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# Regional distribution of a Mediterranean lizard: influence of habitat cues and prey abundance

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**Abstract.** We studied the distribution of a common Mediterranean lacertid lizard, *Psammodromus algirus* (L.) 1758, on nineteen sites within a regional gradient of homogeneous yet contrasted habitats. This scale was large enough to allow line-transect estimates of lizard abundance, which were related to quantitative (and when possible multivariate) measurements of the structure and floristic composition of vegetation, the abundance of arthropod prey, the relative density of other lizard species, and the climatic data obtained from nearby meteorological stations. Neither the climate not the abundance of other lizards seemed to condition the quantitative distribution of the species. The positive influence of broad-leaved forests on the abundance of *P. algirus* appeared to be a consequence of structure attributes more directly related to the ecology of lizards than floristic composition *per se*. Thus, population levels were most highly correlated with the cover of shrubs over 20 cm in height, and once this structural requirement was met, they increased with the abundance of potential prey (itself conditioned by vegetation cover at the ground level and litter cover). We suggest that our results should be interpreted in the context of thermoregulatory, predator avoidance and movement minimization strategies whose influence on survival, and hence abundance, could probably be applied to other insectivorous lizards from temperate zones.

**Key words.** Habitat cues, lizard, Mediterranean, prey abundance, regional distribution.

## INTRODUCTION

A number of broad-scaled studies dealing with the distribution of reptiles and amphibians have used the presence or absence of species to produce distribution maps that have been interpreted in the light of historical and/or climatological factors. Usual subjects of such studies are the variations in species richness and the environmental features associated with the limits of distribution ranges (e.g. Schall & Pianka, 1977; Bock, Bock & Fritz, 1981; Spellerberg, 1982; Watson & Littlejohn, 1985). However, and partly because of methodological limitations, these extensive analyses do not reveal the ecological mechanisms concerning the ultimate causes of distribution patterns (Myers & Giller, 1988; Wiens, 1989a).

Other works have focused on the habitat preferences of particular species or communities, sometimes considering the relationships between habitat features and differential performance of individuals or populations (energy balances, growth rates, survival, etc., e.g. Fox, 1983; Reinert, 1984; Karasov & Anderson, 1984; Huey *et al.*, 1989). These intensive studies require the monitoring of animals in a low number of small, homogeneous areas; this precludes the emergence of covariation patterns between environmental gradients and reptilian abundance.

On the other hand, there is a lack of herpetological studies covering the regional scale used in this paper (but see Thorpe & Brown, 1989; Stockwell & Hunter, 1989). Such intermediate scale should prove useful by offering a number of advantages. It should allow one to identify the environmental cues that condition the between-habitat variations in abundance. It should therefore make clear that distribution is a continuous rather than discrete phenomenon, with an emphasis on the relative importance of the various interacting factors (e.g. structure of vegetation, food abundance, etc.) that could determine population levels. Moreover, as far as abundance is an indicator of habitat suitability (which is expected in seasonally active ectotherms with relatively low dispersal capacities occurring along a gradient of homogeneous habitats; Van Horne, 1983), this approach could lay a bridge between zoogeography and population ecology, so that hypotheses connecting habitat suitability with the biology of a particular species could be postulated and tested.

Within this context, the goal of this study is to analyse the local variations in the relative abundance of a common Mediterranean lizard species, *Psammodromus algirus* (L.) 1758 (Fig. 1). We consider the effects of habitat structure, flora, prey abundance, climate and potential competition with other Lacertidae. Our results are interpreted in the

