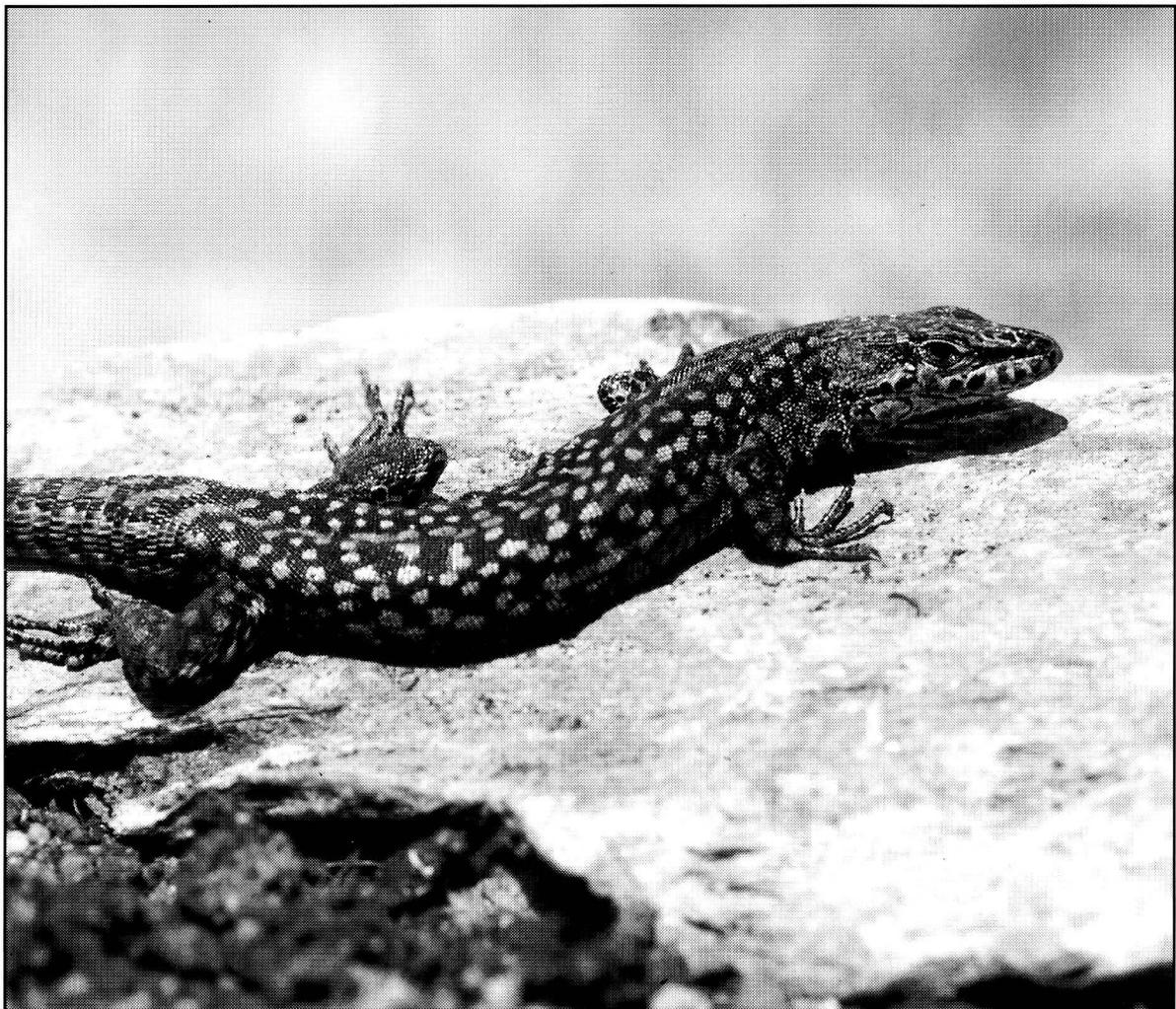


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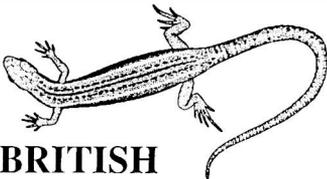
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A PREDICTIVE DISTRIBUTION MODEL FOR THE IBERIAN WALL LIZARD (*PODARCIS HISPANICUS*) IN PORTUGAL

