

Prey Size and Food Selection of *Psammodromus algirus* (Lacertidae) in Central Spain

JOSÉ A. DÍAZ AND LUIS M. CARRASCAL¹

Departamento de Biología Animal I (Vertebrados), Facultad de Biología,
Universidad Complutense, 28040 Madrid, Spain

ABSTRACT.—The summer diet of the lacertid lizard *Psammodromus algirus* and the availability of potential prey were compared at a Mediterranean evergreen woodland in central Iberia. Prey size proved to be the main factor implied in the selection of both prey taxa and individual prey items: lizards were selective in the sizes of the arthropods they captured, their selectivity for different prey types was related to the mean volume of these types, and they tended to capture only the larger items when feeding from the smaller prey types. We conclude that lizards did not assess the taxonomic identity of arthropods but rather relied on prey size in their responses to food availability.

Reptiles are ectotherms whose energy requirements and hence food consumption rates are extremely low relative to endotherms such as birds and mammals (Pough, 1980; Nagy, 1983). In the southern European peninsulas, these low energy requirements translate into population densities that allow members of the family Lacertidae to become an important component of terrestrial vertebrate faunas (Avery, 1978). A further consequence of low energy demands is that maximization of the net rate of energy intake, which is the basic assumption of most optimal diet models (Stephens and Krebs, 1986), might be relatively unimportant for small ectotherms (Stamps et al., 1981; Pough and Andrews, 1985). If true, no marked patterns of prey choice should be expected among lacertid lizards, and dietary differences between species or populations could simply reflect local differences in food availability (Arnold, 1987). On the other hand, previous research on desert communities (see review by Pianka, 1986) has shown that high seasonal abundances of arthropods (such as those typical of hot, dry Mediterranean environments) tend to favor enhanced selectivity on the part of the lizards. These arguments suggest that it would be of interest to consider the relationship between prey consumption and availability on a local scale (see for instance Stamps et al., 1981; Paulissen, 1987); this would help to reveal the criteria, if any, adopted by lacertid lizards when making their foraging decisions.

The present study deals with the feeding ecology of *Psammodromus algirus*, a lacertid in-

habiting forest and scrub habitats in the Mediterranean region of the Iberian Peninsula. In spite of the high abundance of this species (Arnold and Burton, 1978), only a few reports of its diet have been published, usually on a extensive geographical scale (Valverde, 1967; Mellado et al., 1975; Perez-Mellado, 1982; Seva, 1984; Arnold, 1987). In addition, these reports focused on community structure and provide no data on prey availability and hence mechanisms of food choice. The goal of this study is to analyze the food selection patterns of a Mediterranean species of lizard in terms of basic decision rules (Schoener, 1969; Pyke et al., 1977).

MATERIALS AND METHODS

The analysis of prey selection was carried out between 25 June and 23 July 1987, at a time of year when arthropods were fairly abundant (about 21 potential prey per m² according to our estimates; see below), in a Mediterranean continental woodland (40°35'N, 43°45'W) 30 km N of Madrid, central Spain. The area, 700 m above sea level, was a holm-oak woodland in which holm-oaks were also the major components of the shrub layer.

The diet of *P. algirus* was determined from the gut contents of 53 adults and subadults from both sexes that were captured in eight different sampling days; each animal was measured (snout-vent length [SVL] and jaw length) before being killed and dissected. Since no correlation was found between the jaw length of dissected lizards and the mean length of the arthropods found in their stomachs ($r = 0.11$, $N = 53$, $P > 0.2$), all the individuals (with SVLs ranging from 55 to 75 mm) were pooled for the analysis of prey selection. Prey items and identifiable body parts were removed from the stomachs and identified to the ordinal level, with

¹ Present Address: Museo Nacional de Ciencias Naturales, UEI Vertebrados, CSIC, José Gutierrez Abascal 2, 28006 Madrid, Spain.

the exception of Formicidae. Items were classified, when possible, into 3 mm body-length size classes.