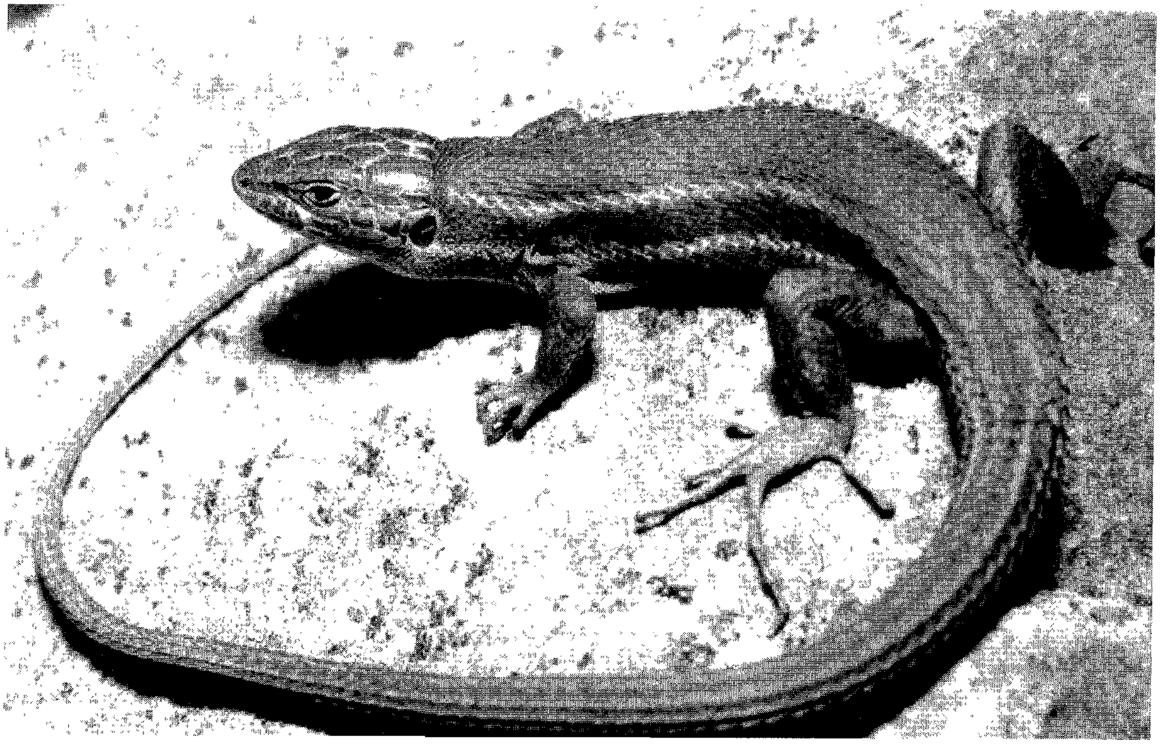

FIG. 1. An adult large psammodromus (*Psammodromus algirus* [L.] 1758). Photograph by A. Salvador.

light of explanatory hypotheses that can probably be applied at a broader geographical scale; although it is always difficult to interpret widespread distribution patterns in terms of the factors causing local abundance, the lack of documented racial variation within the species chosen and its distribution restricted to the western Mediterranean (Böhm, 1981) support the hypothesis that limiting environmental factors should not differ markedly between areas of its distribution range.

## MATERIAL AND METHODS

The abundance of *P. algirus* was estimated in July 1989 at nineteen plots located within an area of 7000 km$^2$ comprising an altitudinal gradient (500–2000 m a.s.l.) between the Tajo Basin and the Sierra de Guadarrama, central Spain. Internally homogeneous sites (grasslands, shrublands and different types of woodlands) were selected so that they could adequately illustrate the variability of the landscape within the regional gradient. Within each plot, we walked 1 km transects counting all lizards seen within a 5 m wide belt; transects were repeated between two and five times and the maximum number of individuals observed was used as a relative index of the abundance of the species. This simple index does not provide a measure of the actual density of lizards, but allows the between-habitats comparison of abundances at a broad geographical scale, facilitating the detection of underlying biogeographical patterns (Caughley, 1977; Tellería, 1986). Thorpe & Brown (1989) and Chase *et al.* (1989) used similar approaches with reptiles. All censuses were carried out in sunny days between 07.00 and 09.00 hours GMT, with air temperatures ranging from 18 to 26°C, i.e. during the daily period and under the thermal conditions in which the summer activity of *P. algirus* reaches its peak (Carrascal & Díaz, 1989). We also noted the observations of other species of Lacertidae (*Psammodromus hispanicus* Fitzinger 1826, *Podarcis hispanica* (Steindachner) 1870, *Podarcis muralis* (Laurenti) 1768, *Acanthodactylus erythrurus* (Schinz) 1833, *Lacerta lepida* Daudin 1802 and *Lacerta schreiberi* Bedriaga 1878) within the survey belt.