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The geographic distributions of two forms of the Iberian wall lizard (*Podarcis hispanicus*) in Portugal were determined through extensive field surveys. Predictive models of probability of occurrence were developed for both forms of *P. hispanicus*, based on multivariate logistic regression of environmental variables. On a coarse scale, the best-fit models suggested that the distribution of the north-western form of *P. hispanicus* can be largely explained by environmental variables such as altitude, mean annual temperature and number of frost days per year. The distribution of the south-western form of *P. hispanicus* is also explained by altitude and temperature, but the type of climate also appears important. Predicted probabilities of occurrence broadly match the known distributions range of the two forms. Where predicted distributions are not confirmed by field surveys, historical and/or interspecific factors may be more important than environmental variables in influencing the distribution of the lizard.

Key words: *Podarcis*, wall lizard, distribution, GIS

INTRODUCTION

Podarcis hispanicus Steindachner 1870 is a small-bodied lizard (adult snout-vent length 65-70 mm), that is found in south-west France (Languedoc-Rousillon and Cévennes; the Iberian Peninsula (except the northernmost border area) and north-west Africa (see Fretey, 1986; Galán, 1986; Guillaume, 1987, 1997). It exhibits pronounced sexual dimorphism (the adult males being larger than the females and having a more intense pattern) and a strong polymorphism between populations (Barbadillo, 1987; Pérez-Mellado & Galindo, 1986; Salvador, 1986). *P. hispanicus* is mainly saxicolous and inhabits rocky shores, stone piles, walls and other stone constructions, with variable vegetation cover (Pérez-Mellado, 1983a, 1997a; Salvador, 1986). Where *P. hispanicus* is the only representative of the genus *Podarcis* (i.e. the centre, the south, and parts of the eastern coast of the Iberian Peninsula), it is ubiquitous and an opportunist, occupying all the available natural or semi-natural habitats (Guillaume, 1997). It feeds mostly on Arachnidae, Diptera, Homoptera, Hymenoptera, Coleoptera, Formicidae and insect larvae (Pérez-Mellado, 1983b; Salvador, 1986; Barbadillo, 1987).

Although *P. hispanicus* is potentially widespread in Portugal, distribution records are not abundant, because the majority of the data refer to the *P. bocagei*/*P. hispanicus* complex (e.g. see distribution maps from Crespo & Oliveira, 1989; Malkmus, 1995). According to Crespo & Oliveira (1989) their "complex" classification was a prudent way of dealing with an incomplete data set, as the classification of *Podarcis* in Portugal is unclear. Moreover, some apparent gaps in the *P.*

hispanicus distribution in Iberia (e.g. "Submeseta Sul" plateau, Andalusia and South of Portugal) have been identified as a result of inadequate sampling (Pérez-Mellado, 1997a). In fact, *P. bocagei* and *P. hispanicus* are morphologically and ecologically distinct species that live sympatrically in Galicia and northern and central Portugal (Arnold & Burton, 1978; Pérez-Mellado, 1981; Galán, 1986; Barbadillo, 1987). Despite the taxonomic controversy concerning *P. hispanicus*, I have studied the morphology of two distinct allopatric forms of this wall lizard in Portugal (Sá-Sousa, 1995 and unpubl. data). Firstly, there exists a north-western Iberian form (*P. hispanicus* 1) found in Galicia, the "Submeseta Norte" plateau, northern and central Portugal, and the "Sistema Central" range (i.e. the form *P. h. lusitanica*) described by Guillaume, 1987). This form has the following characteristics: head and body very depressed; mainly dark, reticulated, marbled and/or striped dorsal patterns; whitish or pearly belly (for details see Pérez-Mellado, 1981; Galán, 1986; Pérez-Mellado & Galindo, 1986; Guillaume, 1987; Galán & Fernández, 1993; Balado, Bas-López & Galán, 1995; Sá-Sousa, 1995). Secondly, there is a south-western Iberian form (*P. hispanicus* 2) first described from the Algarve as *Lacerta muralis* var. (= *Podarcis hispanicus*) *vaucheri* by Boulenger (1905). This form has the following characteristics: head and body moderately robust; mainly light brown and/or pale greenish dorsal patterns, yellow or orange belly (see Klemmer, 1959; the description of the "Andalucia/Portugal meridional" sample in Pérez-Mellado & Galindo, 1986; Salvador, 1986; Malkmus, 1995; Guillaume, 1987; González de la Vega, 1989; Sá-Sousa, 1995). Thus *P. hispanicus* 2 is known at least from the Algarve and Andalusia and for some of these authors it may also be synonymized with the present Maghrebian wall lizard subspecies *P. hispanicus vaucheri*. Moreover, Busack (1986) found a low ge-

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netic distance ($D_{Nei}=0.07$) between Andalusian and Moroccan populations of *P. hispanicus*.