In order to obtain an estimate of prey availability, we walked arbitrary transects within the study area, and then tossed a 20 × 20 cm² wooden frame every 40 steps from a distance of about 1.5 m; we counted arthropods contained within it (or escaping from it, such as grasshoppers) during a 1 min interval. Although there are problems inherent to any method of measuring prey availability (Wiens, 1984), we assume that our sampling protocol reflects the availability of prey in the environment as it is presumably experienced by *P. algirus*. Casual observations of hunting animals showed that most captures took place in the vicinity of bushes; therefore, we tried to concentrate our sampling effort on shrub vegetation edges. *P. algirus* is an active ground forager that uses a wide variety of foraging techniques, from searching within the leaf litter to ambushing more active insects (such as grasshoppers) in the surroundings of the shrub patches. Our availability censuses took into account this variety of foraging modes, so that all arthropods were carefully searched for even when the frame was tossed onto the leaf litter; this should provide a useful index of prey availability regardless of the perceptive cues employed by foraging lizards.

All prey items were identified to order or family and assigned to body size classes as described above. During the last week of July 1987, 240 arthropod samples (i.e., frame tosses) were taken between 2–5 h after local sunrise (when the activity of *P. algirus* reaches its peak in summer months; Carrascal and Diaz, 1989), amounting to a total area of 9.6 m² of sampled ground surface.

Many authors have demonstrated that the relative contribution in biomass (or volume) of different prey types is frequently more meaningful than their relative numbers when assessing their importance in the diet of predators (Griffiths, 1986; Heulin, 1986). Therefore, we assigned a width value to each length size class of each category of prey, according to the width-length ratio provided by the measurement of a representative, intact specimen from the taxonomic group and size class considered. The shape of each prey taxon was then assimilated to an appropriate solid (either a cylinder, an ellipsoid or a hemiellipsoid; see Griffiths, 1986, for a similar approach). The distributions of estimated volumes were normalized by square root transformation prior to their use in *t*-test comparisons.

In order to determine if lizards selected prey items according to their size or taxonomic group, Ivlev's electivity index (IE; Ivlev, 1961) was cal-

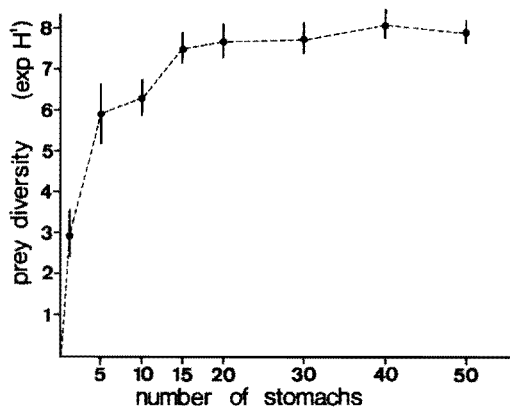


FIG. 1. Accumulated prey diversity (see Table 1 for prey categories) as a function of the number of stomachs examined. For each considered number of stomachs, the mean and 95% CI are represented; stomachs were grouped randomly (20 extractions of N out of 53 stomachs for each value of N) by means of a computer subroutine run on the original matrix of 53 stomachs × 13 prey categories. Diversity is expressed by means of the antilogarithm of Shannon's index (exp H').

culated for each body-length class and for the more common taxa in the diet and frame tosses:

$$IE = (P_s - P_a)/(P_s + P_a),$$

where P_s is the proportion of the considered prey category in the stomachs and P_a is the proportion of the same category in the environment (availability). This simple index varies monotonically between -1 and +1; negative values indicate prey rejection ($P_s < P_a$) and positive ones show active choice ($P_s > P_a$). A value of 0 indicates lack of selection ($P_s = P_a$).

Fig. 1 shows accumulated prey diversity as a function of the number of gut contents examined. Because diversity becomes stable at a low number of stomachs, the sample size was considered representative and no animals were sacrificed unnecessarily.

RESULTS

Prey Size Selection.—Of 167 prey items identified in the stomach contents, 141 could be assigned to 3 mm body-length size classes. The distribution of these was then compared (Fig. 2) with the distribution expected from the size of the arthropods found in the frame tosses ($N = 202$). Ground samples were skewed toward the smaller sizes following the general tendency of the arthropods faunas from temperate regions (Schoener and Janzen, 1968), whereas diet samples were skewed toward larger sizes. The distributions differed significantly (*G*-test: $P < 0.001$), indicating that foraging lizards, when making their food choices, were selective