Habitat structure and floristic composition of survey plots were quantified by means of a scored stick that was stood vertically on the ground at 10 m intervals over the line transect. We used the stick to assess whether vegetation was contacted at 0, 10, 20, 30 or 50 cm; if positive, the identity of the plant(s) contacted was noted. We also considered the presence or absence of leaf litter on the ground and of tree canopy over the vertical projection of the stick (see e.g. Reinert, 1984; Scheibe, 1987; Carrascal, Díaz & Cano, 1989). This technique provided detailed habitat descriptions based on objective percentage covers (number of positive contacts out of 100 sample points).

The relative abundance of arthropod prey was estimated by tossing a 20×20 cm$^2$ wooden frame and counting during 1 min the arthropods contained within it; frame tosses were made at 20 m intervals, providing fifty samples per transect. We only considered arthropods longer than 3 mm (those positively selected by *P. algirus*; Díaz & Carrascal, 1991). Although there are problems inherent to any method of measuring prey availability (Wiens, 1984), we assume that our sampling protocol reflects the abundance of prey experienced by *P. algirus*, an active ground forager that uses a wide variety of foraging techniques, from searching within the leaf litter to ambushing more active insects.

Climatological data were obtained from the weather stations closer to each plot (always within a distance of less than 5 km), considering the mean values for periods of at least 7 years (Elías & Ruiz, 1977). The climatic variables selected were indicative of the amount of sun radiation received (number of cloudy days between March and October, i.e. during the annual activity period of *P. algirus*), the amplitude of the activity period (number of frost-free days), the levels of primary production (annual precipitation and evapotranspiration), the degree of thermal stress by excess or defect in critical months (highest temperature in July and lowest temperature in January), and the mildness of climate at the beginning and end of the activity period (mean temperatures in April and October). Although these data did not include the study year, they adequately represent the climatic differences among sites. They can therefore be used to evaluate the spatial variations of lizard population sizes as a function of mesoclimate, specially since lizard abundances seem to be fairly constant through time (Schoener, 1985).

Patterns of covariation within each subset of data (structural, floristic and climatic variables) were revealed by a series of principal components analyses after having rotated the initial factors by the Varimax procedure. Rotations were performed because the rotated factor loadings were conceptually simpler than the unrotated ones; the ultimate goal was to obtain some theoretically meaningful factors with the simplest possible factor structure (see Harman, 1967, p. 98). Other statistical tools were stepwide multiple regression and simple and partial correlations (Nie *et al.*, 1975).

## RESULTS

The three first principal components emerged from the vegetation structure matrix accounted for 93% of its original variance. These three components (Table 1) defined a tendency towards denser vegetation in the vicinity of the ground (0–20 cm in height; SPC1) and in the low shrub layer (cover 20 cm in height; SPC2), as well as a gradient of forest development associated with increasing covers of trees and leaf litter (SPC3). Floristic composition (Table 2) yielded less clear results probably reflecting a high degree of landscape modification by human influence. The four selected factors (89.5% of variance explained) give high scores to deciduous forests (FPC1), broad-leaved perennial forests (FPC2), and pine forests as opposed to *Cistus* shrublands (FPC3) or open roughlands dominated by forbs (FPC4). Finally, climatic variables (Table 3) were incorporated into a single principal component (CPC: 80.36% of variance explained) giving higher scores to warmer and drier climates.

TABLE 1. Principal components analysis with the structural variables within the nineteen plots surveyed. p.c.: plant cover. significant correlations between original variables and components are in italics.

| | SPC1 | SPC2 | SPC3 |
|---|---|---|---|
| Cover of litter | −0.26 | 0.17 | *0.92* |
| p.c. at the ground level | *0.94* | −0.20 | 0.06 |
| p.c. 10 cm in height | *0.89* | 0.36 | −0.10 |
| p.c. 20 cm in height | *0.69* | *0.69* | −0.01 |
| p.c. 30 cm in height | 0.35 | *0.91* | −0.01 |
| p.c. 50 cm in height | −0.20 | *0.91* | −0.06 |
| Cover of trees | 0.26 | −0.27 | *0.89* |
| Eigenvalue | 2.45 | 2.40 | 1.66 |
| % variance | 35.00 | 34.30 | 23.70 |

TABLE 2. Principal components analysis with the floristic composition of the nineteen plots surveyed. Significant correlations between original variables and components are in italics.