The factors that determine the distributional range of a species are often diverse and subject to complex interactions. According to Wiens (1989), Antúnez & Mendoza (1992) and Cox & Moore (1993), they can mainly be classified as: (1) presence of barriers (e.g. large rivers, mountain ranges, ice caps, sea extensions, etc.); (2) absence of suitable habitat (i.e. scarcity of certain resources or climatic constraints); (3) non-availability of sufficiently large areas to support viable populations; (4) interactions with other species (e.g. interspecific competition, predation, parasitism, mutualism, influence of man); (5) history (if any of the factors cited above have played a role in the past, then their effect will influence the present distribution); and (6) chance events that may have influenced the present distribution.

Climatically, Portugal shows an important latitudinal intergradation between two greater climate domains, the Atlantic (ΣA) and the Mediterranean (ΣM), both interacting with the altitudinal gradient created by relief (Albuquerque, 1954; Ribeiro, 1987). How environmental conditions might influence the *P. hispanicus* distribution was the major aim of this work. This was pursued by (1) updating the distribution in Portugal with recent field surveys; and (2) deriving predictive models for the general distribution, using logistic regression in order to evaluate the probability of occurrence of the two forms of *P. hispanicus* in Portugal.

Given the binary nature of the wall lizard distribution data and the qualitative or non-multivariate normal nature of some available environmental data, logistic regression was considered as more appropriate for modelling the distribution (Press & Wilson, 1978; Hosmer & Lemeshow, 1989; Pereira & Itami, 1991; Austin, Thomas, Houston & Thompson, 1996). Logistic regression is used as a tool for analysing the effects of one or several independent variables, which may be either discrete or continuous, on one dependent binary variable (e.g. presence/absence). It has been used recently for modelling lizard distributions (Brito, Brito e Abreu, Paulo, Rosa & Crespo, 1996); and to study amphibian habitat features (Pavignano, Giacoma & Castellano, 1990; Mann, Dorn & Brandl, 1991; Romero & Real, 1996) as for other vertebrate species (Walker, 1990; Pereira & Itami, 1991; Gates, Gibbons, Lack & Fuller, 1994; Austin *et al.* 1996). The model for logistic regression has the form: $p(y) = e^y / (1 + e^y)$ where e is the base of the Naperian logarithm, and $p(y)$ is the probability of occurrence of the species. The value y is obtained from a regression equation of the form $y = a + b x_1 + c x_2 + \dots + n x_n$, where a is the equation constant and b, c, \dots are the 1 to n coefficients of the x independent variables (Hosmer & Lemeshow, 1989). A multivariate logistic regression model, based on environmental variables, was used to predict the probability of occurrence of each *P. hispanicus* form in Portugal.

Spatial autocorrelation between physical environmental variables is problematical for statistical testing as autocorrelated data violate the assumption of independence of most standard statistical procedures. Moreover, physical environmental variables are not distributed uniformly or randomly (Legendre, 1993). There are two main sources of spatial autocorrelation: (1) geography, whereby adjacent values tend to be strongly related (Augustin, Muggleston & Buckland, 1996); and (2) "spatial structure", whereby the surface pattern or the distribution of physical environmental variables tends to change gradually (Legendre, 1990; Dutilleul, 1993).

MATERIAL AND METHODS

DISTRIBUTION RECORDS

The sampling strategy was mainly based on fieldwork surveys of new *P. hispanicus* 1 and *P. hispanicus* 2 locations in Portugal. Some records were initially obtained by studying preserved specimens in the Museu Bocage (the Natural History Museum of Lisbon). Other data were cited in literature such as Malkmus (1981, 1984a,b, 1985, 1987, 1990a,b, 1991, 1992, 1993a,b, 1995, 1997a), Meek (1983), Pérez-Mellado (1984), Galán (1986), Pérez-Mellado & Galindo (1986), and Ferrand de Almeida (1991). The majority of the new distribution data were obtained during four years of fieldwork, between 1993 and 1997. Two records of *P. hispanicus* 2 were recently obtained from Schwarzer (1998).