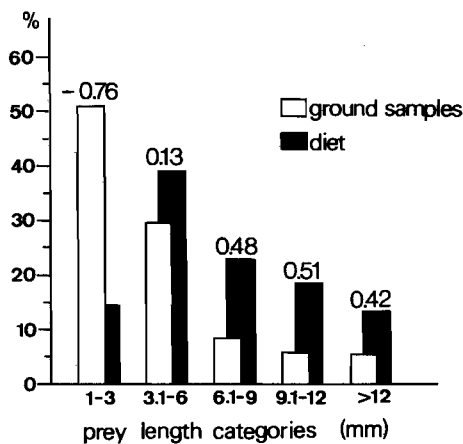


FIG. 2. Utilization of prey length categories by *P. algirus* (shaded columns) in relation to their abundance in the ground samples (white columns). Values of Ivlev's electivity index are shown on top of each pair of columns.

in the sizes of the arthropods that they captured.

Ivlev's electivity index was negative for the smaller prey (<3 mm), fairly close to zero for the 3–6 mm length class and positive for the arthropods longer than 6 mm (Fig. 2). Since the smaller and more abundant arthropods on the forest ground were rarely taken as food, lizards simply did not eat many of the potential prey available in the environment (see Discussion). Arthropods whose length ranged from 3 to 6 mm (which composed the bulk of the diet; see Fig. 2) may have been captured whenever they were found, whereas those longer than 6 mm may have been actively sought by the lizards (they were almost three times as frequent in the diet as it would be expected from their abun-

TABLE 1. Composition of the diet in *P. algirus*. N: number of items in each category; % N: percent by number; % V: percent by volume. % F: frequency of appearance in the stomach samples.

Prey category	N	% N	% F	% V
Araneae	34	20.4	43.4	7.2
Hemiptera	33	19.8	41.5	23.7
Formicidae	29	17.4	47.2	3.1
Orthoptera	28	16.8	49.1	54.0
Diplopoda	11	6.6	20.8	7.9
Other Hymenoptera	10	6.0	18.9	1.4
Larvae	8	4.8	11.3	0.6
Coleoptera	4	2.4	7.5	0.4
Diptera	3	1.8	5.7	0.4
Acarina	2	1.2	3.8	0.1
Lepidoptera	2	1.2	3.8	0.7
Plant material	2	1.2	3.8	0.2
Dermoptera	1	0.6	1.9	0.4

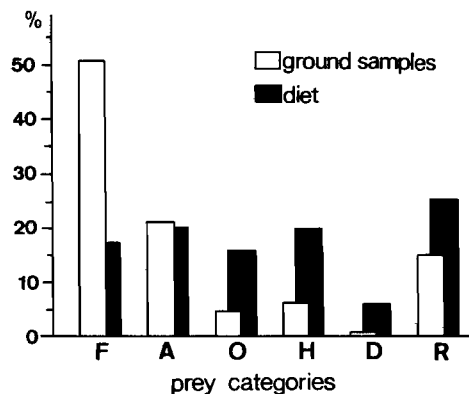


FIG. 3. Utilization of prey categories by *P. algirus* (shaded columns) in relation to their abundance in the ground samples (white columns). F = Formicidae, A = Araneae, O = Orthoptera, H = Hemiptera, D = Diplopoda, R = Rest of prey types.

dance in the ground samples). On the other hand, it should be stressed that there was a prey length selectivity threshold at about 6 mm, upon which threshold selection of prey sizes by *P. algirus* remained unchanged. In other words, selectivity for items longer than 6 mm, though positive, was not an increasing function of prey size.

Prey Taxa Selection.—The diet was almost exclusively made up of arthropods (Table 1), with five taxa (Araneida, Hemiptera, Formicidae, Orthoptera and Diplopoda) accounting for 81% of the total number of prey and for 96% of the estimated volume of ingested food. In addition, these five taxa had also a high frequency of appearance in the stomachs (see % F in Table 1), thus excluding the possibility of biasing our results with the consideration of prey types consumed in large amounts by only a few individuals. The analysis of prey taxa selection was consequently based on these commonest groups.

Ants were the only taxon for which consumption was unequivocally smaller than availability (Fig. 3). The proportion of spiders in the diet closely reflected their relative abundance in the frame tosses. Bugs, grasshoppers and millipedes were positively selected by the lizards. Though the relative contribution of these five prey types to the diet of *P. algirus* was not significantly correlated with their estimated abundance ($r = 0.37$, $N = 5$, $P > 0.5$), their volume percentages in the stomach contents were related to their relative proportion of the estimated prey volume available in the environment ($r = 0.96$, $N = 5$, $P = 0.01$).

Because prey size proved to be important for prey selection by *P. algirus*, and since average body size makes an obvious difference among

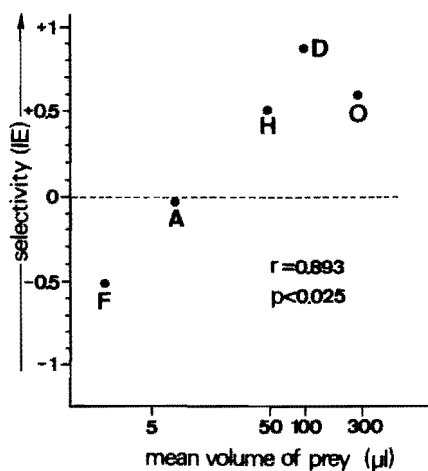


FIG. 4. Logarithmic relationship (one-tailed test) between the selectivity of *P. algirus* for the prey types most often consumed (estimated by means of Ivlev's electivity index, IE) and the mean volume of these prey types in the ground samples. The dashed line indicates no apparent selection. Symbols of prey types as in Fig. 3.

the five considered arthropod taxa, we attempted to interpret the observed pattern of prey selection on the basis of the mean estimated volumes of potential prey. If lizards had selected prey taxa primarily by size, selectivity for the major taxa should have been related to their mean estimated volume in the ground samples (an index of their energy content). The correlation obtained was in fact high and significant ($r = 0.89$, $N = 5$, $P < 0.025$; one-tailed), its logarithmic nature (see Fig. 4) being consistent with the previously described prey-size selectivity threshold.

The importance of prey volume applied not only to differences in selectivity between taxa, but also to selection of individual items within all but the largest taxa (Table 2); the mean estimated volumes of ants, spiders and bugs in the stomach contents were larger than the corresponding mean volumes in the frame tosses (t -tests: $t_{132} = 6.8$ for ants and $t_{72} = 3.81$ for

spiders, $P < 0.001$ in both cases; $t_{44} = 2.18$, $P < 0.05$ for bugs), whereas the consumption and availability means did not differ significantly in the case of grasshoppers ($t_{28} = 0.73$, $P > 0.4$). Diplopods were not included in this analysis due to their scarcity in the ground samples and to the difficulty of accurately estimating the length of individual items from the remains found in the stomachs. It should be noted (Table 2) that the degree of overlap between the available and consumed ranges of estimated prey volumes increased with the mean volume of prey taxa, and that the confidence intervals for diet means were all above the $7.7 \mu\text{l}$ mean volume of a 3 mm prey from the stomach contents (lower limit of positive selection).

DISCUSSION

Several authors (Schoener, 1971; Jaeger and Barnard, 1981) have relied on arthropod size as a rough but useful index of the energy contents of the food taken by insectivores. If we accept that maximal efficiency in energy intake is favored by natural selection (Pyke et al., 1977; Krebs et al., 1983), we should expect prey size to play an important role in the foraging strategies of most insectivorous reptiles and amphibians (Schoener, 1969, 1971; Jaeger and Barnard, 1981; Freed, 1988). Our results were consistent with this viewpoint, showing that prey size provided the basic decision rules for the choice of diet in *P. algirus*. Thus, lizards were selective in the sizes of the arthropods that they captured (Fig. 2), their selectivity for different prey types was related to the mean volume of these types (Fig. 4), and they tended to capture only the larger individuals when feeding on the smaller prey types (Table 2).

Though selectivity for the arthropod taxa most often consumed was positively related to mean prey size, this relationship was not linear. Instead, there was a threshold above which selectivity remained unchanged, thus fitting a logarithmic function of the mean volume of prey available. Similarly, selectivity for items longer than 6 mm did not increase with increased prey size but became stable or even de-

TABLE 2. Means (mean, 95% confidence interval and sample size) for the estimated volumes (in μl) of prey categories in the diet and ground samples.

Prey category	Ground samples			Diet		
	\bar{x}	95% CI	N	\bar{x}	95% CI	N
Formicidae	4.0	2.7-5.3	105	13.4	10.0-16.8	29
Araneae	7.6	3.2-12.0	44	29.5	18.0-41.0	30
Hemiptera	48.7	0 ¹ -111.7	13	90.4	50.7-130.1	33
Orthoptera	280.9	178.9-382.9	9	323.3	262.4-384.2	21

¹ The value obtained (-14.3) was negative and hence meaningless.

creased slightly in the case of the largest prey category (> 12 mm). This can be explained by considering that there could be a trade-off between the benefits of eating larger prey and the costs of locating, capturing and handling these prey that, being relatively scarce (Fig. 2), were probably harder to find and highly time consuming (Schoener and Janzen, 1968; Pough and Andrews, 1985). Assuming that selection of prey types reflects their profitability to the predator (Paulissen, 1987), it follows that profitability should not increase monotonically with prey size. Factors other than net energy gain could become important above a certain threshold; in fact, the bulk of the diet was made up of arthropods between 3 and 6 mm in length.

On the other hand, *P. algirus* appeared to be very consistent in the rejection of prey smaller than the lower (3 mm) limit of positive selection (see Sexton et al., 1972, for a similar result with *Anolis limifrons*). The consumption of small prey in a lower frequency than they occur in the environment could be due to several reasons. For instance, lizards might not be able to encounter, catch or handle such small prey. However, the foraging mode of *P. algirus* and the actual consumption of certain small prey indicate that the ignorance of unprofitable, encountered small prey is probably the most likely explanation (captures < 3 mm were mainly soft bodied spiders, which were almost spherical and hence more voluminous than other arthropods of a similar length).

Although ants, whose average volume (and hence energy content) was very low in the availability samples, accounted for a relatively high proportion of the diet, this does not imply non-fulfillment of the all-or-none rule postulated by optimal foraging models (Stephens and Krebs, 1986). Selection of prey sizes also applied within prey taxa, in such a way that the mean volume of the ants consumed exceeded the mean volume (7.7 μ l) of an average 3 mm prey from the stomach contents (Table 2); only one of 167 prey eaten was an ant smaller than 3 mm. Therefore, the within-types selection of individual items according to their size could explain the consumption of a highly rejectable prey type (Fig. 4) without falling into a partial preference (Stephens and Krebs, 1986).

Since the mean estimated volume of the major prey types accounted for a high percentage ($r^2 = 79.2\%$) of the variance found in the predator's selectivity, it is reasonable to think that prey size was probably the most important factor, though not necessarily the only one, in the series of day-to-day foraging decisions adopted by *P. algirus*. It should be noted that our analysis was restricted to a few prey taxa; the inclusion of other prey types could lead to a more com-

plex situation, with additional variables being needed to explain the observed pattern of prey selection. Other factors such as nutrient constraints (Stamps et al., 1981), chitin content (Skoczylas, 1978; Jaeger and Barnard, 1981) or prey defensive behavior (Rissing, 1981) could also condition the choice of diet performed by *P. algirus*, but it seems unlikely that their influence exceeds the one attributable to prey size. In addition, the five considered arthropod taxa accounted for 81% of the total number of ingested items; this minimizes the probability of disregarding any major decision rule (see Stamps et al., 1981, for a detailed discussion of this topic).

Insectivorous lizards have been shown to behave as opportunistic feeders that capture almost any prey that they encounter (Mitchell, 1979; Barbault et al., 1985; Arnold, 1987). Nevertheless, *P. algirus* seemed to exert a high degree of prey selection, as the consumption of the main prey types was uncorrelated with prey availability. However, because the more abundant but smaller prey items still contributed very little to the total prey volume in the ground samples, the volumetric contribution of prey types to the diet closely tracked their relative contribution to the prey volume available in the environment; this reinforces the importance of prey size as the prime factor implied in prey selection.

The selection of prey according to their size could also be interpreted in the light of a movement minimization strategy, since as mean prey size increases, the number of prey items that a lizard requires eating decreases (Pough and Andrews, 1985). This strategy would allow the lizards to minimize the number of movements that would reveal the presence of the animals to their potential predators, which are numerous in the case of *P. algirus* (Valverde, 1967). Thus, Paulissen (1987) found marked differences between the foraging times of juvenile and adult *Cnemidophorus sexlineatus*, that were associated with differences in the mean length of the prey ingested. Consistent with this viewpoint, Fox (1978), in a detailed study of the survival of juvenile *Uta stansburiana*, suggested that the negative effect of food shortage on survival could be indirectly mediated by a higher predation risk among animals obliged to forage for longer time or in more exposed locations.

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