| | FPC1 | FPC2 | FPC3 | FPC4 |
|---|---|---|---|---|
| Cover of deciduous trees | *0.89* | −0.20 | 0.17 | 0.09 |
| Cover of holm-oaks | −0.10 | *0.90* | −0.27 | 0.07 |
| Cover of pines | *−0.49* | −0.33 | *0.47* | *0.56* |
| Cover of herbs | *0.50* | −0.19 | *0.68* | 0.36 |
| Cover of forbs | −0.25 | 0.02 | 0.10 | *−0.95* |
| Cover of cistus | −0.18 | 0.08 | *−0.94* | 0.17 |
| Cover of holm-oak samplings | −0.29 | *0.84* | 0.05 | −0.20 |
| Cover of deciduous bushes | *0.87* | −0.23 | 0.21 | 0.14 |
| Eigenvalue | 2.23 | 1.76 | 1.72 | 1.45 |
| % variance | 27.90 | 22.00 | 21.50 | 18.12 |

TABLE 3. Principal components analysis with the climatic variables describing the nineteen plots surveyed. All correlations between original variables and components are significant.

| | CPC |
|---|---|
| Annual no. of frost-free days | 0.85 |
| Annual no. of overcast days | −0.55 |
| Precipitation (mm) | −0.89 |
| Evapotanspiration | 0.99 |
| Lowest temperature in January | 0.96 |
| Highest temperature in July | 0.91 |
| Mean temperature in March | 0.96 |
| Mean temperature in October | 0.98 |
| Eigenvalue | 6.43 |
| % variance | 80.36 |

The relative abundance of *P. algirus* was then correlated with the scores of the nineteen study plots on each principal component and with our estimates of prey availability and abundance of other lizard species. We analysed the influence of vegetation structure and floristic composition (SPCs and FPCs) by means of partial correlation within each group of gradients (Table 4). Only the structural components were significantly correlated with the abundance of *P. algirus*, though there were also associations with the two first FPCs and with the estimated abundance of prey at marginal significance levels. Neither the climatic variables (CPC scores) nor the numbers of other lizards seemed to have any influence on the abundance of *P. algirus*.

TABLE 4. Partial correlations between the abundance of *P. algirus* and the scores of the surveyed plots on the structural and floristic components, and simple correlations with the climatic component, food abundance and relative densities of other lacertid species.

| | | |
|---|---|---|
| Structural components | | |
| SPC1 | 0.48 | $P$=0.05 |
| SPC2 | 0.84 | $P$<0.001 |
| SPC3 | 0.63 | $P$<0.01 |
| Floristic composition components | | |
| FPC1 | 0.48 | $P$<0.1 |
| FPC2 | 0.43 | $P$<0.1 |
| FPC3 | 0.15 | $P$>0.1 |
| FPC4 | −0.04 | $P$>0.5 |
| Climatic component | | |
| CPC | 0.07 | $P$>0.5 |
| Food abundance index | | |
| No. arthropods > 3 mm | 0.45 | $P$=0.053 |
| Other lizard species | | |
| No. per transect | −0.02 | $P$>0.5 |

A multivariate approach showed that all the SPCs entered into a stepwise regression model with the abundance of *P. algirus* as the dependent variable and the series of structural scores as the independent variables. This model was highly significant ($P$<0.001) and explained a high percentage of the variance observed in the estimated numbers of lizards ($R^2$=77.4%). A similar model with the floristic components as the independant variables included only the two first FPCs, showing a positive relationship between the abundance of *P. algirus* and the cover of broad-leaved deciduous and perennial forests. Nevertheless, this floristic model had a much lower predictive power ($R^2$=34%, $P$<0.05).

When the stepwise selection was repeated taking into account all possible independent variables, the second structural component (i.e. development of the low shrub layer over 20 cm in height; $P$<0.001) and the abundance of potential prey ($P$=0.0025) were the only variables to enter the final model ($R^2$=75.9%, $P$<0.001). Therefore, the abundance of *P. algirus* on a between-habitats geographical scale increased with the cover of shrubs over 20 cm in height and the abundance of ground arthropods (Fig. 2). It should be noted that the effects of vegetation cover at the ground level (SPC1) and litter cover (SPC3) were at least partially mediated by their influence on food availability, since the estimated abundance of arthropods was positively correlated with these two gradients (partial correlations: $r$=0.58, $P$=0.01 and $r$=0.52, $P$=0.03 for SPC1 and SPC3 respectively), whose combined influence explained 47.1% of the variance found in the numbers of prey.

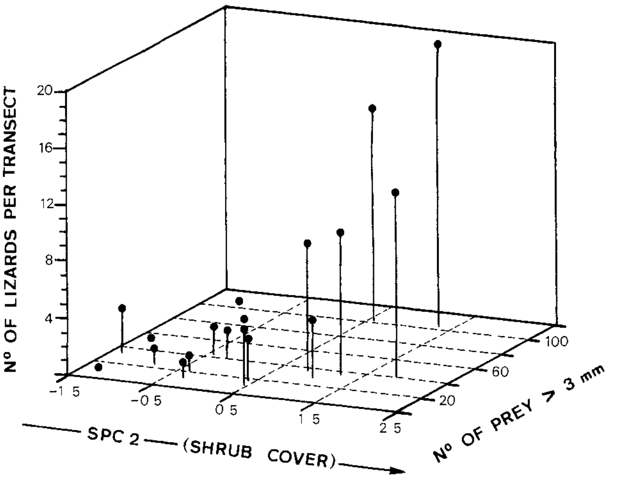

FIG. 2. The number of lizards seen per 1 km transect as a function of the cover of bushes over 20 cm in height (SPC2 scores, see Table 2) and the number of arthropods longer than 3 mm.

In order to check the validity and degree of generality of this overall pattern, we randomly chose ten out of the nineteen study plots, and then tried a multiple regression of the abundance of *P. algirus* on the SPC2 scores and estimated prey abundances of the selected plots. This randomization–regression process was repeated ten different times. SPC2 was significantly correlated with the abundance of *P. algirus* in all trials, whereas the estimate of food abundance entered the regression model in seven out of ten trials. The average percentage of variance explained by these two variables in the ten trials was 73.85% (7 d.f., $P$<0.01). The bivariate equations were subsequently used to predict the abundance of *P. algirus* in the nine plots randomly left unemployed during the building of each model. Predicted and observed values were significantly correlated ($P$<0.05 in one-tailed tests) in eight out of ten simulations, with an average correlation coefficient of 0.698 (7 d.f., $P$<0.05, one-tailed).

## DISCUSSION

The lack of significant correlation between the abundance of *P. algirus* and the scores on the climatic gradient (CPC) indicates that mesoclimate is not truly important for the distribution and abundance of this lizard species. However, more accentuated climatic variations at a larger scale seem to condition its distribution limits. Thus, Castroviejo & Salvador (1970) found that the distribution of *P. algirus* in northwestern Spain closely tracked Mediterranean climatic conditions within a region of Eurosiberian climate. This apparent discrepancy indicates that care should be taken when considering the effects of climate at different biogeographical scales (review in Wiens, 1989b). In addition, it is sometimes difficult to assess if animal distribution patterns are directly attributable to climate through physiological processes (Root, 1988a, b; Thorpe & Brown, 1989), or merely reflect the effects of climate on, e.g., vegetation structure or composition. At a regional scale, structural and trophic factors (i.e. factors that operate at the level of individuals determining such processes as predator avoidance, foraging success or territory holding) seemed to obscure the effects of climatic conditions. Thus, the species would not be present or it would be very scarce at any particular locality that, despite having the appropriate mesoclimate, lacked the structural or trophic conditions required for its survival and reproduction.

The presence of other lacertid species seemed to be unrelated with the distribution and abundance of *P. algirus* at a regional scale. This leads to the conclusion that the role of competition in the structure of lacertid assemblages should at best be analysed at much more reduced spatial scales, by means of experimental studies of interspecific interactions and considering what particular resources are in limited supply (Schoener, 1983; Connell, 1983; Tilman, 1987).

The effects of floristic composition on the abundance of *P. algirus* vanished with the exclusion of other environmental attributes that appear to be more important for the biology of the species. Thus, the cover of perennial oaks (trees and saplings; FPC2) was significantly correlated ($r$=0.48, $P$=0.037, $n$=19) with shrub cover over 20 cm in height (SPC2), and the cover of deciduous shrubs and trees was significantly correlated with the abundance of arthropods ($r$=0.71, $P$<0.001, $n$=19). These results show that floristic gradients positively covariating with the abundance of *P. algirus* did not have true causal effects (Pianka, 1967) but merely reflected underlying biological processes (e.g. influence of SPC2 and arthropod abundance on thermoregulation, predator avoidance or foraging success; see below). This general trend also applied to microhabitat selection by *P. algirus* at a local scale outside the study area (Carrascal *et al.*, 1989).

It should be stressed that a single structural component (SPC2, the development of the low shrub canopy) accounted for more than two-thirds of the variance observed in the abundance of *P. algirus*. Previous research (reviewed in Heatwole, 1977) has shown vegetation structure to play a crucial role in reptilian habitat selection by conditioning features of such vital importance as antipredator escape (Stamps, 1983), foraging (Karasov & Anderson, 1984) or mate access. But why did the number of lizards seen covariate so strongly with a single synthetic aspect of vegetation structure? A look at two basic requirements of lizard biology, thermoregulation and predator avoidance, might provide the clues. Thus, low shrub cover above 20 cm in height generates a continuous sun/shade gradient along which thermoregulating animals would be able to select their position (Grant & Dunham, 1988; Carrascal & Díaz, 1989), and the same low, dense bushes would offer a good refuge for flight no matter what their taxonomical identity. Moreover, the sometimes conflicting demands of basking and finding shelter meet in the distance to shade/protective cover (Carrascal & Díaz, 1989). A high cover of low shrubs produces true thermal gradients (not too short nor too sudden; Strijbosch, 1988) that facilitate to minimize such distance and the length of the movements between sun and shade. This would ultimately enhance survival (by favouring optimal body temperatures and reducing predation pressure) and hence produce more numerous populations.

The development of a thick underbush as a typical feature of the habitats occupied by *P. algirus* has been pointed out by several authors (Mellado *et al.*, 1975; Arnold, 1987), but none quantified its effects with precision. The biogeographical significance of the association found is reinforced, within a more historical perspective, by the complex of characters (imbrication of ventral scales, absence of collar, strongly built keeled dorsal scales) that, following Arnold (1973), have evolved in *P. algirus* as a functional adaptation to locomotion and survival in spiny, dense vegetation.

Similarly, we have observed individual lizards searching refuge into the deep layer of ground litter (twigs and fallen leaves) of the plots in which *P. algirus* was more abundant. Litter is not only the substratum preferred by this species (Mellado, 1980; Arnold, 1987; Carrascal *et al.*, 1989) but also the one in which most foraging activities take place (pers. obs.). In fact, the effects of litter cover (SPC3) and plant cover at the ground level (SPC1, presumably an index of primary production) on the abundance of *P. algirus* seemed to be mediated by their positive association with the abundance of prey (see Results). Thus, the availability of arthropod prey (on the other hand fairly abundant in Mediterranean environments in summer: Herrera, 1980; Tellería *et al.*, 1988) did influence the abundance of the predator over the main effects attributable to habitat structure (SPC2), since the partial correlation obtained was highly significant $r$=0.667, $P$=0.0025). Such a result has been previously reported for endothermic birds (Brush & Stiles, 1986) but rarely for reptiles; the few available observational data (e.g. Heulin, 1985) do not allow one to distinguish between the effects of food abundance on lizard densities and the more casual associations that could be due to converging habitat selection patterns – as it could have been the case of litter cover and plant cover at the ground level in our own study. Notwithstanding, food abundance seemed to play a secondary role in the control of lizard abundance. In other words, once the basic structural requirements for the settlement of *P. algirus* were met, lizard abundance increased with the number of arthropods; but the absence of the species from the localities that, despite their high abundance of arthropods, had low plant covers above 20 cm in height (e.g. pastures, deciduous woodlands with little or no underbrush), could not be explained in terms of low food availability (Fig. 2).

The intriguing effects of food abundance on lizard population levels could again be interpreted as the consequence of a trade-off (Sih, 1980) between the conflicting demands of getting enough food and avoiding the numerous predators that feed on *P. algirus* (Valverde, 1967). Habitats with high arthropod densities would allow the lizards to minimize their gross foraging effort (i.e. number of movements that would reveal the presence of the animals to their potential predators) thus enhancing their survival. This is consistent with the selection of prey according to their size (Díaz & Carrascal, 1991), since as mean prey size increases, the number of times that a lizard requires making a capture decreases (Pough & Andrews, 1985). Another explanation, which is not mutually exclusive (McNamara & Houston, 1987), of the influence of food availability on the abundance of *P. algirus*, could be obtained by considering the effects of food abundance on the growth and fecundity of lizards (Dunham, 1978; Ferguson *et al.*, 1983; Guyer, 1988).

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