

PROCEEDINGS OF THE SECOND WORLD CONGRESS OF HERPETOLOGY:

FORAGING AND FOOD CHOICE SYMPOSIUM

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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			First size class with IE > 0	Size class with highest IE	Maximum SVL	Ref.
	r_s	N	P				
<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 \pm 1.0	High 28.3 \pm 4.2
Size of prey captured (mean dry mass, in mg)	Small 4.6 \pm 0.5	Large 25.8 \pm 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).

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