To determine potential areas of occurrence, a set of environmental characteristics, assumed to be important for wall lizards, was considered. Nine variables were extracted from 1:1 000 000 environmental digital maps published by the Portuguese Ministry of the Environment. Similar environmental charts were previously published as "Atlas do Ambiente" (see CNA, 1983). Both the digital maps and the charts represented annual environmental variables (in classes), illustrated as contours. The environmental variables used were: number of hours of sun per year (*insolation*); annual mean daily temperature of the air in degrees Celsius (*temperature*); mean total precipitation in mm per year (*precipitation*); number of days per year with rainfall (*rain*); relative number of days per year with frost cover (*frost I*), annual period (in months) when frosts may occur (*frost II*); mean annual relative moisture of the air, measured daily at 0900 GMT (*humidity*); amount of water yearly drained in to the river basins (*run-off*); and the amount of water returned to the atmosphere annually (*evapotranspiration*). The type of climate (*climate*) map was firstly digitized from the "Carta Ecológica" chart, and qualitative data were converted to percentage values of Atlantic influence within each type of climate (SA), following Albuquerque's (1954) tables - see correspondence values in the two last columns of Appendix 1. Both location coordinates and *altitude* (above sea level) were recorded during surveys, by consulting 1:250 000 charts. All the digital maps were

imported to a Geographical Information System (GIS; Idrisi for Windows 1.0, following Eastman, 1988). With the GIS, digital maps were equalized and geo-referenced to each other as well as to a digital UTM (Universal Transverse of Mercator) grid. *P. hispanicus* distribution points (UTM 1 x 1 km grid accuracy) were imported by GIS as a separate (raster) layer. The environmental database was extracted by GIS, producing cross-tabulation between the point distribution layer and each of the environmental layers. The *altitude* data column was assigned to this database at the end.

CONSTRUCTING THE PREDICTIVE MODELS

In order to reduce spatial autocorrelation, the sampling involved the selection at random of records (only one record for each UTM 10 x 10 km cell) and the acquisition of one validation sub-sample to be run apart. Thus each *P. hispanicus* distribution set, available as presence (P) / absence (A) data (dependent variable) consisted of two random sub-samples. One main sub-sample (>80%), with 109 present and 112 absent locations for *P. hispanicus* 1; and 112 present and 151 absent locations for *P. hispanicus* 2, was used to build and assess the fit of the models. One validation sub-sample (>20%), with 30 present and 28 absent locations for *P. hispanicus* 1, and 28 present and 43 absent locations for *P. hispanicus* 2, was used to test the prediction accuracy of the final models.

To determine the final regression models, the programme EGRET (1991) was used to undertake a five step procedure of building and evaluating multivariate logistic regressions, as suggested by Hosmer & Lemeshow (1989) and Brito *et al.* (1996). First, univariate logistic regression analysis (maximum likelihood ratio test G) was used to detect relevant environmental variables that showed a significant association with the binary dependent variable, i.e. the Wald test set at $P < 0.25$ and the Odds ratio test with the 95% confidence interval not including 1.00 or not being overestimated (Hosmer & Lemeshow, 1989). The Odds ratio is a measure of association which approximates how likely (or unlikely) it is for the outcome to be present among those with $x=1$, rather than among those with $x=0$ (Hosmer & Lemeshow, 1989). Second, all variables selected by univariate analysis were included in a preliminary multivariate model carried out using a backward elimination procedure: each variable was removed stepwise from the model, in descending order of its previous univariate G -test value (Brito *et al.*, 1996). The only environmental variables that were considered relevant were those that abruptly decreased the G value when they were removed from the multivariate model. Those variables that showed a low level of association between the environmental variable and the presence/absence of the species were also eliminated. Third, up to four variables obtained in this way were checked for linearity. I assumed non-linearity if any transformed variable (i.e. x^2 , $\log(x)$, $x \ln(x)$) provided a better fit according to the G or Wald tests than

the initial variable (x), by univariate analysis. If so, the transformed variable was included in the model, instead of the initial variable, and used in subsequent analyses (see Hosmer & Lemeshow, 1989; Gates *et al.*, 1994, for details). Fourth, any confounding effect was checked for by adding all the initial variables, one after the other, to the last multivariate model in order to find any significant simultaneous increase in the G value. Fifth, significant interactions between variables were assessed again on the basis of significant increments in the G value.

FITTING THE PREDICTIVE MODELS

To assess the fit of the model, the Pearson chi-square and classification tables were used (Hosmer & Lemeshow, 1989; Brito *et al.*, 1996). The Pearson chi-square was calculated as follows: O_i is the observed value and P_i is the predicted value estimated from the model of logistic regression, where $P_i(y) = e^y / (1 + e^y)$.

Classification tables were based on the dependent variable, with presence, absence and total cases of the *P. hispanicus* 1 or *P. hispanicus* 2 forms, using observed values (P, A, T) and predicted values (P , A , T) - the latter representing the estimated probability of occurrence, from the multivariate models. A cut-off point of 0.50 was used as a minimum probability for supporting presence.

TESTING FOR SPATIAL AUTOCORRELATION

According to Legendre (1990), there are various ways of testing the hypothesis of spatial autocorrelation in data. The method used was the simple normalized Mantel (1967) test of matrix correspondence, incorporating the "spatial structure" into modelling using a matrix approach (Legendre, 1990, 1993). First, the spatial structure is assembled into a matrix, called SPACE, comprising geographical distances between the sampling locations (i.e. SPACE contains their Euclidean distances from UTM 1 x 1 km coordinates). Second, each environmental variable matrix is computed comparing locations with the Bray & Curtis (1957) percentage difference as resemblance coefficient. Third, a matrix correlation (simple Mantel test) between SPACE and each environmental matrix is tested by a permutation procedure (e.g. 200 repeated random permutations of the rows and columns), measuring the extent to which the variations in the distances of SPACE correspond to the variations in each environmental matrix. The null hypothesis to be tested is that those variations in the distances do not have linear correspondence with the pair(s) of matrices (SPACE and environmental variable). The matrix comparison was performed with NTSYS-PC 1.8 program (developed by F. James Rohlf).

DISTRIBUTION MAPS

P. hispanicus 1 and *P. hispanicus* 2 distribution maps were updated on a UTM 10 x 10 km based grid, distinguishing the new data (filled circles) obtained

during this work from the data previously known (open circles). The *P. hispanicus* 1 or *P. hispanicus* 2 probability of occurrence maps were generated with contours, using the GIS map algebra to run the model equations. The updated and the predicted distributions were overlain as a composite map. Two classes of probability of occurrence above the cut-off point of 0.5 were illustrated: predictable $P=[0.5-0.8]$ and likely presence $P>0.8$.

RESULTS AND DISCUSSION

KNOWN DISTRIBUTION

Figs. 1-2 illustrate the distribution of *P. hispanicus* (UTM 10 x 10 km grid) in Portugal, including the new data: a total of 173 cells for *P. hispanicus* 1, of which 133 cells (77%) are new records, and a total of 185 cells for *P. hispanicus* 2, of which 164 cells (88%) are new records. Some records from neighbouring regions of Spain (i.e. Galicia, Castilla-Léon Extremadura and Andalusia) are also shown (data from Pérez-Mellado, 1983c; Galán, 1986; Pérez-Quintero, 1990; Palomo,

1993; Balado *et al.*, 1995). The two main reasons that explain why so many records have been added are: (1) that as previously stated, most of the Portuguese data referred only to the *P. bocagei/P. hispanicus* complex (cf. Crespo & Oliveira, 1989; Malkmus, 1995); and (2) that there had been inadequate sampling in Southern Iberia e.g. 'Submeseta Sul', part of Andalusia and southern Portugal were previously little known (Pérez-Mellado, 1997a).

PREDICTED DISTRIBUTION

To obtain final models for both *P. hispanicus* 1 and *P. hispanicus* 2, the input variables *insolation*, *humidity*, *evapotranspiration*, *rain* and *frost II* were initially eliminated in the univariate analyses. In the backward multivariate analysis, the variable *run-off* was excluded, while *frost I* and *climate* were only eliminated in the *P. hispanicus* 1 models. Among many models produced and tested, only the first best-fit model was chosen for each of *P. hispanicus* 1 and *P. hispanicus* 2 (see Table 1). Both models explained significantly

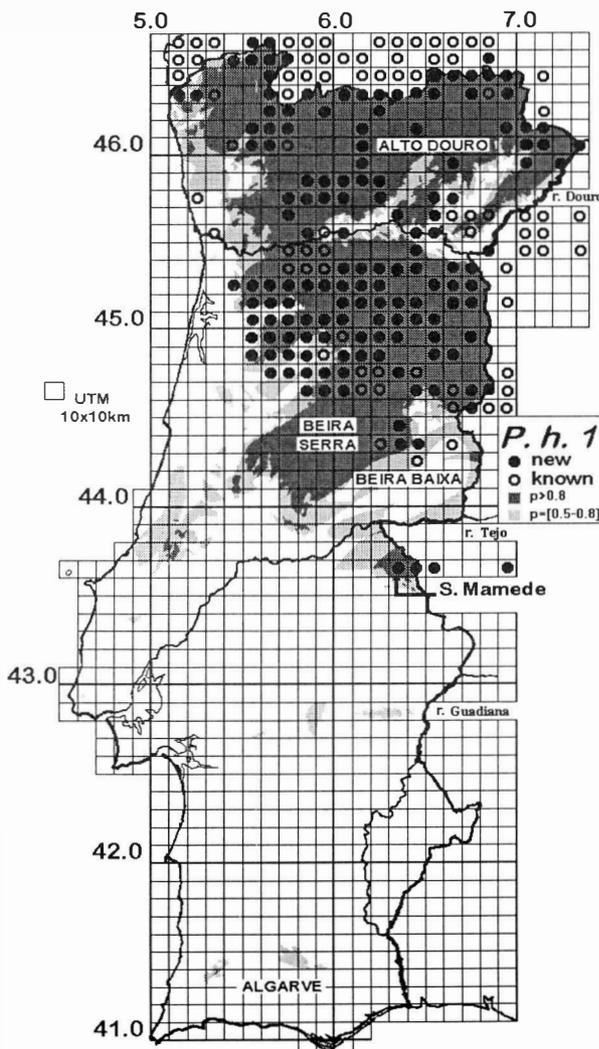


FIG. 1. Both updated (black circles) and predicted (grey contours) distributions of *P. hispanicus* 1 (i.e. NW Iberian form). Probability of occurrence was based on the first best-fit model (Table 1). Grid: UTM 10 x 10 km.

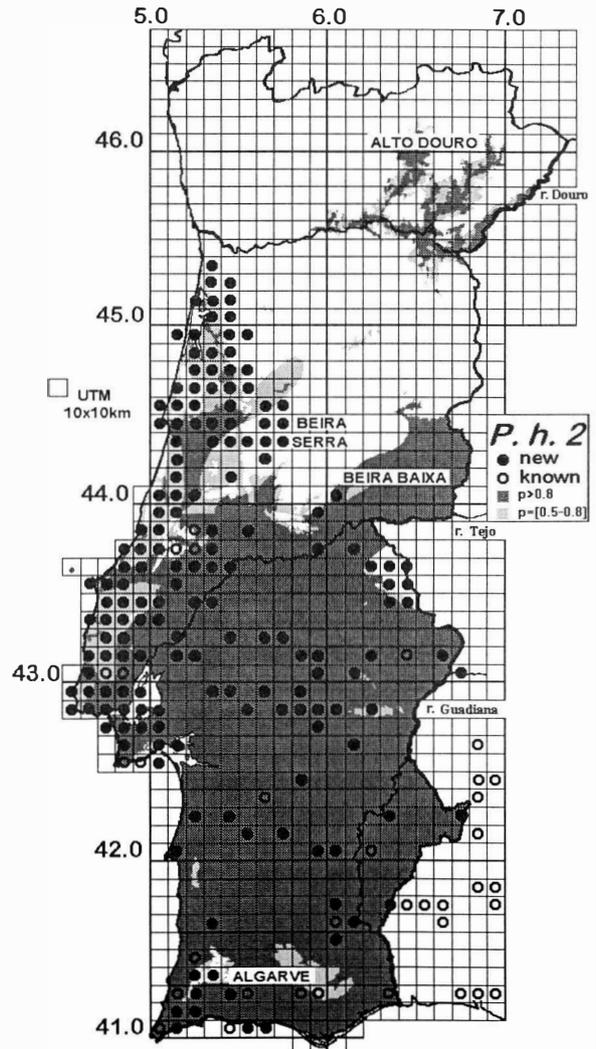


FIG. 2. Both updated (black circles) and predicted (grey contours) distributions of *P. hispanicus* 2 (i.e. SW Iberian form). Probability of occurrence was based on the first best-fit model (Table 1). Grid: UTM 10 x 10 km.

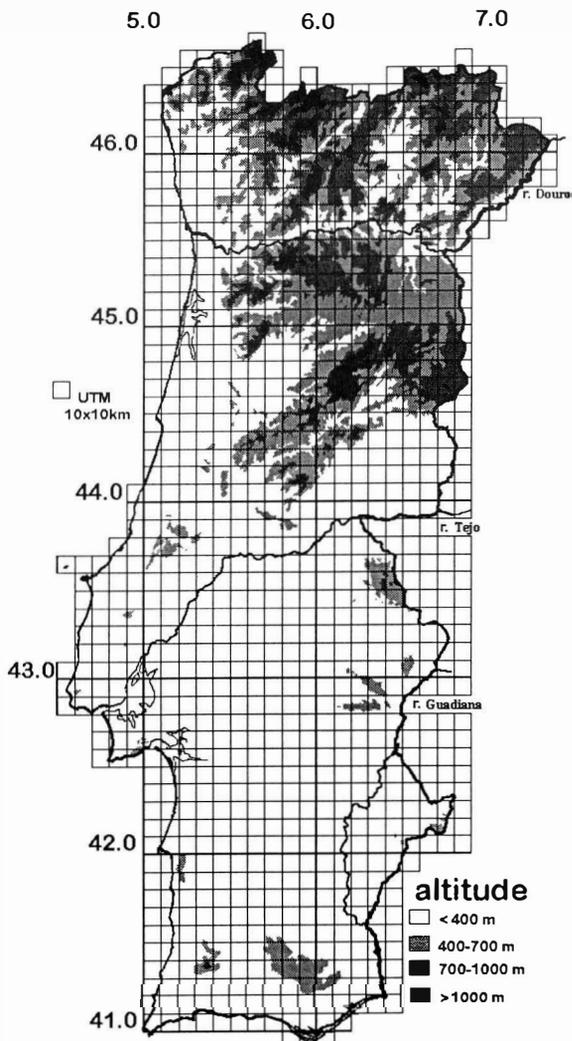


FIG. 3. Altitudinal map of Portugal (adapted from a chart assembled into CNA, 1983).

more variation than other models tested, showing higher values of G but fewer variables (all with significant association), while both agreed closely with the observed values. Pearson chi-square values were significant ($P < 0.001$) and classification table cases correctly classified over 80% of presence, absence and total records, indicating that both final models are good predictors of the distribution of *P. hispanicus* (Table 1). However, as the predictive models are based on broad-scale environmental data, only general patterns should be obtained from them.

The probability of occurrence of *P. hispanicus* 1 in Portugal is shown in Fig. 1. The likely presence contour ($P > 0.8$) broadly matches the known range of this lizard (i.e. northern, central and eastern Portugal), except for the Beira Serra region where no records are available. However, the predictable presence contour ($P = [0.5-0.8]$) extends beyond the known range (e.g. some hilly and mountain areas isolated in western and southern Portugal). Some classes of the environmental variables

such as *altitude* $\geq 400-500$ m (Fig. 3), *temperature* $\leq 12.5-15.0^\circ\text{C}$, *frost* $I \geq 20-30$ days and *precipitation* $\geq 700-800$ mm often determined the minimum probability for supporting presence in the *P. hispanicus* 1 model.

The probability of occurrence of *P. hispanicus* 2 in Portugal is shown in Fig. 2. The likely presence contour extends further than the known range (e.g. Alto Douro - the upper valley of the river Douro basin; Beira Baixa - the frontier region near the river Tejo). Various peripheral records are not covered even by the contour $P = [0.5-0.8]$. *P. hispanicus* 2 only occurs below the river Douro i.e. south and west-central Portugal. In the model, *altitude* $\leq 300-400$ m (see Fig. 3), *temperature* $\geq 15.0-16.0^\circ\text{C}$, *precipitation* $\leq 600-700$ mm and *climate* $\leq 50\%$ often contributed to the minimum probability of occurrence $P > 0.5$.

GENERAL DISTRIBUTION PATTERNS

In brief, five general environmental characteristics may be obtained from the models. (1) *P. hispanicus* 1 predominates in the highlands (> 400 m) and where Atlantic and/or Continental conditions, i.e. rainy and temperate, prevail (CNA, 1984a,b). (2) In contrast, *P. hispanicus* 2 seems to prefer the lowlands (< 400 m) and areas where Mediterranean conditions predominate, in Portugal. (3) The altitudinal variation clearly reflects a more complex set of climatic variables that are interacting (Brown & Gibson, 1983; Cox & Moore, 1993). As a consequence, moderate correlation between environmental variables (Pearson's $r > 0.65$) was found in the final models: positive for *precipitation* vs. *climate*; and negative for both *altitude* vs. *temperature* and *temperature* vs. *climate* (Table 2). On average, when altitude increases by 100 m, temperature decreases by 0.6°C in Portugal (Albuquerque, 1954). (4) The spatial autocorrelation appears not to confound the model results (see significant but lower correlation between SPACE - "space structure" - and each of the environmental distance matrices in Table 3). It should be noticed that correlation between two distance matrices (Table 3) is not equivalent to correlation between the two environmental variables underlying these matrices (Table 2); a distance matrix correlation measures the extent to which the variations in the "distances" of one matrix correspond to the variations in another (Legendre, 1993). (5) The environmental variables used for the models were included because of their likely biological significance, but the final set of model predictions was largely derived on statistical grounds. Subsequent relationships between lizard distribution and specific environmental variables cannot be assumed to imply causal effect. Although macroenvironmental factors may play an important role, they are obviously not the only factors determining *P. hispanicus*' distribution. For example, other habitat features may be unsuitable in areas which are climatically ideal for certain *P. hispanicus* forms.

TABLE 1. Two best-fit models found for each *P. hispanicus* form and associated statistics: maximum likelihood ratio G ; χ^2 and classification tables (P-P means observed versus predicted presences, etc.). $100 \times \text{temperature/precipitation} = K$ corresponds to Emberger's pluviothermic coefficient (used in climatology), which increases with aridity. *** $P < 0.001$.

logistic regression equations	max. likelihood ratio test	validation tests on the sub-samples			
		<i>n</i>	model	<i>n</i>	validation
<i>P. hispanicus 1</i>					
<i>First model:</i>	$G=225.5^{***}$	109	P-P: 92.7%	31	P-P: 80.6%
$Y1=0.2266(\text{altitude})^{0.5} - 0.03188(\text{temperature})^2$		112	A-A: 94.6%	27	A-A: 100%
$-3.1939(100 \times \text{temperature/precipitation})^{0.5} +$		221	T-T: 93.7%	58	T-T: 89.7%
$0.09677(\text{frost I}) + 3.998$		221	$\chi^2=88.6^{***}$	58	$\chi^2=18.2^{***}$
<i>Second model:</i>	$G=205.4^{***}$	109	P-P: 88.9%	31	P-P: 80.6%
$Y2=0.2204(\text{altitude})^{0.5} - 0.04456(\text{temperature})^2$		112	A-A: 94.6%	27	A-A: 100%
$+0.08341(\text{frost I}) + 3.021$		221	T-T: 91.8%	58	T-T: 89.6%
		221	$\chi^2=88.7^{***}$	58	$\chi^2=20.3^{***}$
<i>P. hispanicus 2</i>					
<i>First model:</i>	$G=248.5^{***}$	112	P-P: 92.9%	27	P-P: 88.9%
$Y1=0.7782(\text{temperature}) - 0.008195(\text{altitude})$		151	A-A: 95.4%	43	A-A: 90.7%
$-0.0003807(\text{precipitation}) \times \log(\text{precipitation})$		263	T-T: 94.3%	70	T-T: 90.0%
$-0.0007938(\text{climate})^2 - 5.538$		263	$\chi^2=108.8$	70	$\chi^2=20.7$
<i>Second model:</i>	$G=256.4^{***}$	112	P-P: 93.7%	27	P(27)-P: 85.2%
$Y2=1.268(\text{temperature}) - 0.9493(100 \times$		151	A-A: 95.4%	43	A(43)-A: 95.3%
$\text{temperature/precipitation})^{0.5} - 0.001788$		263	T-T: 94.7%	70	T(70)-T: 91.4%
$(\text{precipitation}) \times \log(\text{precipitation}) -$		263	$\chi^2=116.6^{***}$	70	$\chi^2=21.1^{***}$
$0.008683(\text{altitude}) - 0.0008381(\text{climate}) -$					
$0.0008381(\text{climate})^2 - 3.302$					

BIOGEOGRAPHY

Historical factors could have played an important role in determining present-day distributions (Wiens, 1989; