the "contest" for resources must influence the condition of the competitors. Establishing a relationship between the condition of consumers and their resources is, therefore, the only practical indicator of the presence of competition between species. If resources are not limited, they can be used without competition and no negative effects on the component species will occur. If competition occurs, one or more of the competing species will suffer reduced fitness as a result of (1) less resources being available, and (2) energy used up in direct contests or interference with other competitors. Competition for limited resources may therefore result in reduced fitness of consumers. Such reduced fitness may affect all or only some of the consumers, depending on differential competitive abilities between species.

Thus, the following modification of Milne's (1961) definition has been proposed (Kuzmin & Tarkhnishvili, 1990a, p.47): "Competition is the endeavour of two or more organisms to use the same part of the resource spectrum, when resource supply in this part of the spectrum fails to meet the requirements of both or more organisms, and the endeavour leads to reduced fitness of one or more competitors".

So, there are three main criteria for identifying the presence of competition: (1) food limitation; (2) reduced fitness of consumers; and (3) a relationship between these two parameters. If one or more of these three condition cannot be identified, then competition is not unequivocally demonstrated.

Food is considered to be one of the main resources that animals compete for in nature (e.g. Schoener, 1974). Among amphibians, the presence of food competition is frequently assumed to apply. In this paper, I analyse the main evidence for this supposition in the context of the definition proposed above.

EVIDENCE FOR THE PRESENCE OF FOOD COMPETITION

The evidence for food competition in amphibians may be divided into six main types of study (Table 1). Studies which analyse similarities and/or differences in the biology of syntopic species, infer the presence of competition as a structuring force most frequently. For example, morphological, spatial, and feeding relationships (Szymura, 1974; Miller, 1978; Shlyakhtin, 1986) are often interpreted as indicators of the presence of food competition. Differences between species in these parameters are explained as evidence of past competition or as a way of avoiding competition in the present (Anderson & Graham, 1967; Passmore & Carruthers, 1979; Okochi & Katsuren, 1989, etc.). On the other hand, similarity in feeding may be interpreted as an evidence for the lack of food limitation and competition (e.g. Licht, 1986).

Such relationships may be related to food competition but cannot be regarded as unequivocal evidence for competition, because of the lack of data on resource supply or its depletion by consumers. In the absence of food limitation, amphibian trophic niches may completely overlap without competition (e.g. Kuzmin & Tarkhnishvili, 1987, 1990a,b, 1991, 1992). Food and

TABLE 1. Arguments for presence of food competition among amphibians

Argument	Taxa	Stages	Conditions	References
(1) Similarities/differences in biology of syntopic species	Ambystomatidae Plethodontidae Salamandridae Discoglossidae Bufonidae Pelobatidae Ranidae	Larvae and Adults	Natural	2/11/12/13/16/20
(2) Negative interactions of individuals	Plethodontidae Bufonidae Ranidae	Larvae and Adults	Natural and Experimental	3/4/9/14
(3) Density-dependent reactions without estimation of food resources	Ambystomatidae Plethodontidae Salamandridae Bufonidae Ranidae	Larvae and Adults	Natural and Experimental	1/10/23/24/25
(4) Feeding rate variability	Plethodontidae	Adults	Natural and Experimental	8
(5) Amphibian influences on food resources	Salamandridae Bufonidae Ranidae	Larvae	Natural and Experimental	6/15/22
(6) Density-dependent reactions in relation to food resource limitation	Ambystomatidae Plethodontidae Bufonidae Hylidae Ranidae Leptodactylidae	Larvae and Adults	Experimental	5/7/17/18/19/21/26/27/28

References: 1 - Alford & Wilbur, 1985; 2 - Anderson & Graham, 1967; 3 - Bastakov & Manteifel, 1987; 4 - Boice & Williams, 1971; 5 - Dash & Hota, 1980; 6 - Dickmann, 1968; 7 - Hota & Dash, 1981; 8 - Jaeger, 1972; 9 - Jaeger, 1979; 10 - Kleeberger, 1985; 11 - Miller, 1978; 12 - Okochi & Katsuren, 1988; 13 Passmore & Carruthers, 1979; 14 - Pisarenko, 1987; 15 - Seale, 1980; 16 - Shlyakhtin, 1986; 17 - Steinwascher, 1978a; 18 - Steinwascher, 1978b; 19 - Steinwascher, 1979; 20 - Szymura, 1974; 21 - Travis, 1984; 22 - Viertel, 1981; 23 - Wilbur, 1971; 24 - Wilbur, 1972; 25 - Wilbur, 1977a; 26 - Wilbur, 1977b; 27 - Wilbur, 1987; 28 - Wiltshire & Bull, 1977

spatial differences may result from historically fixed morphological and behavioural differences which are independent of present or past competition, e.g. in larval newt (*Triturus* spp.) and terrestrial anuran guilds (e.g. Kuzmin, 1992; Kuzmin & Tarkhnishvili, 1987, 1990a, 1992).

Evidence from studies in groups 2-4 (see Table 1), are discussed frequently. Differential density-dependent responses of amphibian larvae (Wilbur, 1971, 1972, 1977a; Alford & Wilbur, 1985); frog aggressive behaviour during feeding, and hierarchical feeding behaviour (Boice & Williams, 1971; Bastakov & Manteifel, 1987); cannibalism (Pisarenko, 1987); and feeding rate variability (Jaeger, 1972) are frequently explained in terms of food competition. Some authors (e.g. Jaeger, 1979; Kleeberger, 1985) explain salamander territoriality as the defence of food territories, i.e. the places with the highest concentration of prey in a

patchy environment. However, all these events can be sufficiently explained in other ways: density-dependent responses may, for example, be related to metabolic and behavioural regulation (Shvarts *et al.*, 1976). Different types of behavioural interactions may not depend on food supply, but may be explained in terms of territoriality, dominance behaviour, displacement responses, mistakes in feeding strikes, or defence of refugia (Wrobel *et al.*, 1980; Kuzmin & Tarkhnishvili, 1990b, 1992). Such interactions may negatively affect foraging and the physiological condition of amphibians (e.g. Grant, 1955). Cannibalism can arise when there is a rapid appearance of juveniles, which provide a short-term but more profitable food resource than other unlimited prey. Similarly, variation in feeding rate is influenced by temperature, humidity and aggressive interactions (Kuzmin & Tarkhnishvili, 1990b).

Thus, arguments presented in groups 2-4 (Table 1) are no more persuasive than non-competitive explanations, because these studies do not include data on resource depletion or consumer fitness.

Evidence from studies within group 5 (see Table 1) are more important for our discussion. Anuran tadpoles, for example, have been shown to influence the amount and diversity of periphyton and phytoplankton both in experimental (Dickmann, 1968) and natural conditions (Seale, 1980). This corresponds with data that shows that tadpole growth and developmental rates are higher in ponds with maximum phytoplankton and periphyton concentrations (e.g. Viertel, 1981). However, even in these studies, part of the food resource spectrum (e.g. bottom debris) invariably remains unestimated. In addition, density-dependent interactions between the consumers and their food supply may be unknown. Some experiments have revealed that under certain conditions, tadpoles do not compete for food even if the latter is sharply limited (e.g. DeBenedictis, 1974; Steinwascher, 1979).

Only the arguments based on studies in group 6 (Table 1), i.e. amphibian density-dependent reactions in relation to food resource limitation, may serve as evidence for the presence of food competition. Such events have been demonstrated experimentally for many urodele and anuran species. In these experiments, the influence of amphibian density has been distinguished from density-dependent food limitation. Stewart (1956) first demonstrated more rapid growth and development of well-fed *Ambystoma opacum* larvae than poorly-fed specimens reared at the same population density. Petranka (1984) demonstrated the lack of density-dependent regulation of the growth and development of *Ambystoma texanum* larvae reared with excess food and a regular change of water. In other trials, food was supplied in proportion to the density of larvae, i.e. on a per capita basis. Under such conditions larval growth and development were reduced by the low food levels, but growth inhibition was independent of larval density. It is interesting to note that variation in larval size under food competition was lower than at higher food levels (Petranka, 1984: Fig. 6). Thus interspecific competition for food did not lead to a differentiation in the size of competitors, which is the basis of trophic niche divergence in syntopic amphibians. Fraser (1976) found similar negative effects of food limitation on competing *Plethodon cinereus* and *Plethodon hoffmani*.

Competition for food has also been clearly separated from other mechanisms in laboratory trials (Wilbur, 1977b, 1987; Steinwascher, 1978a,b, 1979; Dash & Hota, 1980; Hota & Dash, 1981; Travis, 1984) and field experiments (Wiltshire & Bull, 1977) in ten species of anuran tadpoles. These experiments showed that food competition extends the duration of larval development and reduces size at metamorphosis. Variation in larval size, growth and developmental rates

has been increased, or decreased, according to species and density.

THE ECOLOGICAL AND EVOLUTIONARY SIGNIFICANCE OF COMPETITION

The problem of food competition has been discussed in many previous studies (e.g. Toft, 1985). However, it has been demonstrated clearly only in laboratory or microcosm experiments but not in nature. All the attempts to explain some natural situations as resulting from food competition were more or less speculative, and did not bring clear evidence for the unequivocal role of competition. Moreover, it is simpler to demonstrate the lack of food competition than its presence. The latter may be demonstrated only if all three conditions stated in the definition (see above) are met. If one or more of these conditions cannot be demonstrated then competition may not be in operation. For example, in many natural situations food resources may be unlimited (Degani, 1982, 1986; Kuzmin & Meschersky, 1989; Kuzmin & Tarkhnishvili, 1987; Taylor *et al.*, 1988). In such cases there will be no competition for food between amphibians.

At low population densities of amphibians, their interactions do not lead to competition. Moreover, there is some indirect evidence of the low influence (or even absence) of food limitation upon amphibian life-history regulation. For example, density-dependent effects in some situations may be sufficiently explained by abiotic factors (Travis & Trexler, 1986) or metabolic influences (Shvarts *et al.*, 1976). The density of *Ambystoma maculatum* eggs in different ponds is not correlated with the amount of food therein (Albers & Prouty, 1987). Moreover, ambystomatid salamanders can change from living in ponds to living in streams, where the food resources are scarcer (Petranka, 1984; Smith & Petranka, 1987). Studies on newts of the genus *Triturus* revealed a convergence rather than a divergence in their trophic niches (Griffiths, 1986; Kuzmin & Meschersky, 1989; Kuzmin & Tarkhnishvili, 1987); such a pattern would not be observed if food competition was operating.

Although competition for food in amphibians has never been unequivocally demonstrated in nature, it appears to be possible in some situations. Theoretically, it is most likely to occur in larvae which have a highly specialised diet, such as the "embryos" of *Salamandra* spp., oophagous tadpoles of Dendrobatidae, and so on. In such situations food competition may be a by-product of specialised reproductive strategies and must ultimately be controlled by them. However, in natural assemblages of opportunistic amphibians, food competition appears to be an unusual event, which plays a minor, or insignificant, role in their structure and dynamics.

This feature of amphibian population interactions may be related to general traits in their evolutionary ecology; those of opportunistic and unspecialised feed-

ing. This feature is based on general morphological and functional similarities in feeding mechanisms in different amphibian taxa. Probably, the main trends in resource use by amphibians have remain unchanged during the course of their evolutionary history. Indeed, an opportunistic feeding strategy may be one of the adaptations which has allowed amphibians to exploit unstable environments. In an environment consisting of a mosaic of small suitable and unsuitable microhabitats, each prey group may be limited in any one patch, but the total prey spectrum as a whole may be not limited. This would obviate selection towards food specialization and perhaps explain the scarcity of this trait in living amphibians.

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Accepted: 28.11.94

ECOLOGICAL CONSTRAINTS ON FEEDING AND GROWTH OF *SCAPHIOPUS COUCHII*

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The ecology of the desert toad, *Scaphiopus couchii*, is very precisely regulated by summer rainfall, such that emergence may be less than 20 nights/year. There are estimates in the literature that, at best, *S. couchii* can obtain its entire annual energy requirement from a single, very large meal, comprising of 50% its body weight in lipid-rich termites. However, our field data from the San Simon Valley in southeast Arizona, show that the toads are generalist feeders, taking prey groups which appear in sequence during the short summer season, including a remarkable range of noxious animals (solpugids, scorpions, centipedes and pogonomyrmid ants). Alate termites emerged briefly after the first rains and seldom represented a major component of the diet. On the other hand, beetles and other hard-bodied insects formed a consistent food type throughout the season. Alate termites represented around 24% of the total food items ingested by *S. couchii* and when prey size (length) was taken into account their contribution to the annual intake was around 20%. Beetles, on the other hand, contributed (by size) around 33% to intake, with ants representing around 19% and all other items each representing less than 8%. Differences in prey type, total food ingested and temperature all significantly influenced the weight change of individual toads fed under controlled laboratory conditions. Animals which were fed more frequently grew more rapidly, since weight increases were correlated with food intake. However, for any given intake, increases in weight were significantly lower at high environmental temperatures (31-33°C compared with 20-24°C), presumably due to increasing metabolic demands with temperature. The nutritional quality of the food significantly influenced body weight change and fat body accumulation: toads amassed excessively large fat bodies (representing up to 14% body weight) when fed with lipid-rich mealworms, compared with those fed crickets (fat bodies up to 10% body weight), and toads fed woodlice had virtually no fat bodies after eating an equivalent number of meals. These studies show that the natural prey range of *S. couchii* varies in time and space, and when toads consume high energy foods, weight increase and fat deposition are very efficient. However, the frequent ingestion of other foodstuffs, lower in calorific value, suggests that a greater number of meals are necessary to accumulate the total annual energy requirement. These other prey items may provide essential nutrients that are lacking from lipid-rich foods.

INTRODUCTION

The desert toad, *Scaphiopus couchii*, inhabits some of the most inhospitably-arid regions of America (Mayhew, 1965). In order to survive here, the toads show remarkable behavioural and physiological adaptations to an extreme environment. They escape the hostile conditions for around 10 months of the year by burrowing up to a metre beneath the ground and accumulate tissue urea to increase osmotic potential (McClanahan, 1967; Shoemaker, McClanahan & Ruibal, 1969; Ruibal, Tevis & Roig, 1969). During hibernation, they do not feed and rely wholly on stored energy reserves for survival. Activity is associated with summer monsoons and rainfall is the key factor correlated with emergence (Mayhew, 1965; Ruibal *et al.*, 1969), but temperature is also important: in parts of California where winter rains occur, *Scaphiopus* does not emerge if temperatures are below 10°C (Mayhew, 1962). At summer temperatures, activity sometimes follows light rains which only dampen the soil surface and this may occur several weeks prior to the arrival of

torrential rainfall which typically stimulates breeding (Ruibal *et al.*, 1969). Moisture in itself does not stimulate arousal of hibernating toads but the key factor for their emergence is the low frequency vibrations of rainfall on the soil surface (Dimmitt & Ruibal, 1980a). Thus, the toads are able to emerge before the surface water has penetrated the desert soil. Breeding occurs in temporary pools formed from run-off and this is the only time the toads enter large water bodies (Bragg, 1967). In southeastern Arizona, USA, the rains occur fairly predictably each year in July and August (Chew, unpublished; Tocque & Tinsley, 1991).

During the activity season, the toads occupy shallow temporary burrows in the daytime and emerge on damp nights to forage on desert invertebrates (Ruibal *et al.*, 1969; Dimmitt & Ruibal, 1980a). Breeding and feeding must take place while environmental conditions are favourable for nocturnal emergence and before the return of harsh conditions, when the toads re-enter hibernation. The amount and frequency of rainfall varies from year to year (Tinsley & Tocque, 1995) and

Tinsley (1990) estimated that in southeastern Arizona the toads have a maximum of 20 nights in the year when conditions are suitable for foraging. These environmental constraints severely restrict the period for resource accumulation and growth in desert anurans. *Scaphiopus* typically emerges to feed after long periods of dormancy and starvation. The depletion of stored reserves during hibernation is reflected by the fact that the majority of toads have virtually no fat bodies upon emergence (Seymour, 1973; Tocque, 1993). Nevertheless, a previous study (Dimmitt & Ruibal, 1980b) has determined that the feeding ecology of *Scaphiopus couchii* may be so efficient that the toads can survive one year on a single, albeit very large, meal equalling 55% of the toad's body weight and consisting solely of lipid-rich alate termites. A more realistic estimate was that a toad eating meals of half termites and half beetles, corresponding to 29% its body weight, needed just 2-3 meals to provide the total annual energy requirements.

The present studies were carried out during long-term research on the ecology and parasitology of *Scaphiopus couchii*, in a region of Chihuahuan desert scrub in southwestern Arizona, USA (Tinsley, 1990, 1993; Tocque, 1993; Tinsley & Tocque, 1995 and references therein). The aims were to estimate the overall contribution of alate termites to the toads' annual intake and to measure the effects of different food types and environmental conditions on resource accumulation. This involved analysis of gut contents throughout the entire feeding season and laboratory studies recording the voluntary intake of toads and their growth under different feeding and temperature regimes.

MATERIALS AND METHODS

NATURAL PREY RANGE

Fieldwork was carried out during 1990 and 1991 in one area of the San Simon Valley in southeastern Arizona described by Tinsley & Jackson (1988). Frequent rainstorms occurred throughout July and much of August in both these years, providing ideal circumstances for foraging by desert amphibians. Animals were collected from the desert surface on nightly excursions, along transects covering approximately 50 km. However, in 1990, collections of juvenile toads in particular were concentrated along one stretch of road running from the Arizona / New Mexico border to Portal. After capture, the toads were transferred to the Southwestern Research Station during the same night and maintained in soil-filled terraria. The following day, animals were either dissected (as part of ecological and parasitological studies; e.g. Tocque, 1993; Tinsley & Tocque, 1995) or their stomachs were 'flushed' with water until a food bolus was regurgitated. The stomach contents were weighed and preserved in 70% alcohol until prey items could be analysed. The individual items were identified with the aid of field guides (White, 1983; Borro & White, 1970) and museum

specimens of the Southwestern Research Station, and were assigned to size classes based on body length.

LABORATORY FEEDING EXPERIMENTS

Animals collected in the San Simon Valley were transported to the UK by air freight during August and were maintained in soil-filled terraria at relatively low temperatures (15-20°C) until the start of feeding experiments. Prior to feeding, the toads were weighed (after removal of urine by catheter) and randomly assigned to different groups (see below and Table 3). Each toad was maintained individually in a plastic tube partially filled with moist soil and with a perforated base to allow water uptake (Tinsley & Earle, 1983) and moved to a controlled environment room two days before feeding commenced. Groups of toads were fed according to the following regimes:

Experiment 1 : The effect of temperature. Male and female toads were maintained at either 20 or 33°C and fed with laboratory-raised crickets approximately every three days (a total of 16 meals in 51 days).

Experiment 2 : The effects of temperature and feeding rate. Male and female toads were maintained at either 24 or 31°C and fed with laboratory-raised crickets, either once a week (a total of 6 meals in 42 days) or four times a week (a total of 24 meals in 42 days).

Experiment 3 : The effect of food quality. Male and female toads were maintained at 25°C and fed with either laboratory-raised crickets or mealworms or wild-caught woodlice every other day (a total of 28 meals in 56 days).

At each feeding session, individual toads were removed from their soil-filled tubes and transferred to plastic aquaria (50 x 60 x 80 cm), with a number of pre-weighed food items. The animals were then left to feed at their maintenance temperature under lighted conditions (with the exception of animals at 31°C in Experiment 2, which were fed in the dark) for two hours. After this time, the toads were washed to remove any urine, which otherwise burns the delicate skin, returned to their individual tubes and remained undisturbed until their next feed. The food items remaining in each aquarium were recovered and re-weighed to determine the amount eaten by each animal. Several days after the end of the feeding period, each toad was weighed and animals from Experiment 3 were dissected after a further two weeks (during which they were maintained at 10-15°C) to determine fat body weights.

RESULTS

PREY SELECTION IN THE DESERT ENVIRONMENT

The range of prey items found in the combined sample of stomach contents from 158 animals collected in 1990 and 1991 shows the opportunistic nature of *S. couchii* feeding (Table 1). The toads were typically generalist insectivores with a wide range of genera ingested but arachnids were also a major food source.

TABLE 1. The total contribution of different prey types to the nutrition of *Scaphiopus couchii* during the entire feeding season (data collected in July/August, 1990 and 1991).

Prey item	Common name used in text	% of total food items (n = 2180)	% toads eating item (n=158)	Mean No. items ingested	Mean length of food item (cm)	^a Relative contribution to annual intake (%)
Order & Family						
<i>Insecta</i>						
Coleoptera:	Beetles:					
Carabidae	Ground	0.83	8.23	1.38	0.75	0.82
Cicindelidae	Tiger	0.05	0.63	1.00	0.75	0.05
Curculionidae	Weevil	1.74	17.09	1.41	0.58	1.33
Elateridae	Click	2.71	7.59	4.92	0.77	2.74
Eucnemidae	False-click	0.05	0.63	1.00	0.75	0.05
Scarabidae	Scarab	17.20	59.49	3.99	0.70	15.83
Pairs elytra		11.70	49.37	3.27	0.70	10.78
Unknown		0.83	8.23	1.38	0.90	0.98
Diptera	Flies	0.28	3.80	1.00	0.56	0.20
Hemiptera	Bugs	1.42	17.09	1.15	0.80	1.50
Homoptera	Hoppers	0.32	4.43	1.00	1.00	0.42
Hymenoptera:						
Scolioidae	Ants					
alates		5.92	13.92	5.86	0.78	6.07
workers		5.73	18.35	4.31	0.36	2.72
heads only		11.83	40.51	4.03	^b 0.62	9.66
Apoidae	Bees	0.41	3.80	1.50	0.75	0.41
Isoptera:	Termites					
alates		24.27	8.86	37.79	0.61	19.49
workers		1.51	1.90	11.00	0.25	0.50
Lepidoptera	Caterpillars	2.52	17.72	1.96	1.95	6.47
Neuroptera	Lacewings	0.14	1.90	1.00	1.00	0.18
Orthoptera:						
Gryllidae	Crickets	3.94	37.97	1.43	1.42	7.37
Phasmatidae	Stick-insects	0.55	7.59	1.00	1.25	0.91
Mantidae	Mantids	0.14	1.90	1.00	1.25	0.23
Insect larvae		0.09	1.27	1.00	1.00	0.12
<i>Arachnida</i>						
Araneida	Spiders	1.65	15.19	1.50	0.53	1.15
Acarina	Mites	0.83	5.70	2.00	0.75	0.82
Chelonethida	Pseudoscorpions	0.05	0.63	1.00	0.25	0.02
Phalangida	Harvestmen	0.05	0.63	1.00	0.25	0.02
Scorpionida	Scorpions	0.23	3.16	1.00	2.75	0.83
Solpugida	Solpugids	2.75	29.11	1.00	1.72	6.23
<i>Chilopoda</i>	Centipedes	0.28	3.80	1.00	5.75	2.08
<i>Reptilia</i>						
Teiidae	Whiptail lizard	0.05	0.63	1.00	-	-

^a calculated from the average length and the relative occurrence of individual food items.

^b calculated as the average length of all ants

Beetles (scarabs and weevils in particular) formed the most substantial prey and were eaten by 83.3% of toads and represented 35.1% of food items. Ants, Orthoptera (particularly crickets) and solpugids were ingested by 57.9, 44.7 and 29.1% of toads (representing 23.5, 4.6 and 2.8% of food items), respectively. Several other food groups were also eaten by over 15% of toads: these were caterpillars, bugs and spiders. Alate termites were only eaten by 8.9% of toads but they represented 24.3% of food items since they were consumed in large numbers: a maximum of 200 items ingested per animal (average 37.8 termites/toad). Some prey types, such as, worker termites, lacewings, mantids, pseudoscorpions, harvestmen and some beetles were consumed rarely (by less than 2% of toads) which reflected either their low abundance or chance encounters. The most interesting of these occurrences was the ingestion of a hatchling whiptail lizard (*Cnemidophorus* sp.) by one animal. A range of particularly noxious animals was ingested by *S. couchii*, including, solpugids, scorpions, centipedes and pogonomyrmid ants.

From the combined data, the average contribution (by size) of different prey types to the intake of *S. couchii* during the entire feeding season has been estimated (Table 1). In total, beetles represented 32.6%, alate termites 19.5%, ants 18.5%, crickets 7.4%, caterpillars 6.5% and solpugids 6.2% of the overall prey intake.

A total of 81 toads was collected along Portal road throughout July and August, 1990, which provided an indication of the change in prey availability over the entire feeding season (Table 2a,b). The prey types eaten most frequently (scarabs, crickets, ants, spiders, weevils and solpugids) were found consistently throughout the two month feeding season (ingested by at least 55%, 30%, 20%, 13%, 13% and 12.5% of toads, respectively). However, alate termites were confined to the first week following the onset of the summer rains (in the second week of July), when they represented a major food source and were consumed by 33% of toads. Another group of toads ($n = 12$) was also collected in the second week of July, less than 5 km away, but not a single animal had eaten termites. No alate termites were ingested during the subsequent five weeks of *S. couchii* activity. Similarly, alate ants were eaten in abundance following the first rains and decreased dramatically thereafter. Flies, bees, mites, pseudoscorpions and mantids also decreased in occurrence after the first week of rain. By contrast, caterpillars, lacewings and unidentified beetles were ingested in increasing numbers and by a greater proportion of toads as the summer season progressed.

FOOD INTAKE AND GROWTH UNDER LABORATORY CONDITIONS

The effects of varying prey type, as well as feeding rate and temperature, on weight changes and resource accumulation were investigated under controlled laboratory conditions. There was no consistent difference

between the intake and weight changes of male and female toads. In some groups, males consumed more and increased in weight more than females and in others the reverse occurred. Therefore, the sexes have been combined for the following analysis (Table 3). The total intake of laboratory-raised crickets increased as the number of meals eaten increased: overall means of 7.8, 21.2, 38.3 and 41.2 g of food were ingested by toads fed 6, 16, 24 and 28 meals, respectively. There was a corresponding increase in the average weight change of the animals with increasing intake: 2.4, 5.2, 12.5 and 17.5 g, respectively.

The influence of feeding rate and temperature. In Experiment 2, toads were fed either 6 or 24 times over the same time period. There was little obvious effect of these different feeding rates on the efficiency of food conversion, since animals increased in weight by 1 g after eating around 3.0 and 2.6 g of food, respectively, at 24°C and 3.8 g in both groups at 31°C. However, intake varied considerably between individuals and temperatures. In Experiment 1, the toads fed at 33°C ate more than those fed at 20°C (Table 3) whereas in Experiment 2, the toads ate less at the higher temperature (presumably because they were fed in the dark). Therefore, since toad size varied as well as intake, the efficiency of food conversion at different temperatures was analysed as the relationship between intake and weight change relative to initial body weight (Fig. 1). In both Experiments 1 & 2, for any given intake, toads showed smaller weight increases at the higher temperature. Multiple analyses of covariance (with intake as the covariate), showed that weight changes were significantly different between the temperatures in both experiments ($F = 4.76$, $P < 0.05$ and $F = 8.39$, $P < 0.01$, respectively). The difference between temperatures was more pronounced as the toads ate more. This was especially true in Experiment 2 (Fig. 1b) for which there was no significant difference between weight changes at the different temperatures in toads fed once a week ($F = 0.24$, $P > 0.6$; Fig. 1).

The influence of prey type. Toads fed with mealworms ate around the same weight of food as those fed with crickets over the same period (Experiment 3) but woodlice were not readily eaten by *S. couchii* (see Table 3). Weight changes were slightly greater in toads eating mealworms compared with those eating crickets but there was wide individual variation in intake, such that some toads trebled in weight during the eight week period. The animals eating woodlice did not, on average, increase in weight despite eating a mean of 11.5 g of food (Table 3). In fact, half these toads lost weight during the experiment. The relationship between relative intake and weight change (Fig. 2) shows that mealworms were converted to body weight more efficiently than crickets (MANCOVA: $F = 9.74$, $P < 0.01$) and woodlice provided a very poor diet for the toads compared with crickets (MANCOVA: $F = 10.88$, $P < 0.01$).

TABLE 2 (a). The prey intake of *Scaphiopus couchii* ($n = 81$) collected from Portal Road over the entire feeding season in 1990, represented as the percentages of total prey items eaten.

		Occurrence of prey (% total prey items)			
Prey item		7-13 July (<i>n</i> = 766)	14-29 July (<i>n</i> = 318)	3-13 Aug (<i>n</i> = 123)	14-22 Aug (<i>n</i> = 114)
<i>Insecta</i>					
Coleoptera:					
	Carabidae	0.0	0.0	0.81	0.0
	Cicindelidae	0.0	0.31	0.0	0.0
	Curculionidae	0.52	2.2	2.44	7.89
	Elateridae	0.13	15.09	1.63	0.0
	Eucnemidae	.013	0.0	0.0	0.0
	Scaribidae	12.14	31.45	24.39	30.7
	Pairs elytra	2.61	16.35	22.76	16.67
	Unknown	0.0	0.63	3.25	3.51
Diptera		0.39	0.31	0.0	0.0
Hemiptera		0.52	3.14	2.44	0.88
Homoptera		0.26	0.0	1.63	1.75
Hymenoptera:					
	Scolioidae				
	alates	15.14	0.31	0.0	0.0
	workers	2.87	5.98	2.44	3.5
	heads only	18.54	7.86	4.88	3.51
	Apoidae	0.91	0.0	0.0	0.0
Isoptera:					
	alates	32.25	0.0	0.0	0.0
	workers	3.79	0.0	0.0	3.51
Lepidoptera		0.26	6.6	11.38	10.53
Neuroptera		0.0	0.0	0.81	1.75
Orthoptera:					
	Gryllidae	1.31	3.14	6.5	7.89
	Phasmatidae	0.13	0.63	0.0	0.0
	Mantidae	0.26	0.31	0.0	0.0
Insect larvae		0.0	0.0	0.81	0.88
<i>Arachnida</i>					
Araneida		1.83	1.89	4.88	1.75
Acarina		1.83	0.0	0.0	0.0
Chelonethida		0.13	0.0	0.0	0.0
Scorpionida		0.0	0.63	0.81	0.0
Solpugida		0.91	3.14	7.32	5.26
<i>Chilopoda</i>					
		0.13	0.0	0.81	0.0

Accumulation of stored reserves. Animals from Experiment 3 were dissected to determine the weight of fat body accumulated after feeding with different food types. Despite the fact that toads ate, on average, similar weights of crickets and mealworms (Table 3), the fat bodies of those fed mealworms were considerably heavier (Table 4): animals eating crickets had fat bodies weighing to up to almost 10% of their body weight but those fed lipid-rich mealworms had fat bodies weighing up to 14% of

their body weight. The amount of fat body amassed was positively correlated with intake ($R^2 = 0.69$, $F = 15.4$, $P < 0.01$ and $R^2 = 0.59$, $F = 7.10$, $P < 0.05$, for crickets and mealworms, respectively) but the efficiency of fat accumulation was almost three times greater in toads eating mealworms compared with those eating crickets (Table 4). Toads eating woodlice did not accumulate fat and probably utilised previously stored fat body during the experiment.

TABLE 2 (b). The prey intake of *Scaphiopus couchii* collected from Portal Road over the entire feeding season in 1990, represented as the percentages of toads ingesting each prey item.

		Occurrence of prey (% toads eating each item)			
Prey item		7-13 July (n = 24)	14-29 July (n = 23)	3-13 Aug (n = 20)	14-22 Aug (n = 14)
<i>Insecta</i>					
Coleoptera:					
	Carabidae	0.0	0.0	5.0	0.0
	Cicindelidae	0.0	4.4	0.0	0.0
	Curculionidae	12.5	26.1	15.0	28.6
	Elateridae	4.2	17.4	10.0	0.0
	Eucnemidae	4.2	0.0	0.0	0.0
	Scaribidae	75.0	91.3	55.0	71.4
	Pairs elytra	45.8	78.3	40.0	50.0
	Unknown	0.0	8.7	10.0	14.3
Diptera		12.5	4.4	0.0	0.0
Hemiptera		16.7	39.1	10.0	7.1
Homoptera		8.3	0.0	10.0	14.3
Hymenoptera:					
	Scolioiðae				
	alates	66.7	4.4	0.0	0.0
	workers	45.8	21.7	10.0	21.4
	heads only	62.5	52.7	20.0	28.6
	Apoidae	16.7	0.0	0.0	0.0
Isoptera:					
	alates	33.3	0.0	0.0	0.0
	workers	8.3	0.0	0.0	7.1
Lepidoptera		8.3	21.7	50.0	35.7
Neuroptera		0.0	0.0	5.0	14.3
Orthoptera:					
	Gryllidae	41.7	30.4	30.0	50.0
	Phasmatidae	4.2	8.7	0.0	0.0
	Mantidae	8.3	4.4	0.0	0.0
Insect larvae		0.0	0.0	5.0	7.1
<i>Arachnida</i>					
Araneida		41.7	13.0	20.0	14.3
Acarina		29.2	0.0	0.0	0.0
Chelonethida		4.2	0.0	0.0	0.0
Scorpionida		0.0	8.7	5.0	0.0
Solpugida		12.5	39.1	35.0	21.4
<i>Chilopoda</i>					
		4.2	0	5	0

DISCUSSION

For any terrestrial amphibian, activity and foraging take place only when environmental conditions are suitable: generally when it is wet and warm enough for emergence (Poynton & Pritchard, 1976; Toft, 1980; Galatti, 1992). For a desert anuran, such as *Scaphiopus couchii*, the occurrence of these conditions is more limited than for most other amphibians. It has already been determined that *S. couchii* ingests a wide range of invertebrate prey but takes advantage of the mass

emergence of alate termites, enabling efficient accumulation of lipid reserves (Dimmitt & Ruibal, 1980*b*). Our data confirm the generalist nature of *S. couchii* feeding patterns, with a wide range of prey types being ingested (Table 1). However, the collection of gut contents throughout the entire feeding season has shown that the prey ingested varies throughout the activity season, presumably reflecting variations in invertebrate abundance. Some prey types were eaten consistently throughout the two month feeding season (scarabs, crickets, ants, spiders, weevils and solpugids)

TABLE 3. Food intake and weight changes of *Scaphiopus couchii* maintained at different temperatures and feeding regimes. Values show means (with standard deviation in parentheses) and range for percent weight change.

Expt. No.	n	Total No. of meals	Duration of feeding (days)	^a Food type	°C	Starting body weight (g)	Total weight of food eaten (g)	Change in body weight (g)	Percent weight change (%)
1	8	16	51	Cr	20	21.9 (6.2)	24.3 (10.6)	5.3 (2.8)	9-38
	8	16	51	Cr	33	22.6 (6.6)	28.8 (12.5)	6.2 (3.4)	13-60
2	10	24	42	Cr	24	20.3 (4.2)	41.8 (12.8)	15.9 (5.7)	43-123
	10	24	42	Cr	31	21.7 (5.2)	34.9 (9.5)	9.2 (2.7)	31-58
	10	6	42	Cr	24	21.2 (4.0)	8.8 (5.0)	2.9 (3.1)	-12-37
	10	6	42	Cr	31	24.7 (6.6)	6.9 (3.7)	1.8 (2.0)	1-33
3	9	28	56	Cr	25	21.0 (6.8)	41.2 (15.5)	17.5 (6.8)	25-204
	8	28	56	Mw	25	21.1 (4.5)	43.0 (14.9)	24.9 (9.4)	63-217
	6	28	56	Wl	25	21.8 (6.8)	11.5 (6.0)	0.3 (2.9)	-14-30

^a Cr = crickets; Mw = mealworms; Wl = woodlice

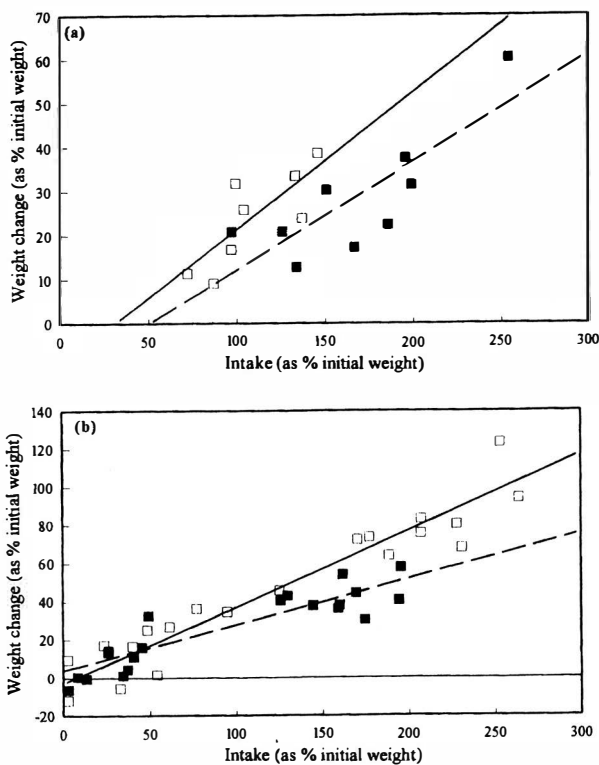


FIG. 1. The effect of temperature on the weight change of *Scaphiopus couchii* fed (a) 16 meals in 51 days at 20°C (open squares, solid line $R^2 = 0.94$, $F = 103$, $P < 0.001$) or 33°C (filled squares, dashed line $R^2 = 0.92$, $F = 97.6$, $P < 0.001$) and (b) 6* or 24 meals in 42 days at 24°C (open squares, solid line $R^2 = 0.91$, $F = 173$, $P < 0.001$) or 31°C (filled squares, dashed line $R^2 = 0.65$, $F = 32.7$, $P < 0.001$). * toads fed 6 meals consumed equivalent to less than 100% their body weight.

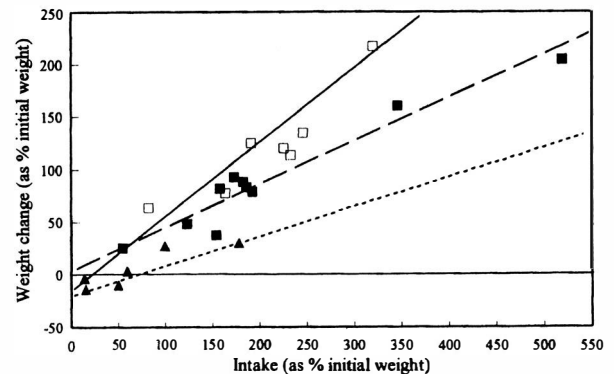


FIG. 2. The effect of food quality on the weight change of *Scaphiopus couchii* fed with crickets (open squares, solid line $R^2 = 0.98$, $F = 494$, $P < 0.001$), mealworms (filled squares, dashed line $R^2 = 0.98$, $F = 293$, $P < 0.001$) or woodlice (filled triangles, dotted line $R^2 = 0.59$, $F = 7.3$, $P < 0.05$) at 25°C.

but others increased in abundance with time (caterpillars, lacewings and unidentified beetles); and some were present only after the first rains and decreased dramatically afterwards (alate ants, mites, bees, pseudoscorpions and mantids). This was also true for alate termites which were ingested only in the second week of July in 1990 and not at all in the following 5 weeks of toad activity.

The opportunities for feeding on high energy foodstuffs are a direct result of localised thunderstorms which stimulate insect reproductive flights: both temporal and spatial constraints influence the ingestion of alate termites by *S. couchii*. Thus, the toads cannot rely on the presence of such prey items to ensure that they eat a few high energy meals. Harder-bodied inver-

TABLE 4. Variation in fat body accumulation by *Scaphiopus couchii* fed with different food types.

Food Type	N°of meals	Duration of feeding (days)	°C	Intake (as % of initial body weight)	Fat body weight (as % of final body weight)	*Mean fat body accumulation efficiency (%)
Crickets (<i>n</i> = 9)	28	56	25	54 - 519	2.6 - 9.8	3.7
Mealworms (<i>n</i> = 9)	28	56	25	82 - 320	6.1 - 14.2	10.6
Woodlice (<i>n</i> = 5)	28	56	25	14 - 178	0.02 - 0.09	0.2

* calculated as fat body weight (g) as a percentage of intake (g)

tebrate prey (particularly beetles but also ants, crickets and solpugids) are more reliable in occurrence throughout the summer but these represent an inferior energy source (Dimmitt & Ruibal, 1980b). The toads may ingest one or two meals composed of large numbers of alate termites in the first week of the summer season but thereafter intake consists of foodstuffs with lower calorific values. Over the entire feeding period, alate termites represented around 24% of the total number of food items ingested. Given their smaller size, compared with beetles and crickets for instance, their actual contribution to nutrition may be less than this. Based on prey length, it is estimated that alate termites contribute 19.5% to the entire annual intake of *S. couchii*, with beetles, ants, crickets, caterpillars and solpugids contributing 32.6, 18.5, 7.4, 6.5 and 6.2%, respectively. However, the calorific and nutritive value of the different prey cannot be determined from the present study. The occurrence and distribution of termite swarms is likely to vary from year to year since environmental conditions promoting their, and other invertebrate, emergence also vary considerably from year to year (Tinsley & Tocque, 1995). These annual variations are also evident in the natural growth patterns of *S. couchii*, presumably because of variations in prey abundance and foraging opportunities (Tocque & Tinsley, submitted).

Varying the quality of prey items significantly influenced resource accumulation by *S. couchii* under controlled laboratory conditions, as did varying environmental temperature. However, the efficiency with which food was converted to body weight seemed to be regardless of feeding rate, since weight changes were proportional to total food intake whether toads were fed once or four times a week. The fact that there was a significant decrease in weight changes as temperature increased is to be expected for an amphibian in which the metabolic rate increases with environmental temperature (McClanahan, 1967; Seymour, 1973). Presumably a greater proportion of absorbed energy is utilised for maintenance at higher temperatures (31-33°C) than at lower temperatures (20-24°C). Bush (1963) found that *Bufo fowleri* did not amass more lip-

id at 31°C compared with 21°C but did convert more food to lean tissue. It seems unlikely that this was the case for *S. couchii*, since the conversion of food to body weight was significantly lower at higher temperatures than at lower temperatures (Fig. 1). In the present study, animals were continuously maintained at the same temperature during the feeding period but under natural conditions the toads feed at cooler night time temperatures (average 20°C) and remain in temporary burrows during higher daytime temperatures (average 34°C) (Ruibal *et al.*, 1969; Tocque & Tinsley, 1991). It is not known how fluctuating daily temperatures would affect metabolic energy demands, digestion efficiency or resource accumulation.

By far the greatest influence on weight changes and the accumulation of fat bodies, was the type of the food ingested. Toads fed crickets and mealworms, at 25°C, ate similar amounts of food but weight increases were greater in animals fed mealworms, and fat body was amassed three times more efficiently than by toads eating crickets. Woodlice, on the other hand, proved to be an inferior food source: animals eating them did not increase in weight and virtually no fat was accumulated. A similar relationship between food quality and weight change has been observed in juvenile *Bufo woodhousei*, for which lipid-rich mealworms produced the greatest growth (Claussen & Layne, 1983). In juvenile *B. bufo*, feeding with mealworms leads to excessive fatness since lipid deposition predominates over protein deposition (Jørgensen, 1989). The lipid content (wet weight) of mealworms may be as high as 16% compared with 10-11% in crickets and beetles (Dimmitt & Ruibal, 1980b). However, mealworms are known to be low in digestible calcium (Mattison, 1993). Fat reserves, which provide all the energetic needs of spadefoot toads during their long hibernation (Seymour, 1973; Dimmitt & Ruibal, 1980b), may be accumulated more effectively when the toads feed on lipid-rich food but it is not known how a nutrient imbalance may adversely effect the growth of other tissues, such as gonad or bone.

The desert environment provides only a short summer season during which conditions are suitable for

Scaphiopus couchii activity and feeding. Erratic environmental conditions during this period limit the occurrence of high energy foodstuffs in both time and space and other harder-bodied prey are ingested consistently throughout the feeding season. The toads show an exceptional ability to accumulate their annual energetic reserves in the form of excessively large fat bodies when ingesting lipid-rich foods. However, the opportunistic nature of feeding and the ingestion of a large variety of prey is likely to provide other essential nutrients which may be lacking from a diet restricted to alate termites.

ACKNOWLEDGEMENTS

The considerable time and effort of Charlotte Henderson and Beverley Brayson for help with the feeding and maintenance of toads is greatly appreciated. We are also grateful to Drs. Stephan Cover and Doug Eifler for the identification of some prey items. Fieldwork facilities were provided by Southwestern Research Station of the American Museum of Natural History and financial support by the Natural Environment Research Council.

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Accepted: 23.1.95

SENSORY BASIS OF FORAGING BEHAVIOUR IN CAECILIANS (AMPHIBIA, GYMNOPTERON)

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The caecilian *Ichthyophis kohtaoensis* is able to localize prey objects by chemical cues only. On the surface of the ground *I. kohtaoensis* moves faster and on a more direct path towards prey than does the newt *Triturus alpestris*. Blocking the tentacles in the caecilian does not impair this ability. Within artificial tunnels, however, caecilians with blocked tentacles took longer to reach the prey than control animals did. Blocking the nostrils led to complete failure of prey localization on the surface of the ground.

INTRODUCTION

Compared to other amphibian groups, caecilians (Gymnophiona) are rather poorly investigated. The subterranean mode of life makes these limbless tropical animals relatively inaccessible. It is extremely difficult to observe their behaviour and to study sensory physiology. We keep *Ichthyophis kohtaoensis* (Family *Ichthyophiidae*) in our laboratory and have begun to investigate sensory functions involved in feeding behaviour. As in other caecilian species the eyes of *I. kohtaoensis* are rather small (about 0.5 mm in diameter) and they are covered by skin. Vision does not guide feeding; the only visually guided behaviour in *I. kohtaoensis* is a negative phototaxis (Himstedt & Manteuffel, 1985). In front of each eye caecilians possess a tentacle. This organ is unique among vertebrates and is possibly involved in tactile and chemoreceptive functions. The structure of the tentacle skin suggests a

tactile function (Fox, 1985). During development, the tentacle is constructed from parts of the eye muscles and nerves, and of the accessory eye glands (c.f. Engelhardt, 1924; Billo & Wake, 1987; Wake, 1993.) Tentacle ducts connect the tentacle sac to the vomeronasal organ (Fig. 1) and it is presumed that by means of this path substances from the surrounding medium may be transported to the olfactory epithelium (c.f. Badenhorst, 1978; Billo, 1986). Until now, however, there is no experimental evidence for function of the tentacle. Therefore it was the aim of this study to investigate a possible role of the tentacle in identifying and localizing prey objects.

MATERIAL AND METHODS

Adult specimens of *I. kohtaoensis* were collected in north-eastern Thailand and kept in terraria in moist soil and moss at about 27°C and a 12 hr : 12 hr light-dark cycle. They were fed earthworms and pieces of meat. For experiments, 10 specimens (about 18 to 20 cm total length) were kept individually in perspex boxes measuring 25 x 20 cm, 13 cm height filled with soil 10 cm deep. The soil was covered by a perspex plate with a central hole 1 cm in diameter. This hole was the only exit to the surface. During experiments, animals were fed daily at the beginning of the dark phase, with one piece of meat (bovine heart) weighing 0.05 g. This meat was placed on top of the perspex surface, and during four to five weeks the caecilians learned to search for food outside their burrows on the surface after "sunset". During experiments the perspex plate was covered by a sheet of paper and the piece of meat was placed in one corner of the rectangular surface, 12 cm away from the central hole. The corners were changed in random sequence, and the paper was replaced after each trial.

Searching and feeding behaviour were observed and recorded under infra-red illumination, by means of an infra-red sensitive video camera (Fig. 2). The paths of the experimental animals could be tracked on a monitor screen so that the time and the length of path from the exit hole to the target were recorded. In control experiments each animal was presented with a prey target 10 times. Subsequently, the tentacles were

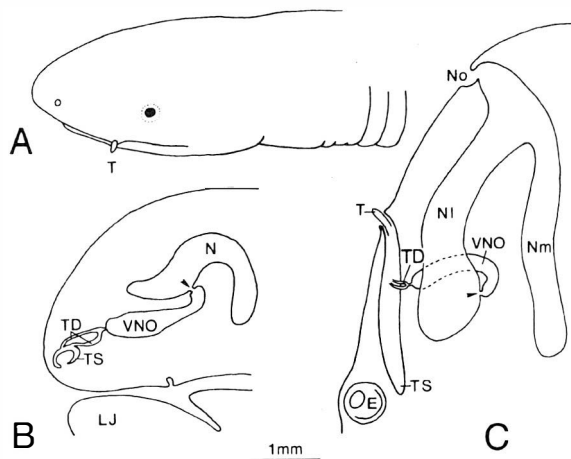


FIG. 1. Anatomy of nasal cavities and tentacle apparatus in *Ichthyophis kohtaoensis*. A. Lateral view of the head; between eye and nostril, the tentacle is visible. B. Cross section at the level of the tentacle ducts. C. Dorsal view of the nasal cavities. Abbreviations: E = eye; LJ = lower jaw; N = nasal cavity; Nm = nasal cavity, medial part; NI = nasal cavity, lateral part; No = nostril; T = tentacle; TD = tentacle ducts; TS = tentacle sac; VNO = vomeronasal organ: The arrowhead points to the connection between nasal cavity and vomeronasal organ.

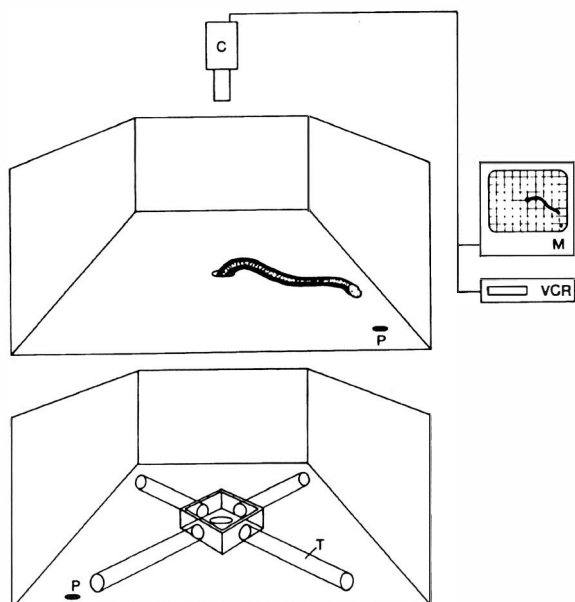


FIG. 2. Diagram of the experimental set-up to test chemical orientation. Above: on the surface of the ground. Below: in a tube system. C = Video camera; M = monitor; P = prey object; T = glass tubes; VCR = video cassette recorder.

blocked by closing the tentacle opening with a surgical glue (Histoacryl®). After three days, the glue scaled off the skin and the tentacles could be protruded as before. Experiments with blocked tentacles were likewise performed 10 times on each animal. In other experiments, the nostrils were blocked by filling the external and internal nostrils with a two-component polyvinyl (Dentagum®, a dentist's material for taking impressions). The tentacle and vomeronasal organ were not influenced by this treatment. After an experiment the plugs were removed with fine forceps.

In order to compare the ability of *Ichthyophis* to localize prey objects by means of chemical cues, with that of other amphibians, adult terrestrial newts of the species *Triturus alpestris* were tested in the same experimental situation. Ten newts were fed in darkness with pieces of meat as described above for *Ichthyophis*. During experiments, a newt was placed in the center of a rectangular box, with the prey object in a corner 12 cm away from the animal's head.

In another series of experiments caecilians were not tested on the surface of the ground but within tubes (Fig. 2, below). Here a situation was simulated in which a caecilian follows a prey within its tunnel. After leaving the exit hole, the animal had the choice to enter one of four glass tubes leading to the four corners of the test box. One of the tubes was scented by pulling the piece of meat through it so that the inner wall of this tube was contacted by the odorous substances. After each trial the tubes were cleaned thoroughly. In this setup each of the ten experimental animals was tested 10 times as controls and 10 times after blocking the tentacles.

The Wilcoxon matched-pairs signed-ranks test was used to compare samples.

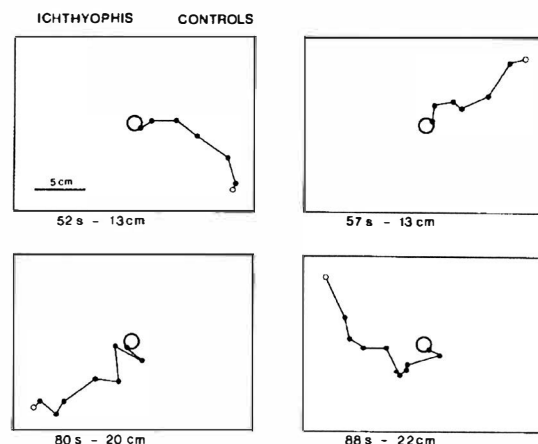


FIG. 3. Examples of paths of four control animals (*I. kohtaoensis*). The position of the animal's head was marked by a dot every 10th second. The total time from leaving the exit until reaching the prey and the length of the path are indicated.

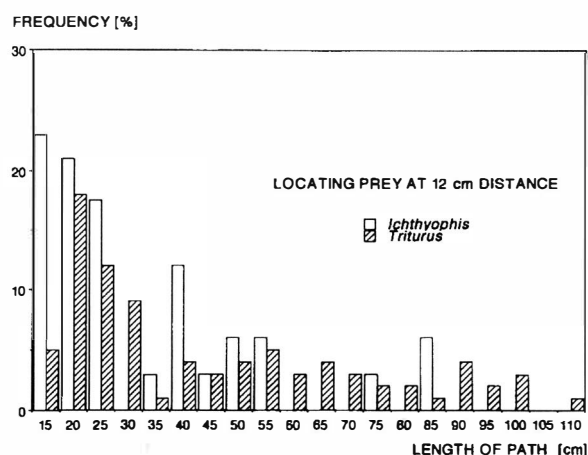
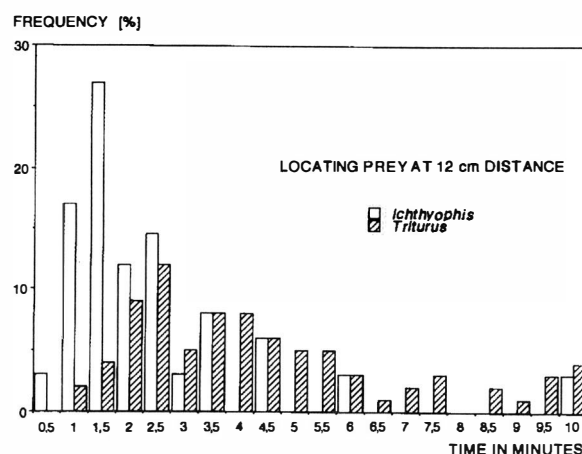


FIG. 4. Comparison of chemical orientation in the caecilian *I. kohtaoensis* and in the newt *Triturus alpestris*. Above: Time to reach the prey. Below: Length of the path.

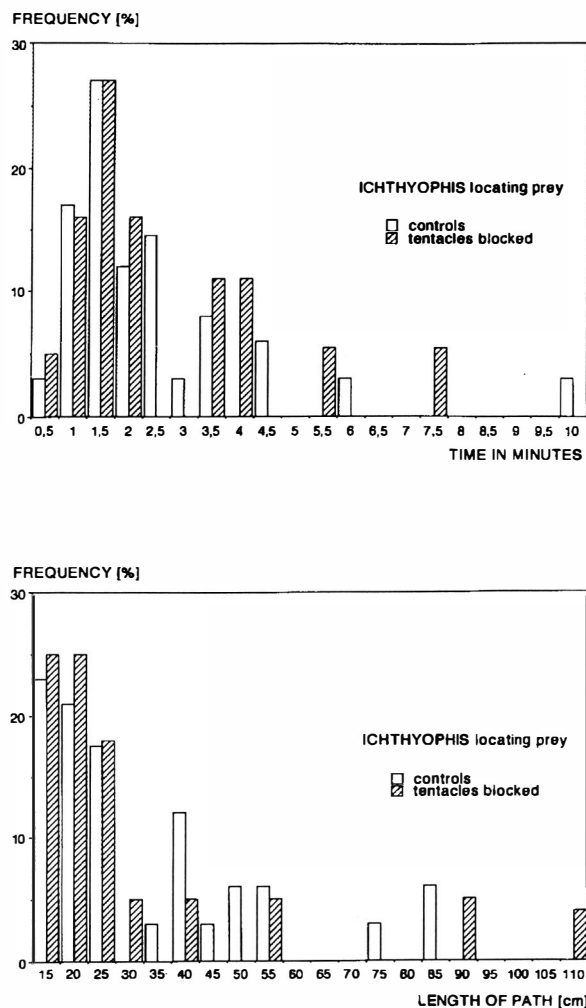


FIG. 5. Comparison of chemical orientation in caecilians with functioning tentacles (controls) and with blocked tentacles. Above: Time to reach the prey. Below: Length of path.

RESULTS

The movements of *I. kohtaoensis* on the surface, toward the prey object, appeared rather straight and fast. Fig. 3 shows four typical paths of control animals which reached the targets without many detours and within quite a short time. The direct distance from exit to prey object was 12 cm, and in these four examples the length of the path ranged from 13 cm to 22 cm, while the time elapsed until seizure of the meat ranged from 52 s to 88 s. In Fig. 4 the responses of *Ichthyophis* are compared to the data for *Triturus*. It is clear that *Ichthyophis* moved faster to the target; most animals reached it within one to two minutes, while only a few newts seized the prey so soon. Only six caecilians needed more than 5 min to reach the target, whereas 24 newts were counted in the intervals from 5.5 to 10 min. The lengths of the path also clearly differed. Most caecilians (61%) went 25 cm or less whereas the newts walked longer distances, making more detours. Only 35% of the newts needed 25 cm or less; 9% of the caecilians covered more than 60 cm, but 25% of the

newts exceeded this path length. The differences between *Ichthyophis* and *Triturus* regarding the time as well as the length of path are significant ($P < 0.01$).

Caecilians with blocked tentacles showed normal feeding behaviour one day after surgery. These animals behaved much like the controls in the experiments. The movements during searching from the exit hole toward the piece of meat appeared not to be affected by the restriction of the tentacles. Indeed, as can be inferred from Fig. 5, neither the length of path nor the searching time is longer in animals with blocked tentacles. Regarding the length of path, there is a slight predominance of blocked individuals at the intervals from 15 to 25 cm, suggesting that without tentacle use the path might be even more straight. This difference, however is not significant ($P > 0.3$).

Differences occurred, however, if *Ichthyophis* had to follow a scented track within the glass tube system. Generally, the caecilians responded quite precisely and quite quickly in this situation. In 100 trials respectively, control animals entered the scented tube 79 times, blocked animals entered it 78 times. So the frequency of errors in the first orienting decision was nearly the same in animals with and without blocked tentacles. But the velocities within the tube differed significantly ($P < 0.01$). After entering a scented tube, caecilians with functioning tentacles moved distinctly faster than those with blocked ones. As can be seen in Fig. 6, the proportion of controls that reach the target within the first minute, is nearly three times that of the blocked animals.

Blocking the nostrils resulted in remarkable effects. These experiments were performed on the surface of the ground only, but not in the tube-system. As can be seen in Fig. 7, the paths were no longer directed towards a target but were totally random. None of the 10 animals, which again were tested 10 times each, seized the prey object. Even if the path led close to the prey the caecilian did not turn towards it but passed by.

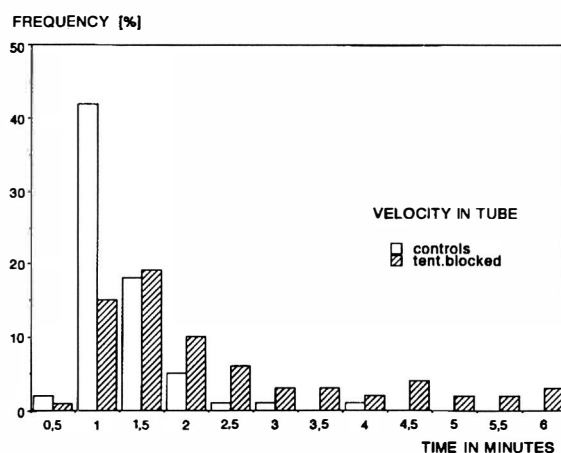


FIG. 6. Reactions of caecilians with functioning or blocked tentacles following a scented path within the tube system.

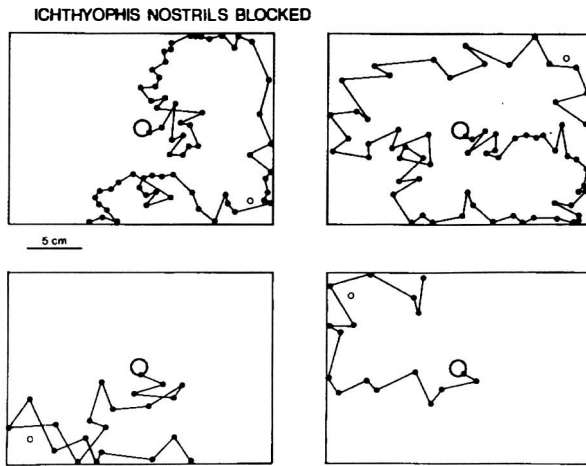


FIG. 7. Examples of paths of four caecilians with blocked nostrils. As in Fig. 3, the position of the animal's head was marked every 10th second.

DISCUSSION

The experiments reported here show that the caecilian *I. kohtaoensis* is able to localize prey objects by chemical cues only, quite precisely. Compared to terrestrial newts the caecilians reached a prey object on the ground surface within a shorter time and by a more direct route. The fact that *Ichthyophis* in this situation reached the target faster, does not necessarily indicate greater sensory abilities but might also be a result of a different mode of locomotion. The fact, however, that the newts took courses with larger deviations (resulting in longer paths) may be interpreted in terms of better chemical orientation by the caecilians. Presumably *I. kohtaoensis* is able to detect smaller differences in odour concentration reaching the left or right olfactory epithelia.

Blocking the tentacles had no effects on behaviour on the surface, so we conclude that feeding on the surface of the ground is guided by olfaction with the nose. In the experiments with blocked nostrils, the tentacles and the vomeronasal organs were not influenced. But these organs were apparently unable to detect the prey and to guide the animal to it. In this situation, the tentacles probably have no function. Indeed, they are so short that a protruded organ does not touch the ground when *Ichthyophis* is moving horizontally on a flat surface. This is different in a subterranean tunnel.

Burrows built by *Ichthyophis* consist of tubes with a lumen that matches the body diameter of the animal. Within them, the moving tentacles can contact the substrate and might pick up odour molecules and transport them towards the olfactory epithelia. This may explain the results of our experiments in the glass tube system. Here, animals with blocked tentacles reached the target after a significantly longer time than the controls with functioning tentacles. We conclude that within a tube the tentacles may support olfactory orientation when the molecules to detect are not only gaseous but also dissolved in substrate humidity. In

reptiles, the vomeronasal organ is involved in chemoreception during tongue-flick behaviour which may pick up odorants from the substrate but also may sample air (c.f. Simon, 1983; Halpern, 1992). Whether or not the tentacles in *Ichthyophis* are involved in detection of air-borne odorants is an open question and has to be tested.

With tentacles blocked, the caecilians in the tubes seemed not to be seriously handicapped. They still reached their prey within a rather short time. The role of the tentacles in chemical orientation probably might be more important if caecilians have to burrow in the soil. In our experiments, animals moved within pre-made tubes, like caecilians travelling through their gallery-system. In terraria *I. kohtaoensis* does not dig new tunnels continuously. When placed in fresh soil they spend about two weeks burrowing and from then on move within the same tubes.

During burrowing in the soil the external nostrils are closed, and half a century ago Marcus (1930) presumed that the physiological function of the caecilian tentacle is not only to serve as a tactile sense organ but also to provide a side-path for breathing and olfaction during burrowing behaviour. Marcus thought that gaseous scents enter the tentacle opening and that the movements of the tentacle itself had the function of removing soil particles from the opening. Badenhorst (1978) suggested that particles clinging to the moist tentacle are deposited into and dissolved in the secretions of the orbital glands covering the tentacle and conveyed via the tentacle ducts to the vomeronasal organ. He also postulated that the tentacle opens a bypass in the event of closure of the external nostrils, while burrowing. This hypothesis was adopted by recent anatomists such as Billo (1986) and Schmidt & Wake (1990).

Our data are consistent with this hypothesis: In our tube experiments, the tentacles might have transported dissolved substances which they could not do on the ground surface where only gaseous scent was present.

The function of the tentacles during burrowing must be investigated in further experiments. In contrast to Ramaswami (1941), who reported that *Ichthyophis* is no burrower but lives under decaying vegetation, our own observations show that *I. kohtaoensis* stays in tunnels built by burrowing. Not only does it live in subterranean burrows in terraria; in the natural habitat in Thailand as well, most specimens were found about 10 to 20 cm deep in the soil, although some stayed on the surface under wood or leaves. Also Ducey, *et al.*, (1993) reported that *I. kohtaoensis* in terraria was not detectably a less effective burrower than caecilians of other genera. We therefore presume that chemical orientation mediated by the tentacles might be of biological significance in this species while moving in existing tunnels as well as during burrowing in the soil.

A possible function of tentacles and vomeronasal organs in caecilians might also be detection of pheromones.

ones. In salamanders, chemosignals in courtship behaviour and territorial interactions are mainly perceived by the vomeronasal organ (c.f. Dawley & Bass, 1989; Houck, 1986). Until now, these behaviours have not been observed and studied in caecilians.

ACKNOWLEDGEMENTS

We thank M. Elsell and K. Weishaupt for performing parts of the experiments, and R. Frank-Bauer for technical assistance.

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Accepted: 15.2.95

CONTRIBUTION TO THE SYSTEMATICS OF THE LIZARD *ACANTHODACTYLUS ERYTHRURUS* (SAURIA, LACERTIDAE) IN MOROCCO

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We have analysed several scalation characters and the geographic distribution of lizards of the *Acanthodactylus erythrurus* group to verify the validity of these criteria. These data are collated with biogeography to demonstrate the existence of two distinct species within what are known as common fringe-toed lizards: *Acanthodactylus erythrurus*, consisting of three subspecies, and *Acanthodactylus lineomaculatus*, monotypic and endemic to Morocco. Hypotheses concerning the population history of these animals are proposed.

INTRODUCTION

At the beginning of the last century common fringe-toed lizards were described from Europe (*Lacerta erythrura* Schinz 1833, and *Acanthodactylus vulgaris* Duméril & Bibron 1839) and from North Africa (*Acanthodactylus lineomaculatus* Duméril & Bibron 1839). Since then, they have been the subject of many investigations. Boulenger's revision in 1878 was the first attempt to introduce some order to the genus *Acanthodactylus*, often considered as one of the most difficult in the Palearctic. The increase in the number of specimens collected, and the use of often contradictory terminology by different authors, led Salvador (1982) and Arnold (1983) to make a revision of the numerous species that this genus comprises and to clarify the phylogenesis. Other authors have confined their research to a single group, e.g. Squalli-Houssaini (1991) on the fringe-toed lizards of the *erythrurus* group.

Since we had access to abundant material from North Africa and precise data on these animals' ecology and distribution in Morocco, our intention was to readdress the problem, restricting our analysis to certain scalation characters that, in our opinion, are discriminative. These characters were then collated with the ecological and biogeographical characteristics of the populations being studied. We restricted our study to the different forms of the common fringe-toed lizard in Morocco because it is the country where the widest diversity of forms and habits is found.

The common fringe-toed lizard, *Acanthodactylus erythrurus* (Schinz 1833), is the only representative of the genus occurring in Europe, where it is confined to the southern two thirds of the Iberian Peninsula, extending its range as far north as Gerona (Barbadillo Escrive, 1987), Zaragoza, Burgos (old record) and Leon (old record) (Salvador *in* Böhme, 1981). It is also the only fringe-toed lizard to occupy the whole of Morocco, north and west of the Atlases. This distribution stretches eastwards along a large part of the Algerian

coast. However, it does not appear to be known from Tunisia.

Morphologically, it is characterised by the presence of three complete rows of scales round the fingers and small dorsal scales, either keeled or unkeeled, on the back, with the underside of the tail bright red in juveniles and subadults. The combination of these three characters distinguishes *Acanthodactylus erythrurus* within the genus. Three subspecies have been recognised in Morocco (Pasteur & Bons, 1960; Bons & Girot, 1962):

— ssp. *belli* Gray 1845, in the Rif, on the coast and plateaux east of the Atlases, the southern slopes of the High Atlas and the far west of the Anti-Atlas (this subspecies is the only representative of *Acanthodactylus erythrurus* in Algeria; Salvador, 1982).

— ssp. *atlanticus* Boulenger 1918, in the Middle Atlas, the northern slopes of the High Atlas and the plains situated north of the High Atlas (endemic to Morocco).

— ssp. *lineomaculatus* Duméril & Bibron 1839, on the Atlantic coast from Tangiers to Essaouira (endemic to Morocco).

The nominate subspecies is confined to the Iberian peninsula.

The two recent revisers of the genus, Salvador (1982) and Arnold (1983), do not retain the subspecies *atlanticus*. They consider it as intermediate between *A. erythrurus belli* and *A. erythrurus lineomaculatus*. Whereas Squalli Houssaini (1991), without adopting a definite position, considers that the Moroccan subspecies have little taxonomic value and are only a reflection of their distribution, and that the Iberian fringe-toed lizards are sufficiently differentiated from their Moroccan counterparts to merit a distinct specific status.

MATERIALS AND METHODS

We examined 496 Moroccan individuals from 22 localities, or groups of localities, throughout the country. For comparative purposes, we added 11 individuals

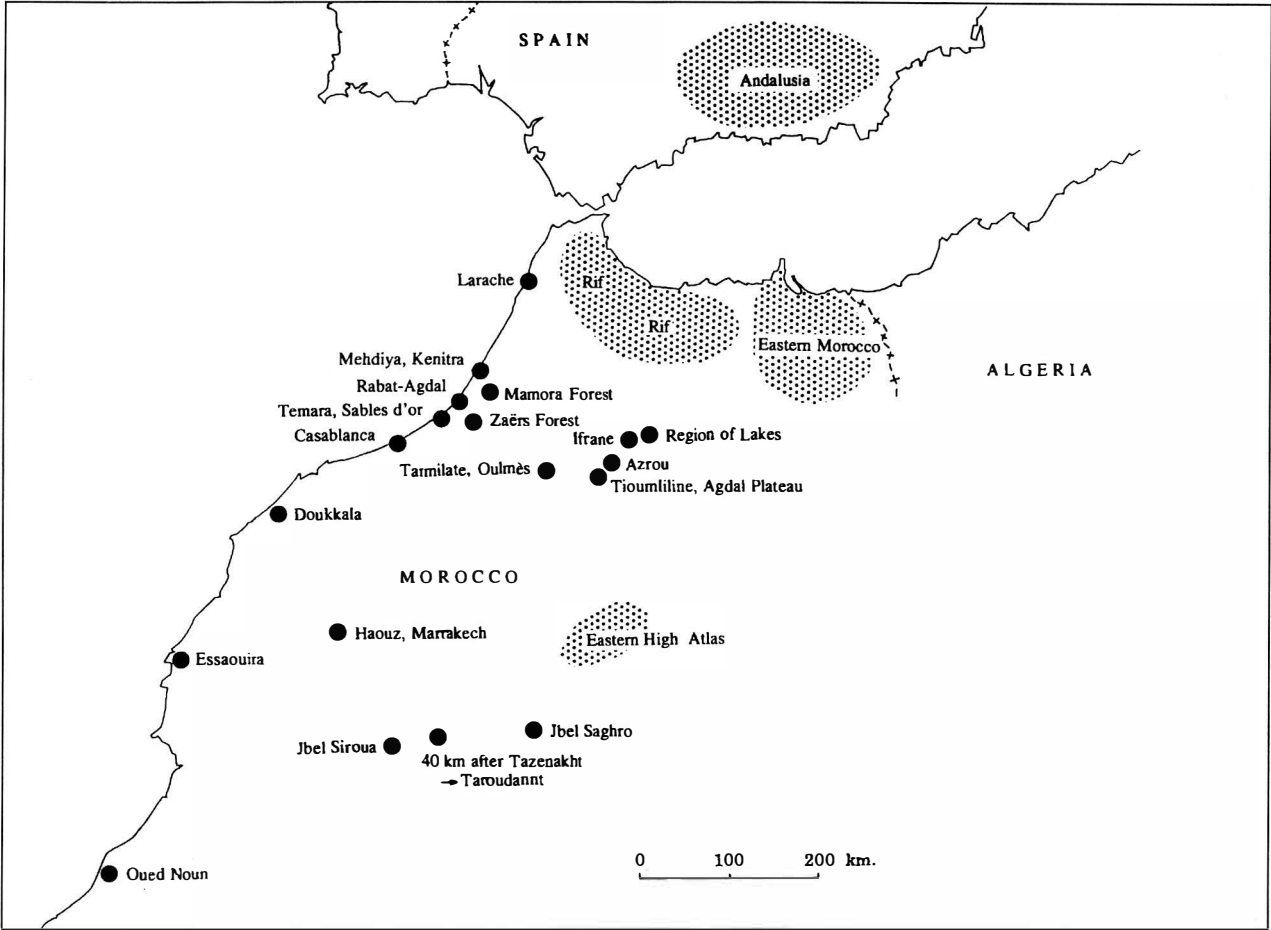


FIG. 1. Location of populations studied.

from Andalusia (Spain) (Fig. 1). The samples varied in size depending on the localities, ranging from 1 to 69 specimens (average : 22.55). The examined samples are as follows :

MOROCCO

Larache	(47 individuals)
Mehdiya, Kenitra	(36 individuals)
Mamora Forest	(41 individuals)
Rabat-Agdal	(55 individuals)
Temara, Sables d'or	(14 individuals)
Zaërs Forest	(47 individuals)
Casablanca	(47 individuals)
Doukkala	(4 individuals)
Essaouira	(6 individuals)
Region of Lakes	(5 individuals)
Ifrane	(34 individuals)
Azrou	(17 individuals)
Tioumliline, Agdal Plateau	(9 individuals)
Tarmilate, Oulmès	(69 individuals)
Haouz, Marrakech	(3 individuals)
Rif	(18 individuals)
Eastern Morocco	(13 individuals)
Eastern High Atlas	(13 individuals)
Jbel Saghro	(4 individuals)
40 km W. of Tazenakht	(11 individuals)

Jbel Siroua	(2 individuals)
Oued Noun	(1 individual)

SPAIN

Benidorm	(1 individual)
Almeria	(2 individuals)
Huescar	(2 individuals)
Torre de la Higuera	(3 individuals)
unknown locality	(3 individuals)

Five scale characters were monitored: (1) dorsal scales strongly keeled or not; (2) position of the subocular in relation to the edge of the upper lip; (3) number of scales and granules arising from the fragmentation of the first supraocular, right and left; (4) number of interprefrontal granules; and (5) internasal divided or not.

We then compared the percentage of individuals within each population that presented different configurations of each character.

The specimens examined come from the collection of the Laboratoire de Biogéographie et Ecologie des Vertébrés de l'E.P.H.E., Montpellier, France. The results of these examinations were collated with numerous observations made in the field in Morocco and the Iberian Peninsula.

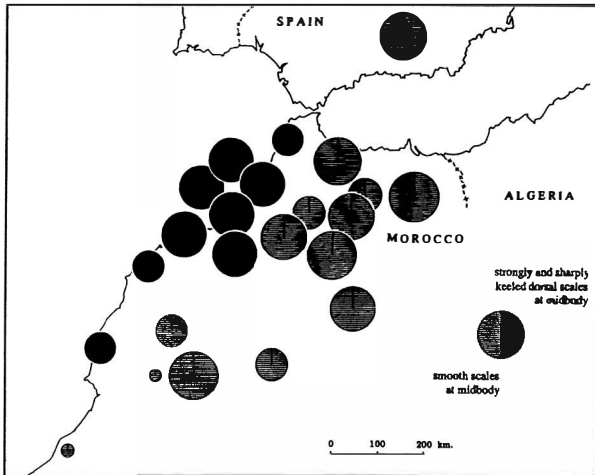


FIG. 2. Texture of dorsal scales, expressed in percentages of individuals per site.

RESULTS

The results of the pholidotic analyses are ordered according to scale characters.

DORSAL SCALATION (FIG. 2)

An examination of the dorsal scales reveals a partition of our samples into two groups: (1) lizards from the Atlantic coastal area, between Tangiers and Essaouira, possess strongly and sharply keeled dorsal scales, starting on the back and sides of the neck; (2) lizards from all other localities (Morocco and Spain) possess smooth scales on the anterior part of the back. In some populations they become tectiform or weakly keeled at the rear of the back.

We did not observe any individuals presenting intermediate characters between these two types of scalation, nor any mixed populations. Consequently, strongly keeled dorsal scales make it possible to distinguish with certainty Atlantic coast animals from all the other common fringe-toed lizards examined from Morocco and Spain. A later examination of a sample (c. 30 individuals) from the Aurès in Algeria, put at our disposal by Laurent Chirio, also confirmed our findings for Algeria.

POSITION OF THE SUBOCULAR (FIG. 3)

Four positions of this scale in relation to the upper lip were observed. This is the most commonly used character for the recognition and distinction of the North African subspecies (Bons & Girot, 1962).

Position 1: The subocular is wedged between the 4th and 5th upper labials, but does not touch the lip (labials 4 and 5 are still in contact). This is characteristic of the form *lineomaculatus*.

Position 2: The subocular is separated from the lip by a small trapezoidal scale that appears to result from the fragmentation of the 4th supralabial.

Position 3: The subocular is separated from the lip by a small "independent" rectangular scale. This position is characteristic of the form *atlanticus*.

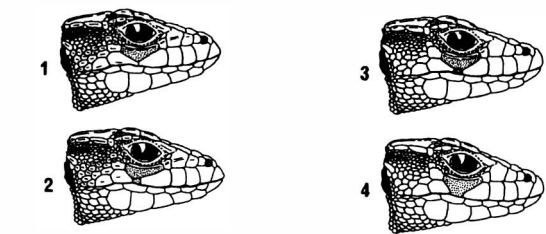
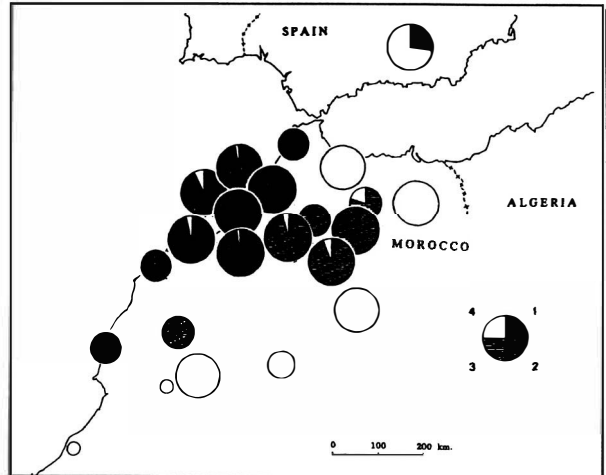


FIG. 3. Position of subocular scale, expressed in percentages of individuals per site.

Position 4: The subocular is in wide or narrow contact with the upper lip. This subocular/edge of lip contact is characteristic of the form *belli*.

The analysis of our samples shows that only animals from the Rif, the southern slopes of the High Atlas and the east of Morocco are 100% consistent with position 4.

Position 3 is characteristic of animals from the Middle Atlas and the Haouz plain, in percentages varying from 87 to 100%. The other situations are infrequent in these regions: 0 to 8.7% of position 1, 0 to 20% of position 4.

The coastal animals are distributed along a band running north-east/south-west. In localities north of Rabat they mostly (75 to 95%) possess a small trapezoidal upper labial (position 2) that is usually absent (57.1 to 95%) in specimens from south of Rabat (position 1).

Consequently the traditional criterion of the position of the subocular used to distinguish subspecies of *Acanthodactylus erythrurus* should be used with care. Position 4 certainly enables animals from the Rif, eastern Morocco, the southern slopes of the High Atlas and the far west of the Anti-Atlas, (i.e. belonging to the subspecies *belli*), to be identified unequivocally. However, positions 1 and 3, that were traditionally used to identify respectively the *lineomaculatus* and *atlanticus* forms, are not absolute and cannot be used for the determination of all individuals:

Position 3 (small rectangular supralabial) is peculiar to the form *atlanticus*, but a small percentage of individuals from the Middle Atlas present situations 1 and 4.

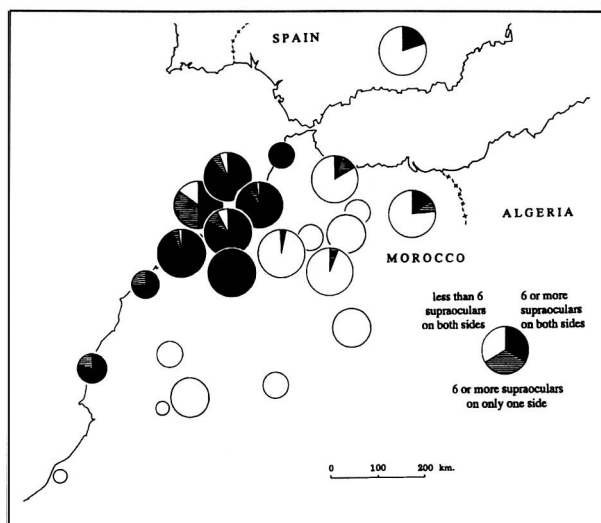


FIG. 4. Number of fragments of the 1st supraocular scale, expressed in percentages of individuals per site.

Position 1, characteristic of *lineomaculatus*, can be used to identify a large proportion of animals from the Atlantic coastal area south of Rabat, but becomes infrequent north of Rabat. It is replaced by position 2 (fragmented supralabial), a configuration that may sometimes be confused with position 3.

SUPRAOCULAR SHIELDS (FIG. 4)

The genus *Acanthodactylus* is characterized by the presence of four large supraocular shields that have a tendency to fragmentation. In common fringe-toed lizards, only shields 2 and 3 remain entire, while the 4th, and to a lesser extent the 1st, are fragmented into granules or small scales.

The Atlantic samples are the most affected by this fragmentation, since between 85.7% and 100% of specimens, depending on localities, have the 1st supraocular fragmented into over five scales and granules on at least one side. (From 50 to 100% of individuals possess over five scales in the place of the 1st supraocular on both sides).

In samples from the Rif, the Atlases, western Morocco and Iberia, the 1st supraocular is nearly always fragmented into fewer than six scales on both sides (from 76.9 to 100% of individuals, depending on localities).

The division of the 1st supraocular into more than five fragments is an identifying feature for individuals from the Atlantic coast. However, this situation is also found, though in very low percentages, in Andalusia, the Rif, the Middle Atlas and the East.

EXISTENCE OF INTERPREFONTAL GRANULES (FIG. 5)

In some fringe-toed lizards, one or several granules are intercalated between the prefrontal scales. These granules exist in 75 to 95.8% of individuals from the Atlantic coast, except those from the extreme north (Mehdiya, 47.2%; Larache, 25%).

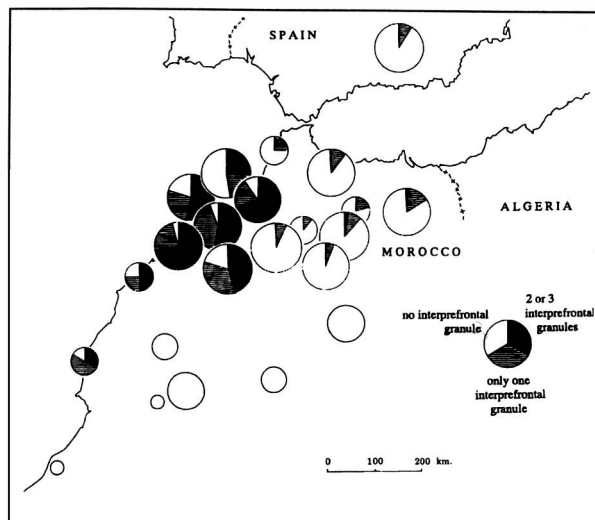


FIG. 5. Presence or absence of interprefrontal granules, expressed in percentages of individuals per site.

On the other hand, the absence of interprefrontal granules is the most common situation in animals from the rest of Morocco and Andalusia (80 to 100% of individuals, depending on localities, with values always higher than in the Atlantic localities). Some animals from the Rif, the Middle Atlas, the East and Spain have one granule (5.9 to 20% of individuals depending on localities), while it is absent in all specimens examined from the High Atlas, Haouz and the far west of the Anti-Atlas.

The presence of one or two interprefrontal granules, characteristic of the form *lineomaculatus*, is therefore predominant in animals from the coast south of Rabat and infrequent in the north. It is rare or exceptional in animals from other areas.

DIVISION OF THE INTERNASAL (FIG. 6)

The division of the internasal is a recognition character of the subspecies *lineomaculatus*.

With the exception of those from the extreme north (Larache and Mehdiya), the majority of individuals from the Atlantic coast have a divided internasal (66.7 to 85.7%, depending on localities), whereas the other populations show few cases of internasal division (Middle Atlas, 2.9 to 5.9%, depending on localities), or none (Anti-Atlas, High Atlas, Haouz, Rif, East and Spain).

All the fringe-toed lizards from the Atlantic coast between Tangiers and Essaouira, i.e. those that always present strongly keeled scales, when compared to the other forms, also have a much more pointed snout, a more slender head, a sharper angle between the pileus and the cheeks, more angular lateral edges to the frontal, which is markedly concave, and variably keeled temporal scales. Squalli-Houssaini (1991) adds other distinctive characters such as the number of rows of supraciliary granules (two for *lineomaculatus*, one for the other taxa of the group), and the frequent pres-

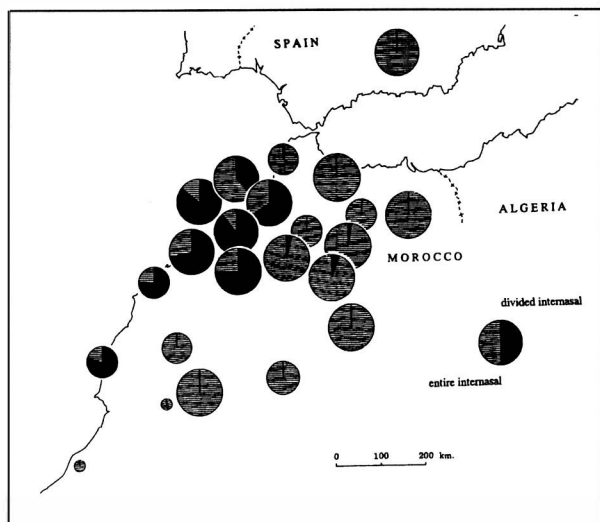


FIG. 6. Division of internasal scale, expressed in percentages of individuals per site.

ence (41%) of occipital granules in the former and their rarity in the others. These characters were not monitored during our analyses but they have been largely confirmed by our studies in the field.

DISCUSSION

It is therefore established that the head scalation criteria used to identify the subspecies of *Acanthodactylus erythrurus* should not be taken into account if used in isolation or on a single specimen. On the other hand, if applied together, they are very interesting and easy to use. They also make it possible to show up three geographic regions, which are occupied by three morphologically different types. These correspond to the three traditionally accepted subspecies of Morocco: ssp. *lineomaculatus*, ssp. *belli* and ssp. *atlanticus* (Pasteur & Bons, 1960; Bons & Girot, 1962). In spite of the total confirmation of these characters and percentages by Squalli-Houssaini (1991), this author could not adopt the same conclusions as ours because of the low number of populations studied.

Concerning the form *atlanticus*, it should be noted that it is not recognised by Salvador (1982) and Arnold (1983). They consider it an intermediate between *A. erythrurus belli* and *A. erythrurus lineomaculatus*. Yet the homogeneity of its scalation characters, distributed over a well defined geographical area (the Middle Atlas, northern slopes of the High Atlas and Haouz), make it quite different from the other subspecies. Furthermore this form, usually considered as mountainous (Pasteur & Bons, 1960; Bons & Girot, 1962), is found in plains at Haouz of Marrakech. The hypothesis that the form *atlanticus* could be a mountain ecotype of *Acanthodactylus erythrurus* can therefore not be retained. Lastly, the absence of intermediate animals between the subspecies *lineomaculatus* and *belli*, as well as the absence of intermediate morphological characters between these two forms, is contrary to the

claims of Salvador (1982) and Arnold (1983). *Acanthodactylus erythrurus atlanticus* is therefore a valid subspecies perfectly consistent with the definition of a subspecies.

We then investigated the nature of contacts and relations between these different subspecies. A large number of specimens, observed in many localities (cf. Fig. 2), enabled us to make the following clarifications.

Contact zones between the forms *atlanticus* and *belli* exist in the northern foothills of the Middle Atlas. The transition from one subspecies to the other occurs via a mosaic of small populations in which all the individuals possess either the labial character of *atlanticus* (position 3) or of *belli* (position 4). Thus, 5 km north of Dayet Ifrah (region of lakes, north of the Middle Atlas), all individuals of *Acanthodactylus erythrurus* possess the headscale pattern of *belli*, while the surrounding populations belong to the subspecies *atlanticus*.

We have no knowledge of contacts between *atlanticus* and *belli* along the ridge of the High Atlas, even though the two subspecies are separated by only a few kilometres. The very high altitude of the High Atlas mountains may mean that the supposed contacts do not exist, the two subspecies being allopatric in the southern part of their range.

We know several areas where populations of *lineomaculatus* and *belli* or *atlanticus* live in immediate proximity. No morphologically intermediate animals have been observed. This apparent absence of intermediates between the two forms, together with diagnostic morphological differences (dorsal scalation, head shape) and other important differences (position of subocular, divided internasal, shape of frontal) indicate that we are dealing with two distinct species: *Acanthodactylus lineomaculatus* on the one hand, and *Acanthodactylus erythrurus*, represented in Maghreb by the subspecies *belli* and *atlanticus*, on the other.

Within the range of *Acanthodactylus lineomaculatus*, disparity in several characters is observed between animals from south of Rabat and those from the north: divided internasal, number of interprefrontal granules, fragmented 4th supralabial. However these variations are of a clinal nature, with the transition consisting of a progressive inversion of frequency, so the town of Rabat is only a reference mark. Consequently, it is impossible to establish the existence of two subspecies for *A. lineomaculatus*. Besides, other characters are invariable throughout the whole of this species range (keeled dorsal scales, slim pointed snout, concave frontal, strongly fragmented 1st supraocular), providing supplementary evidence for *A. lineomaculatus* specific status.

Of course, there are no contacts between the nominal subspecies, confined to the Iberian peninsula, and the other forms that are peculiar to the Maghreb. However, from a strictly morphological point of view, the European animals are very similar to *A. erythrurus*

belli and *atlanticus*, to such an extent that the Spanish animals, whose subocular is in contact with the lip, are practically indistinguishable, apart from slight colouration variations, from *A. erythrurus belli*. They have a rounded snout, low headscale fragmentation and smooth dorsal scales. So *A. erythrurus belli* and *A. erythrurus atlanticus* should be considered as conspecific with *A. erythrurus erythrurus*, in spite of the electrophoretic differences observed by Squalli Houssaini (1991) between animals from the Iberian peninsula and those from Morocco.

In fact, this author has found a D_{Nei} genetic distance of 0.327 between his Spanish samples (Alicante) and those from Morocco. This distance is higher than that observed between his oceanic coast population and both Rifain and Middle Atlas samples ($D_{\text{Nei}} = 0.081$). In Busack's (1986) study of *Acanthodactylus erythrurus*, the genetic distance between different samples from Tingitane Peninsula (north of Morocco) was no different from that between Tingitane and Andalusia ($D_{\text{Nei}} = 0.10$ and 0.09 respectively). The genetic similarity between Spanish and Moroccan populations found by Busack (1986) is in partial contradiction of those of Squalli-Houssaini (1991) but agrees with our morphological results: we observe a closer phenotypic similarity between *Acanthodactylus erythrurus erythrurus* (Spain), *A. e. belli* (northern, eastern and southern Morocco) and *A. e. atlanticus* (central Morocco) than between these and *A. lineomaculatus*.

Moreover, the weaker electrophoretic polymorphism in Spanish populations (six diagnostic alleles for 10 individuals, $D_{\text{Nei}} = 0.01$) compared to one of the Moroccan populations (12 diagnostic alleles for 9 individuals, $D_{\text{Nei}} = 0.10$) (Busack, 1986), suggest the Iberian peninsula was colonized from North Africa by a small number of individuals. This led to a 'founder effect' characterized by the large genetic homogeneity of Spanish populations. This homogeneity approaches the phenotypic uniformity observed in Andalusia.

SYSTEMATIC REVIEW OF THE FRINGE-TOED LIZARDS OF THE GROUP *ERYTHRURUS*

Common fringe-toed lizards are distributed in the Iberian peninsula and the Maghreb, except Tunisia. They are represented by two geographically parapatric species, one of which is monotypical and the other comprising three subspecies. They are all characterized by three entire rows of scales round the fingers, small dorsal scales, and the bright red underside of the tail in juveniles and subadults.

Acanthodactylus erythrurus erythrurus (Schinz, 1833)

Diagnosis: Smooth dorsal scales (or weakly keeled on rear of back), rounded snout, barely concave frontal, entire internasal, usually no interprefrontal granules (exceptionally one), 1st supraocular generally fragmented into fewer than six scales on both sides (sometimes into six scales on both sides), subocular usually in contact with lip (sometimes it is separated

from the lip by the 4th and 5th labials that are joined in this case).

Distribution: The southern two-thirds of the Iberian Peninsula, extending northwards along the Mediterranean coast as far as the environs of Gerona.

Acanthodactylus erythrurus belli Gray, 1845

Diagnosis: Smooth dorsal scales (or weakly keeled on rear of back), rounded snout, barely concave frontal, entire internasal, usually no interprefrontal granules (exceptionally one), 1st supraocular generally fragmented into fewer than six scales on both sides (exceptionally six on one or both sides), subocular in contact with lip.

Distribution (Fig. 7): Rif mountains and foothills, eastern Morocco, southern slopes of the High Atlas and far west of the Anti-Atlas (Foum Assaka, Ifni), as well as Mediterranean Algeria.

Acanthodactylus erythrurus atlanticus Boulenger, 1918

Diagnosis: Smooth dorsal scales (or weakly keeled on rear of back), rounded snout, barely concave frontal, internasal nearly always whole (exceptionally divided), no interprefrontal granules (sometimes one, exceptionally two), 1st supraocular generally fragmented into fewer than six scales on both sides (exceptionally six on one or both sides), subocular generally separated from the lip by a small rectangular or oval scale (exceptionally this small scale is absent and the subocular may or may not be in contact with the lip).

Distribution (Fig. 7): Morocco only; Middle Atlas including the Central Plateau, northern slopes of the High Atlas, plains to the north and west of the Atlases, with the exception of an Atlantic coastal fringe.

Acanthodactylus lineomaculatus Duméril & Bibron, 1839

Diagnosis: Strongly keeled dorsal scales, slim pointed snout, concave frontal (with sharply angled lateral edges), internasal usually divided, except north of Rabat, usually one or two granules, except north of Rabat where they are generally absent, 1st supraocular usually fragmented into more than six scales or granules, subocular usually separated from the lip by the 4th and 5th supralabials, the 4th being usually fragmented at the rear by a small trapezoidal scale in localities north of Rabat.

Distribution (Fig. 7): Moroccan endemic along the Atlantic coast from Tangiers to Essaouira.

Acanthodactylus (erythrurus) lineomaculatus has been frequently reported from Agadir and the plain of the Oued Souss. However, all fringe-toed lizards of this area that we examined in collections or in the field, belong to the *pardalis* group, especially *Acanthodactylus busacki* Salvador, 1982. Raxworthy *et al.* (1984) also mentions the problem in identifying Cap Rhir's animals (northern Agadir) and suggests that only

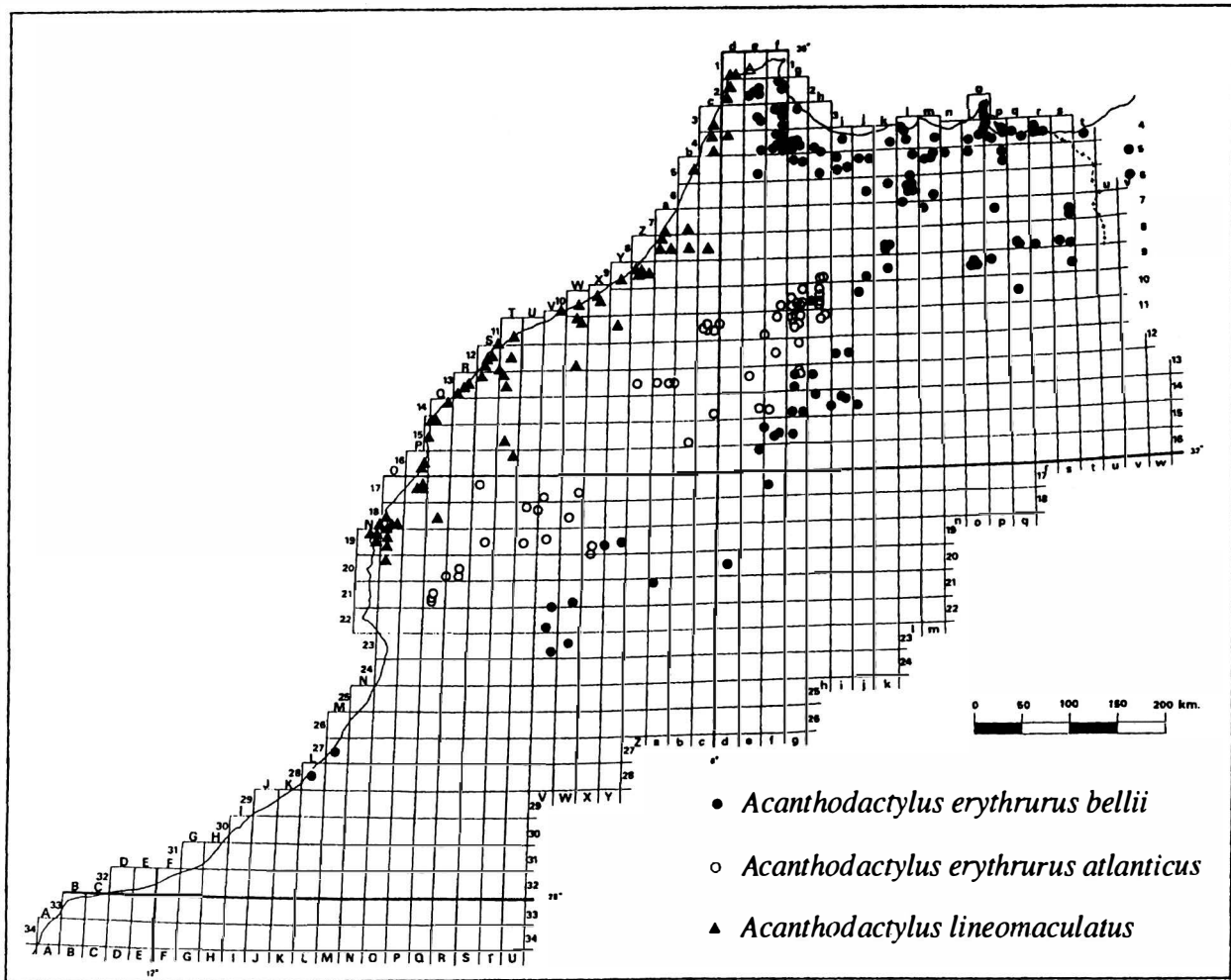


FIG. 7. Distribution of common fringe-toed lizards in Morocco (from Bons & Geniez, in press).

Acanthodactylus pardalis s.l. was present in this area. So we must accept that *A. lineomaculatus* reaches its geographical limit 15 km south of Essaouira and that further south it is replaced by another species, *A. busacki*. This taxon is found in the plain of Oued Souss and the Atlantic coast from Tamri, in the North, to Boujdour, in the South.

CONCLUSION

On the basis of several scalation characters, we have been able to demonstrate that there is a larger disparity between animals from the Atlantic coast of Morocco and those from the rest of the country, than exists between the latter and the fringe-toed lizards from the Iberian Peninsula. This disparity is largely confirmed by the morphological analysis of Squalli Houssaini (1991) but is contrary to her genetic findings. This author used electrophoresis, to show that the Iberian animals she studied differ from those from Morocco in two diagnostic loci (*FUM* and *ME.1*) and by a fixed allele [*LDH-2(90)*] that is not shared by their Moroccan counterparts. On the other hand, the three Moroccan forms are barely distinguishable from each other on the

basis of electrophoresis with the exception of *lineomaculatus*, which presents a more developed enzymatic polymorphism with a higher number of rare alleles.

We have also observed that animals from the Mediterranean coast of Morocco, and those from both the Mediterranean and Atlantic coast of Iberia, did not display any of the morphological characters of *Acanthodactylus lineomaculatus*. This suggests that these lizards have been isolated on the Atlantic coast for a long time and enables us to reject the hypothesis of a single ecotypical adaptation to sandy habitats, where thermal variations are mitigated by the proximity of the Atlantic. This also suggests that Spain was colonised by a small group of individuals from Morocco. This idea is reinforced by Busack (1986) who obtained an insignificant genetic distance ($D_{Nei} = 0.01$) between his different Iberian samples and found for Spanish samples only six diagnostic alleles for 10 individuals, as opposed to 12 diagnostic alleles for nine individuals in northern Morocco. This type of biogeographical scenario is found in other species, for example *Podarcis hispanica*, *Lacerta lepida* and

Macroprotodon cucullatus (cf. Busack, 1986; Table 3).

The presence of *Acanthodactylus erythrurus atlanticus* in the plains to the north-west of the Atlases suggests the recent colonisation of this low altitude habitat by a form that could have been differentiated by long isolation in high mountains and selective pressures associated with these extreme conditions. It is conceivable that this colonisation is still taking place and that this form could come into contact with *A. lineomaculatus*. Would this develop into competition between the two forms, or even lead to the elimination of the coastal form with its more demanding ecological requirements? Alternatively, will the present situation stabilise, with the sandy substrate and the presence of a well-adapted species to this environment proving an insuperable barrier for *A. erythrurus atlanticus*?

Another hypothesis can be put forward to explain the presence of the form *atlanticus* in the plains. This subspecies could have been much more widespread during the pluvial periods and the last glaciations than at present. The general warming and aridification that have led to the present climate could have reduced the range of *atlanticus* to small isolated populations, in which case this form would be retreating in the plains to the north-west of the High Atlas.

Patterns of interspecific diversity within other species groups which are comparable to *Acanthodactylus erythrurus* are known from Morocco. In the *Acanthodactylus* genus, two species groups are known (Salvador, 1982; Bons & Geniez, in press). The *pardalis* group contains one species, *Acanthodactylus maculatus*, which has a wide extension in arid steppes

in the East of the Atlas (and in Algeria), where there are cold or cool winters (*sensus* Brignon & Sauvage, 1962). The same species group also includes an endemic Moroccan species, *Acanthodactylus busacki*, which is restricted to the oceanic coast from Tamri to Boujdour and the plain of Oued Souss, an area with hot winters.

Within the *scutellatus* group, *Acanthodactylus dumerili* is linked to the Sahara's sand dunes with temperate winters. On the other hand, *Acanthodactylus aureus*, also in the *scutellus* group, occurs from the Sahara's Atlantic littoral sands (from Agadir to Senegal), where winters are hot.

These patterns are also observable in other reptile genera (in particular *Saurodactylus*, *Chalcides* and *Sphenops*; cf. Table 1), as well as some mammals (Aulagnier & Thévenot, 1986), members of the Gerbillidae belonging to the genus *Gerbillus* and *Gerbillus pyramidum* group. They are represented in Morocco by a Saharan and sand-loving species, *Gerbillus pyramidum*, located in all the Sahara, and four endemic species in sand from both the Moroccan oceanic coast and western Sahara (from the north to the south, *Gerbillus hesperinus*, *G. hoogstralli*, *G. occiduus* and *G. riggenbachi*) where there are hot winters.

Caputo *et al.* (1993) used Suc's works (1984, 1989) to explain the history of the specific distinction between *Sphenops sepsoides* and *S. sphenopsiformis*. These authors state that "these two species may have diverged as a result of allopatry during the drastic climatic fluctuations of the Plio-Pleistocene. During the most mesic climatic periods, the pluvial phases in the

TABLE 1. Bioclimatic characteristics of ranges of several vicariant species. end., endemic to Morocco; temp., substage with temperate winter; **, species well represented in substage; *, marginal species in substage.

Species	endemic?	Atlantic sides of Morocco & W. Sahara				Eastern and southern sides of Morocco			
		hot	temp.	cool	cold	hot	temp.	cool	cold
<i>A. erythrurus</i>	N					*	**	**	**
<i>A. lineomaculatus</i>	Y	**	**						
<i>A. maculatus</i>	N						*	**	**
<i>A. busacki</i>	Y	**	*						
<i>A. dumerili</i>	N						**	**	
<i>A. aureus</i>	N	**							
<i>Sph. boulengeri</i>	N						**		
<i>Sph. sphenopsif.</i>	N	**							
<i>Saur. mauritanicus</i>	N						**	**	
<i>Saur. brossei</i>	Y	**	**	*					
<i>Ch. ocellatus</i>	N					**	**	**	
<i>Ch. polylepis</i>	Y	**	**	**	*				
<i>Ch. minutus</i>	?						**	**	**
<i>Ch. pseudostratus</i>	Y	*	**	**	*				

Saharan region (corresponding to high-latitude glaciations) would have caused the contraction of the once more-or-less continuous desert into separate arid refuges". The explanation given by these authors may also apply to taxa listed in Table 1.

These examples illustrate the biological originality of the north-west African Atlantic littoral region. This originality is reinforced by the existence of a cortege of species endemic to this area. *Pelobates varaldii* (Amphibia, Anura, Pelobatidae), *Geckonia chazaliae* (Reptilia, Sauria, Gekkonidae), *Chalcides mionecton* (Reptilia, Sauria, Scincidae) and *Crocidura tarfayensis* (Mammalia, Insectivora, Soricidae) are some examples of this cortege. These last species do not present oriental or non coastal vicariance.

In the Miocene, the climate of palearctic Morocco was arid, with vegetation consisting of mainly sclerophyll forests (Axelrod, 1978). This period coincided with the start of orogenic movement leading to the formation of the Atlas mountains. We believe that these two events played a major role in the differentiation of endemic species. This differentiation was accelerated by alternate pluvial and dry periods which isolated populations in either mountains or plains. Moreover, Morocco is the only north-west African country which has both Mediterranean and Atlantic coasts. The arid depression of Oued Moulouya and the Sahara Desert provide further barriers to the east and south respectively. Populations tend to be separated by these geographical partitions. In addition, Morocco itself can be divided into nine distinct geographical units: the Rif; the Oued Souss valley; the Middle Atlas; the Mediterranean coastal fringe between Melilla and Oran; the High Atlas; the Hauts Plateaux; the Anti-Atlas; the Sahara; and the Atlantic plains.

This geographical partitioning has induced an exceptional diversification of the Moroccan herpetofauna (105 species of amphibians and reptiles, of which 22 are endemics (Bons & Geniez, in prep.). The fringed lizards of the *erythrurus* group follow the same pattern, with one endemic species on the oceanic coast (*Acanthodactylus lineomaculatus*) and another one living in the rest of palearctic Morocco (*A. erythrurus*). The latter is split into two subspecies: one, an endemic (subsp. *atlanticus*) in the mountains and the hills of the Atlantic side, the other one found everywhere else in the Moroccan mountains. With nine species, including two endemics in Morocco (Salvador, 1982), the *Acanthodactylus* genus is less diversified than the *Chalcides* genus which has no less than 11 species, eight of which are endemic to Morocco (Mateo *et al.*, in prep.).

ACKNOWLEDGEMENTS

The authors would like to express their thanks to Philippe Roux and Laurent Chirio for their original data and the samples they kindly provided, as well as Claude P. Guillaume, Stéphane Boissinot and Tristan Guillosson for their advice on evolutionary systematics,

Nicolas Privat for the map treatment, and Véronique Jallageas for the re-reading of the English manuscript. Translated from the French original by Elizabeth Guillosson.

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Accepted: 9.7.94

THERMOREGULATION OF THE AMPHISBAENIAN *ZYGASPIIS QUADRIFRONS*

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The mean selected temperature of *Zygaspis quadrifrons* in a thermal gradient was 23.1°C, similar to other amphisbaenians. Body temperatures of amphisbaenians are lower than those of other squamates, but are similar to those of fossorial snakes and lizards, apart from skinks. The precision of thermoregulation in *Z. quadrifrons* was low; body temperatures had a SD of 3.8°C and an interquartile range of 6.0°C.

INTRODUCTION

Studies of the body temperatures and thermoregulation of reptiles are heavily biased towards diurnal, heliothermic lizards (Avery, 1982). Nocturnal and fossorial lizards, and other suborders and orders of reptiles, have been neglected. Perhaps the most neglected are the fossorial reptiles of the suborder Amphisbaenia. Gatten & McClung (1981), Abe (1984) and Martin, Lopez & Salvador (1990) all reported mean body temperatures of amphisbaenians of 21–23°C, rather low for reptiles from warm climates. The aim of this study was to determine the mean and variability of selected body temperature of the tropical amphisbaenian *Zygaspis quadrifrons* from Zimbabwe. Two different thermal gradients were used to test whether body temperature was being regulated or reflected random movements of the animals within the apparatus.

METHODS

Amphisbaenians were collected from May to July 1992, under small rocks in degraded miombo woodland (mixed *Brachystegia* and *Julbernardia*) at Arcturus, 25 km east of Harare (approximately 17°50'S). The temperatures in the soil from which an amphisbaenian had been captured was measured on five occasions in July 1992. The amphisbaenians were maintained at a constant 25°C, with a 12 hr photoperiod, in stock cages with 5 cm depth of wood shavings, dampened periodically. They were fed mealworms weekly. Experiments were performed in April and May 1994.

The thermal gradient consisted of a metal floor of 183 x 45 cm, with wooden sides. It was heated from below by two electric hot plates, the whole being in a constant temperature room at 12°C, with a 12 hr photoperiod. The floor was covered by 3 cm of dry wood shavings. Substrate temperatures were measured with mercury thermometers placed next to the metal floor. The temperatures available in the gradient were mapped at 10 cm intervals on an 18 x 4 point grid. Observations on the amphisbaenians were made over two weeks in the initial configuration of the gradient (A),

then for two weeks when modified by turning off one of the hot plates (gradient B).

Measurements followed a weekly routine. Amphisbaenians were placed in the gradient at about 14.00 hr on a Monday, and measurements were made at about 09.00 hr and 15.00 hr on the next four days (though some sampling occasions were missed). On Friday afternoon, the amphisbaenians were placed in 2–3 mm depth of water for 10 min to allow them to drink, then returned to the stock cages with food. They were replaced in the gradient on the following Monday. The amphisbaenians were allowed a week in the stock cages between gradients A and B.

Ten adult amphisbaenians (mean mass 4.9 g, range 4.0–6.7 g) were used throughout. Each was removed from the gradient and its cloacal temperature measured to the nearest 0.5°C with a Schultheis quick-reading mercury thermometer. The amphisbaenians were placed in a plastic bucket until all ten had been measured, then they were returned to the gradient. The data are thus pooled observations from the ten animals. Statistical analysis was by Minitab

RESULTS

Substrate temperatures where amphisbaenians were captured in the field ranged from 16.4 to 27.8°C, with a mean of 23.8°C and SD of 4.4°C. These measurements were made in sandy soil, where thermal conduction between substrate and animal was probably high; see Hailey, Rose & Pulford (1987) and Daut & Andrews (1993) for the close relation between substrate and body temperatures of small reptiles buried in sand.

Substrate temperatures differed significantly between the two gradients (Mann-Whitney test, $W = 6147$, $P = 0.0002$). Maps of temperatures available in the two gradients are shown in Fig. 1. Gradient B was more difficult for thermoregulation, in terms of the area falling within the selected temperature range (found from gradient A). Ninety-two percent of body temperatures were between 19.0 and 28.5°C; 44% of substrate temperatures were in this range in gradient A, but only 24 % in gradient B.

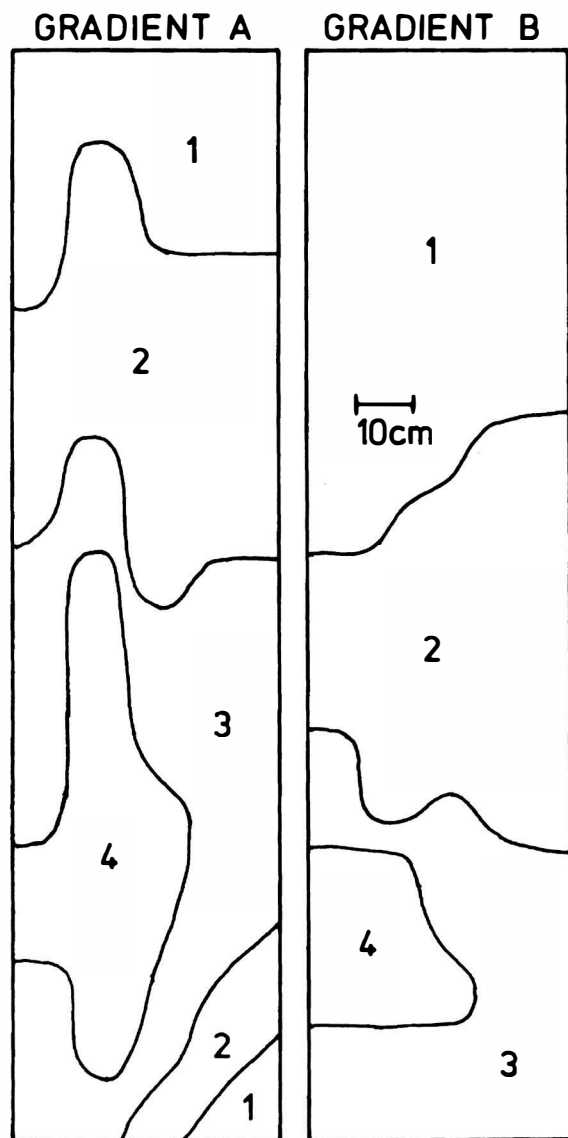


Fig. 1. Map of substrate temperatures in thermal gradients A and B. 1 = 15°C or lower, 2 = 16–20°C, 3 = 21–29°C, 4 = 30°C or greater.

One hundred and thirty body temperatures were measured in each gradient, with a mean of 23.5°C in A and 22.7°C in B. The difference between the two was not significant (Mann-Whitney test, $W = 17986.5$, $P = 0.092$), suggesting that the amphisbaenians were indeed regulating their body temperatures. The overall mean was 23.1°C, with a SD of 3.8°C and range of 15–32°C. The interquartile range (calculated to exclude the 25% lowest and the 25% highest points) of the laboratory measurements was 6.0°C, from 20.0 to 26.0°C.

DISCUSSION

Zygaspis quadrifrons had a mean selected temperature similar to those of the two species of amphisbaenians previously studied in thermal gradients, *Amphisbaena mertensi* from Brazil and *Trogonophis wiegmanni* from Tunisia (Table 1). The limited field data on both *Z. quadrifrons* and *A. mertensi* suggest that field body temperatures are simi-

lar to those selected in a thermal gradient. The only amphisbaenian studied intensively in the field is *Blanus cinereus* from Spain, which has field body temperatures similar to those of *Z. quadrifrons* and *A. mertensi* (Table 1).

The mean body temperature for the four species of amphisbaenians is thus about 22°C, rather low for reptiles from warm climates and lower than body temperatures of the other two suborders of the Squamata. Brattstrom (1965) has reviewed body temperatures of many species of snakes and lizards; the interspecific mean was 25.6°C for snakes (54 species), and 29.1°C for lizards (93 species). Is the difference between amphisbaenians and other squamates phylogenetic or ecological, due to the fossorial habit of amphisbaenians?

This question can be resolved by examining body temperatures of fossorial lizards and snakes (Table 1; habits were checked in Cogger (1986), where necessary). Several fossorial snakes and non-scincid lizards have mean field or mean selected temperatures in the range 20–24°C, similar to amphisbaenians. Two fossorial skinks, *Eremiascincus fasciolatus* and *Hemiergis decresiensis* also have mean body temperatures below 24°C. However, most fossorial skinks have mean body temperatures above 24°C; this includes other species of *Eremiascincus* and *Hemiergis*. The fossorial pygopodid *Delma fraseri* also has a high mean body temperature (Table 1).

Amphisbaenians thus do not have particularly low body temperatures compared to other fossorial reptiles. If a taxonomic distinction is to be made, it should be between fossorial skinks (and the pygopodid), and other fossorial reptiles. Skinks in general used to be thought of as having low body temperatures, but more recent data show them to be similar to heliothermic lizards (Huey, 1982). It is clear that fossorial skinks have retained high body temperatures, possibly due to a shallow depth of burrowing.

The precision of regulation in *Z. quadrifrons* was low, with a SD of 3.8°C and an interquartile range of 6.0°C. These values are similar to those for *Amphisbaena mertensi* (SD 2.7°C; Abe, 1984), and to other reptiles normally thought of as imprecise thermoregulators. For example, the anguid *Ophisaurus apodus* had a SD of 2.7°C (Hailey, 1984), and five species of gecko had an average interquartile range of 5.0°C in the field (Huey, Niewiarowski, Kaufmann & Herron, 1989). These values can be compared with those for diurnal, heliothermic lizards. *Mabuya striata* and *Lacerta vivipara* had SD's of 1.6°C and about 1.0°C, respectively (Patterson, 1989; Patterson & Davies, 1978). The average interquartile range for field temperatures of 13 species of diurnal lizards was 2.8°C (Huey *et al.*, 1989).

TABLE 1. (opposite) Mean selected temperatures (MST) and mean field temperatures (T_b) of fossorial reptiles (°C). * Approximate.

Species	MST	\bar{T}_b	Reference
Amphisbaenidae			
<i>Amphisbaena mertensi</i>	21.4	21.1	Abe, 1984
<i>Blanus cinereus</i>	-	22.5	Martin et al., 1990
<i>Trogonophis wiegmanni</i>	22.4	-	Gatten & McClung, 1981
<i>Zygaspis quadrifrons</i>	23.1	23.8	This study
Anguidae			
<i>Anguis fragilis</i>	23	-	Spellerberg, 1976
Anniellidae			
<i>Anniella pulchra</i>	21	20	Brattstrom, 1965
<i>Anniella pulchra</i>	24.2	-	Avery, 1982
Scincidae			
<i>Chalcides bedriagai</i>	-	28.5	Hailey et al., 1987
<i>Chalcides ocellatus</i>	32*	-	Daut & Andrews, 1993
<i>Eremiascincus fasciolatus</i>	22.8	-	Heatwole & Taylor, 1987
<i>Eremiascincus richardsoni</i>	-	26.2	Pianka, 1986
<i>Eremiascincus richardsoni</i>	26	-	Heatwole & Taylor, 1987
<i>Eumeces egregius</i>	-	30*	Avery, 1982
<i>Hemiergis decresiensis</i>	21.2	20.3	Heatwole & Taylor, 1987
<i>Hemiergis peronii</i>	24.3	26.3	Heatwole & Taylor, 1987
<i>Hemiergis quadrilineatum</i>	26.8	-	Heatwole, 1976
<i>Lerista bipes</i>	-	31.2	Pianka, 1986
<i>Lerista bougainvillii</i>	-	30.7	Heatwole & Taylor, 1987
<i>Lerista bougainvillii</i>	31	-	Spellerberg, 1976
<i>Lygosoma laterale</i>	-	28.8	Brattstrom, 1965
Pygopodidae			
<i>Delma fraseri</i>	-	31.7	Pianka, 1986
Leptotyphlopidae			
<i>Leptotyphlops dulcis</i>	20.6	-	Avery, 1982
Typhlopidae			
<i>Typhlops nigrescens</i>	-	14.2	Heatwole, 1976
Uropeltidae			
Various species	-	20*	Avery, 1982
Boidae			
<i>Charina bottae</i>	-	23.3	Avery, 1982
Colubridae			
<i>Carphophis amoenus</i>	23	-	Avery, 1982

ACKNOWLEDGEMENTS

This study was undertaken during a Scripps-Pitzer exchange visit (M.E.). We thank Peter Clarke for access to his farm, and Roger Avery and John Loveridge for comments. Supported by the Research Board of the University of Zimbabwe.

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Accepted: 2.12.94

SHORT NOTES

HERPETOLOGICAL JOURNAL, Vol.5, pp. 285-286 (1995)

OBSERVATIONS ON PERCH USE IN
TWO LIZARDS (*ANOLIS SCRIPTUS*
AND *LEIOCEPHALUS*
PSAMMODROMUS)

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Schoener (1975) and Schoener & Adler (1991) briefly noted the relationships of *Leiocephalus* spp. and *Anolis* spp. in the Bahamas; however these studies did not provide a detailed, quantitative assessment of the microhabitat use of these species, but they do suggest there are differences in how these species use their environment. Here I examine perch use patterns of two sympatric lizards (*Anolis scriptus* and *Leiocephalus psammodromus*) on Pine Cay in the Turks and Caicos Islands, British West Indies.

Anolis scriptus is distributed throughout the Turks and Caicos Islands, as well as the Bahamas (Schwartz & Henderson, 1991). Very little has been published on this lizard except for a description of perch use on Inagua in the Bahamas (Laska, 1970). *Leiocephalus psammodromus* is distributed throughout the Turks and Caicos Islands (Schwartz & Henderson, 1991). It is sexually dimorphic (Smith, 1992), and is reproductive from April to November (Smith & Iverson, 1993).

Pine Cay is a small (350 ha), relatively low (highest point < 3 m above mean sea level) island found in the Caicos Islands at the southeastern end of the Bahamian archipelago. The island is primarily covered with "dense scrub" and "mixed woodlands", however, "open scrub" and "beach" habitats are prevalent on the leeward coast (see Iverson, 1979 for a more detailed description of the island).

I made observations on Pine Cay between 13 July and 28 July 1991. Observations were made from 0700 to 1800 EDT. However, lizards were not individually marked to reduce the influence of the human observer on their behavior (see Marcellini & Jenssen, 1991). Therefore, I only use one day's data (22 July) to ensure that all observations are independent of each other. Because I did not sample an area more than once a day, each observation represents a different individual. I walked slowly along the edge of a path or road, or along the beach, looking for lizards. Upon observing a lizard, I recorded the species, time, and several characteristics of the perch. Substrate characteristics recorded were: (1) rock, (2) litter, (3) bare ground or sand, (4) on tree, (5) on wall, and (6) other. In addition, I noted whether the lizard was using an open or covered perch, and whether the lizard was in full sun, in a sun-shade mosaic, or in full shade. In some cases, one or more perch characteristic was not recorded.

Anolis scriptus was most often seen on trees (61.3%; 65/106), followed by rocks (24.5%; 26/106). Anoles were rarely observed on walls (5.7%; 6/106), bare/sand (4.7%; 5/106), and litter (1.9%; 2/106). *Leiocephalus psammodromus* was most often found on litter (38.6%; 27/70), followed by trees (22.8%; 16/70), bare/sand (18.5%; 13/70), and rocks (11.4%; 8/70). It was never found on walls. Niche breadths for substrate use (Simpson's $B = 1/\Sigma p_{ij}^2$; Levins, 1968) were 2.26 and 3.91 for *A. scriptus* and *L. psammodromus*, respectively. Niche overlap using Schoener's (1970) proportional overlap ($PO = 1 - 0.5 (\Sigma |p_{ij} - q_{ij}|)$) was 0.428. *Anolis scriptus* were first observed in full sun 36.2% (29/80) of the time, 13.8% (11/80) of the time in sun/shade mosaic, and 50% (40/80) of the time in full shade. *Leiocephalus psammodromus* was located in full sun 18.5% (12/65) of the time, 38.5% (25/65) of the time in sun/shade mosaic, and 43.0% (28/65) of the time in full shade. *Anolis scriptus* was first observed in the open 49.5% (49/99) of the time, whereas *L. psammodromus* was first observed in the open 19.4% (13/67) of the time.

Anolis scriptus is definitely more arboreal than *L. psammodromus*. However, on Pine Cay the former may be less arboreal than on other islands. Laska (1970) found that on the island of Inagua, *A. scriptus* used trees 86.3% of the time (145 of 168 observations), which is substantially higher than the value reported here ($G = 22.24$, $P < 0.001$).

The two lizards examined in this study did not exhibit a high degree of overlap in microhabitat use. *Anolis scriptus* also showed shifts in perch use during the day such that their use of terrestrial habitats decreased when *L. psammodromus* began to be active and using terrestrial habitats (Smith, 1994). Why *A. scriptus* and *L. psammodromus* show the patterns of habitat and microhabitat use observed in this study is unknown. There at least two possible explanations. The first is that there is or has been competition between *A. scriptus* and *L. psammodromus*. The different habitat and microhabitat use of these two species may represent resource partitioning (see Schoener, 1977). Schoener (1975) found that habitat shifts by *Leiocephalus* sp. appeared to have taken place in 44% of cases involving sympatry between *Anolis* sp. and *Leiocephalus* sp., suggesting that there is at least the potential that competition has played a role in structuring the microhabitat relations in these two lizards. On Inagua, *A. scriptus* is the only anole (Laska, 1970) as it is on Pine Cay. As on Pine Cay, *A. scriptus* on Inagua is sympatric with only one curly-tail (*Leiocephalus inaguae*; Schwartz & Henderson, 1991). Whether or not the differences in tree use (mentioned above) reflect differences in the habitat use of the two species of *Leiocephalus* is uncertain, but is certainly a possibility as the limited information available on *Leiocephalus inaguae* (see Schwartz & Henderson, 1991) and the data presented here suggest differences in habitat use. A second possible explanation is that each species has a

set of specific physiological, nutritional, or social requirements, and their microhabitat and habitat use patterns are simply reflections of these requirements (see Barbault, 1991). For example, use of different microhabitats during the day may result from thermoregulation (e.g., Davis & Verbeek, 1972; Carrascal & Diaz, 1989; Marcellini & Jenssen, 1989; Castilla & Bauwens, 1991).

While the present study cannot provide direct answers to whether or not competition is occurring or whether abiotic factors are influencing the interaction (or lack thereof), it does suggest that an investigation into the mechanism(s) driving perch use and selection in these two species would be valuable in understanding their ecology.

ACKNOWLEDGEMENTS

I thank J. Garis, manager of the Meridian Club, P. Neis & the residents of Pine Cay for their assistance and hospitality during my stay on Pine Cay. J. Iverson generously provided his field notes. R. Ballinger, D. J. Bullock, R. A. Griffiths, T. Joern, J. Rowe & anonymous reviewers provided helpful comments on earlier versions of this manuscript. Support was provided by a National Science Foundation predoctoral fellowship, a Gage Fund award from the American Society of Ichthyologists and Herpetologists, the H. Holck fund of the UNL School of Biological Sciences, and T. & J. Smith.

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Accepted: 6.1.95

SHORT NOTES

HERPETOLOGICAL JOURNAL, Vol.5, pp. 287-289 (1995)

RECURRENT MASS MORTALITY OF LARVAL MIDWIFE TOADS *ALYTES OBSTETRICANS* IN A LAKE IN THE PYRENEAN MOUNTAINS.

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In July 1992, an episode of mass mortality of larval and metamorphic midwife toads *Alytes obstetricans*, was recorded in a lake in the Pyrenean mountains (Márquez & Lizana, 1993). We report another event of mass mortality in the same site in July 1994 and we present evidence that infection by the bacterium *Aeromonas hydrophila*, a disease commonly known as "red leg", may be responsible for the occurrence.

The decline of populations of amphibians in their natural habitats in the absence of identifiable direct causes is of increasing concern for the scientific community (Blaustein & Wake, 1990; Wyman, 1990; Wake, 1991; McCoy, 1994). Recent studies have provided solid evidence of disappearances of populations of species that were common only a few decades ago throughout hundreds of kilometres of their range, particularly in montane habitats in Western USA (Carey, 1993; Fellers & Drost, 1993). In addition to these general trends, isolated events of mass mortality of amphibians have been reported in several montane populations and in some cases an infection by the bacterium *A. hydrophila* has been reported to be the cause (Dusi, 1949; Reichenbach-Klinke & Elkan, 1965; Shotts, 1984; Nyman, 1986; Bradford, 1991). So far the evidence gathered for the amphibian populations of the Pyrenean Mountains does not allow the identification of any general trends and no episodes of mass mortality have been reported. This report documents the recurrence of high death rate, involving premetamorphic overwintering larvae of the midwife toads *A. obstetricans* in the Pyrenean Mountains.

In July 1992, the Ibón de Piedrafita was visited by the authors. This is a montane lake (1600 m a.s.l.) near the town of Tramacastilla de Tena (UTM 30TYN1630, Huesca, Aragón, Spanish Pyrenean Mountains). The lake is relatively shallow, approximately 150 m in diameter, and sustained a large number of (huge) overwintering *A. obstetricans* tadpoles in July of 1988 and 1989 (RM, personal observation). Large numbers

of dead and dry tadpoles were visible on the shore of the lake in 1992. In an area of 2 m of shore the remains of over 100 dead tadpoles could be counted. Some of these we found more than 2 m away from the shore indicating that the water level had receded substantially in the last weeks. Some individuals were still alive in the water near the shore, but most of them were floating and apparently in distress. Among the recently dead and dying tadpoles, those individuals with fully developed hind legs had haemorrhagic, grossly swollen limbs and some also had areas of haemorrhage around the eyes. Metamorphic individuals were also found dead on the shore at different stages of development.

Dry, dead, adults were found under rocks, mummified in the vicinity of the water. The single fresh corpse of an adult individual found did not show signs of violent death (i.e. predation) but had an unusually conspicuous dark coloration to the thorax. The other two anuran species that bred in the same lake appeared to be unaffected. Only a single dead tadpole of *Bufo bufo* was found in 1992 and areas of the shore were teeming with juveniles of *B. bufo* and *Rana temporaria*. The only urodele that occurs in the lake, *Euproctus asper*, has never been observed in large numbers. In 1992 one apparently healthy adult individual was observed in the water during our visit. As for other aquatic vertebrates, a single species of fish is known to inhabit the lake: an introduced population of the cyprinid fish (*Chondrostoma toxostoma*). Although schools of these fishes are usually visible from the shore of the lake, we could not see any living individuals in 1992. Only one dead specimen of *C. toxostoma* was found floating near the shore. It did not show obvious signs of illness.

While no evidence of death of midwife toads was obtained in the summer of 1993, in July 1994 another episode of *A. obstetricans* tadpole die-off was observed. The dying tadpoles in the water presented similar signs to those observed in 1992. The general conditions of the lake were similar to those in 1992: large numbers of live postmetamorphic *R. temporaria* and *B. bufo* could be found on the shore, no *E. asper* were found, and only schools of fry but no adults of *C. toxostoma* could be seen from the shore.

Two samples of tadpoles were collected: a sample of eight individuals showing advanced stages of ill-health, and a sample of five healthy tadpoles from a nearby population located in the same watershed (less than 13 km north west of the lake), which did not suffer a die-off in 1992 nor in 1994. The tadpoles were kept at 5°C for transportation to Madrid; however, the diseased tadpoles died during the trip and were analysed the day after. Blood samples (1 ml) were obtained from a vein at the insertion of the hind-limb of four diseased and three healthy tadpoles. Two samples of water (1 ml), one from each of the two sites were tested as well. All samples were diluted in 20 ml of alkaline peptone wa-

ter (APW, pH 8.4-8.6). The samples were enriched by incubation at 30°C for 24 hours. They were then plated on two growth media specific for *A. hydrophila*. The first medium (Shotts & Rimler, 1973) developed yellow colonies which were used in an additional medium, specific for *A. hydrophila* (Millership & Chattopadhyay, 1984). The colonies that grew in this second medium were further tested for oxidase production, ability to ferment glucose and growth in nutrient broth without NaCl. Positive results confirmed the identification of the yellow colonies as *A. hydrophila*.

This methodology determined that the bacteria were present in the blood of all four diseased tadpoles as well as in the water samples from both sites. Only one of the three healthy tadpoles had *A. hydrophila* in its blood. A sample of the bacterial culture was collected by scraping the tip of a sterile hypodermic needle directly on the growth medium. The needle was used to cause a small rupture in the skin of the healthy tadpoles to provoke infection. Both tadpoles died in 48 hours and one of them showed clear lesions of "red leg" (haemorrhagic areas in the swollen hind limbs and lower abdomen).

Additionally, a sample of tadpoles from the Ibón de Piedrafita was collected by the Dirección General del Medio Natural de Huesca of the Diputación General de Aragón, and analysed in the facilities of the Depto. de Patología Animal, Facultad de Veterinaria, Universidad de Zaragoza. Their independent analyses confirmed the presence of *A. hydrophila* in the blood of the tadpoles in addition to other bacteria such as *Aeromonas sobria*, *Hafnia alvei*, *Pseudomonas alcaligenes*, *Micrococcus albus*, *Alteromonas putrefaciens*, *Campylobacter* spp., *Bacillus* spp. and *Aeromonas* spp.

The results of our observations and analyses are in agreement with previously reported events of mortality of montane populations of anurans in North America where the bacterium *A. hydrophila* has been identified as a cause of the die-off (Dusi, 1949; Nyman, 1986). *Aeromonas hydrophila* occurs naturally in waters that provide habitat for amphibians and it is debatable whether the infection by this bacterium is the ultimate cause or whether the bacterium acts as an opportunistic pathogen, that infects animals with weakened immunological defences due to stressors of different origins such as temperature extremes (Nyman, 1986; Carey, 1993). However, in the four nearest meteorological stations, the records of daily maximum and minimum temperatures in May, June, and July do not indicate extreme values for the year of the die-offs (1992 and 1994) when compared with the recent years where the lake was surveyed and mass mortality did not occur (1988, 1989, 1991, 1993). The maximum and minimum monthly values for the years of the die-offs are close to the average monthly extremes in the period 1971-1994. Other potential causes of stress such as an eventual change in water acidity after a fast thawing of the snow, or possible presence of toxins, remain

to be considered. The present study demonstrates that die-offs can be recurrent in natural habitats, although it must be emphasized that these episodes occur in a specific lake, since other populations of *A. obstetricans* periodically visited in the near vicinity (Márquez, 1992, 1993) did not show any signs of disease in 1992 nor in 1994. This report also extends the list of species of amphibians naturally affected by "red leg" to *A. obstetricans*. Furthermore, it is of interest to consider the differences in vulnerability between coexisting species of amphibians in the lake, with *B. bufo* and *R. temporaria* being apparently unaffected by the disease in the Ibón de Piedrafita in the years of the midwife toad die-off. Perhaps the much shorter aquatic phase of these amphibians rendered them less vulnerable to the disease that affected midwife toads or to the potential stress that lowered the defences of the midwife toad tadpoles against infection by the bacterium. In any event, the potential vulnerability of other species in the genus *Alytes*, which are also characterized by long larval periods, is of some concern, considering the endangered status of the Mallorcan midwife toad *Alytes muletensis* and the efforts devoted to its captive reproduction program (Bush, 1993; Tonge & Bloxam, 1989).

Acknowledgements. We thank P. Barrachina, J. Fabo, V. Juste and the Dirección General del Medio Natural de Huesca (Diputación General de Aragón) for their help with the monitoring of the site and the collection and analysis of the samples, and for the expeditious granting of the collecting permits. C. Franco helped with the bacteriological analyses. Meteorological data was kindly provided by E. Rodríguez from the network of the Estación Pirenaica de Ecología (Jaca, Huesca). Field work was funded by project CYCIT PB 92-0091 (PI: P. Alberch) Ministerio de Educación y Ciencia (Spain). Logistic support was provided by the Estación Bio-Geológica El Ventorrillo (C.S.I.C.).

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Accepted: 6.1.95

BOOK REVIEWS

Health and Welfare of Captive Reptiles. C. Warwick, F. L. Frye and J. B. Murphy (Eds). (1995). 299pp. Chapman & Hall, London. £45.00 (cloth).

As a graduate student in the 1980s the subject of ethics rarely came up. I recall the controversial naturalist and philosopher John Livingston debating the ethics of wildlife conservation with science faculty members. Livingston elicited extreme agitation, almost anger, in his scientific colleagues. Although on the same 'side' — in favour of wildlife conservation — the biologists disagreed with Livingston's view that emotional experiences were the only honest reason for wildlife conservation (Livingston, 1981). The scientists feared that Livingston's thesis interfered with convincing the public that conservation was an economic and a scientific imperative, free of emotive value. Ethical considerations in dealing with captive animals are not new, but they have rarely been extended to reptiles. *Health and Welfare of Captive Reptiles* is an edited volume of papers contributed for the most part by American academic biologists, with a smattering of zoo biologists and veterinarians. The tone and quality of the chapters presented in this volume vary immensely. Many of the chapters are informative and detailed, presenting physiological and behavioural information that should make everyone dealing with either captive or free-living reptiles look again at their charges and the way in which researchers and conservation managers interact with them. The chapters dealing explicitly with the biology of stress, veterinary perspectives and techniques for husbandry and research, and with empirical animal behaviour are particularly interesting.

Louis Gillette, Alison Cree and Andrew Rooney have provided a great deal of detail on the biology of stress in reptiles. Their chapter, backed by 12 pages of references, demonstrates that our understanding of stress is better advanced than one might at first expect. They present convincing evidence that stress plays a major role in the suitability of particular species to captivity, and make suggestions on how the environment can be manipulated to reduced physiological stress.

The chapter on veterinary aspects of reptiles in captivity by John Cooper and David Williams is essential reading for anyone contemplating physical manipulation of a reptile, either in captivity or in the wild. Cooper and Williams review the levels of intervention which need to be weighed against pain or other discomfort. They direct the reader to consider such psychological factors as length of time in captivity as well as types of physical contact undertaken.

The normal behaviour of reptiles is reviewed by James Gillingham. He highlights the need to have a good, empirical understanding of the normal behaviours and routines of a species under free-living conditions, and that behaviour in captivity cannot be

taken as a reliable indication of the behaviour of the specimen under wild conditions. Gillingham notes that behavioural signs are often the first indication of physiological or medical problems, and thus an understanding of both normal and abnormal behaviour is an important tool for veterinarians and biologists alike.

Other chapters are confusing, presenting little in the way of factual information, relying instead on generalizations and jargon to create the impression that there is a scientific discussion underway. The chapter by Clifford Warwick and Catrina Steedman which compares the merits of clinical and naturalistic environments for captivity of reptiles is particularly perplexing in this regard. Why, for example, are none of the claims for the superiority of naturalistic environments supported with any empirical data on longevity or other objective measures of the animals' condition?

Sadly, this book is let down by its weak ending. One has to wonder why the closing chapter by Phillip Arena and Clifford Warwick is a miscellany of factors potentially affecting the health and welfare of reptiles in captivity, when this was an excellent opportunity to break new ground. They could have given their readers constructive recommendations, a comprehensive synthesis, a plan for future research, or a balanced, scholarly treatment of the ethics of keeping reptiles in captivity. Instead, the final chapter recapitulates stress-related problems in captivity, and then touches on some areas that must be regarded as speculation at best. This includes suggestions that electromagnetic fields should be investigated for their effects on the health of reptiles, and that postulated 'Neo-Lamarckian' inheritance of acquired characteristics may somehow interfere, in unspecified ways, with *ex situ* conservation efforts.

The authors of the final chapter also appear to have a negative and uninformed opinion of reintroduction programs for reptiles, stating "While intentions and endeavours of many 'reintroduction' supporters have to be viewed with great sympathy, the extent of any valuable contribution to wildlife protection and, relatedly, animal welfare, is probably more perceived than real" (p.277). In fact, documented reintroductions of reptiles are at least as successful, if not more so, than similar programs for mammals and birds (Beck *et al.*, 1994), are undertaken with great caution given the known risks of introducing diseases and other problems to wild populations (Woodford & Rossiter, 1994) and are being actively and critically reviewed by the IUCN Re-introduction Specialist Group (Kleinman *et al.*, 1994).

Although flawed, this book is an interesting early examination of the animal welfare aspects of working with reptiles in captivity and also in nature. Those of us who work with reptiles in nature or in captivity need to be aware of the physical and psychological impact of our actions on the well-being of the animals themselves. On the surface *Health and Welfare of Captive Reptiles* deals with stress and other biological aspects

of human interactions with reptiles. After reading this volume I felt that there is a deeper agenda at work, that of trying to distance the discussion of the welfare of reptiles from our human reactions because rational arguments sound better than relying on honest emotions. Such an agenda will fail if Livingston is correct. After an exhaustive review of the agenda of rationalizing conservation, Livingston wrote "Neither you nor I need accept any obligation to rationalize those universes of emotional responses to wildlife; indeed such experiences have a way of being severely self-defeating."

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Captive Management and Conservation of Amphibians and Reptiles. James B. Murphy, Kraig Adler & Joseph T. Collins (Eds.). (1994). 408 pp. Society for the Study of Amphibians and Reptiles, Ithaca, New York, USA. (Contributions to Herpetology No. 11) \$58.00 (cloth).

This book is based on the proceedings of the symposium with the same title held at the joint meeting of the SSAR and Herpetologists' League at Pennsylvania State University in 1991. Dedicated to Roger Conant and with a foreword by Gerald Durrell, it is intended to be reasonably comprehensive, covering a broad range of issues. Particular emphasis is placed on new and special techniques, and on endangered species.

Whilst the vast majority of contributors are inevitably American, they are drawn from a relatively wide range of backgrounds: university zoology departments are particularly strongly represented, as are museums, zoological gardens and aquaria, with an assortment of conservationists, ecologists and private individuals making up the bulk of the rest. Together they present a

snapshot of state-of-the-art herptile management, as well as providing a broader perspective of herpetological conservation and an indication of desirable future developments. Although an immense amount of practically useful information is contained in this book, it is also sufficiently authoritative to raise problems to which no immediate solutions are available.

Obtaining written papers from the speakers at symposia is a notoriously difficult task, but the editors of this volume have successfully negotiated with no fewer than 70 authors. A number of these did not contribute to the original symposium, but were subsequently recruited in order to improve the balance of its contents. The result is some 40 or so chapters, grouped under the broad headings of: General Issues, Management Issues, Reproductive Biology, Model Programs for Amphibians, Model Programs for Reptiles, Future Directions and Special Techniques. The weight of material concerning reptiles is considerably in excess of that on amphibians, but there are families from within both classes that are notably absent; this is simply a reflection of the lack of available material, however.

The proof of good editorship is in the cohesiveness, consistency and plain readability of this sort of composite work. Murphy, Adler and Collins clearly started out by commissioning wisely, but have also taken great care subsequently in compiling the volume. Although some of the papers necessarily require a certain level of specialist knowledge on the part of the reader, others would be quite accessible to the interested layman. The standard of contributions is always high, though, with little in the way of unsubstantiated argument or vague generality.

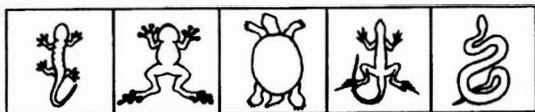
Extremely well produced (even the production specifications make interesting reading!), this book represents excellent value for money. There are 35 photographs and an attractive colour plate depicting specimens of two taxa of water snakes. Numerous tables and diagrams add to the impressive amount of information in the text, and most chapters carry extensive bibliographies. A more unusual, and rather helpful, touch is the provision, at the start of each chapter, of a list of the acronyms used.

This is not a controversial book; any consideration of ethical matters is largely incidental. Whether reptiles and amphibians should be kept in captivity and, if so, whether captive breeding is a legitimate, let alone an effective, tool in conservation, are issues on which various herpetologists inevitably have strongly opposing views. It is to be hoped, however, that all would agree with the sentiment that any captive animals should be managed as well as possible. *Captive Management and Conservation of Amphibians and Reptiles* is certain to prove of great value in achieving this goal.

Leigh Gillett
British Herpetological Society

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be included at cost to the author. 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 camera-ready for uniform reduction of one-half on A4 size paper. Line drawings should be drawn and fully labelled in Indian ink, dry-print lettering or laser printed. A metric scale must be inserted in micrographs etc. Legends for illustrations should be typed on a separate sheet.

8. References in the text should be given as in the following examples: "Smith (1964) stated —"; "—as observed by Smith & Jones (1963)." "—as previously observed (Smith, 1963; Jones, 1964; Smith & Jones, 1965)". 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 should 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 of post. Alterations should be kept to the correction of errors; more extensive alterations will be charged to the author.
11. Twenty-five offprints and one complimentary copy of the Journal 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.
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THE HERPETOLOGICAL JOURNAL

Volume 5, Number 3 1995

CONTENTS

Foraging and Food Choice Symposium Proceedings

Prey selection by lacertid lizards: a short review	J. A. DÍAZ	245
The problem of food competition in amphibians	S. L. KUZMIN	252
Ecological constraints on feeding and growth of <i>Scaphiopus couchii</i>	K. TOCQUE, R. TINSLEY & T. LAMB	257
Sensory basis of foraging behaviour in caecilians (Amphibia, Gymnophiona)	W. HIMSTEDT & D. SIMON	266

Full Papers

Contribution to the systematics of the lizard <i>Acanthodactylus erythrurus</i> (Sauria, Lacertidae) in Morocco	J. BONIS & P. GENIEZ	271
Thermoregulation of the Amphisbaenian <i>Zygaspis</i> <i>quadriifrons</i>	A. HAILEY & M. ELLIOT	281

Short Notes

Observations on perch use in two lizards (<i>Anolis</i> <i>scriptus</i> and <i>Leiocephalus psammodromus</i>)	G. R. SMITH	285
Recurrent mass mortality of larval midwife toads <i>Alytes obstetricans</i> in a lake in the Pyrenean mountains	R. MÁRQUEZ, J. L. OLMO & J. BOSCH	287

<i>Reviews</i>	290
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<i>Announcements</i>	292
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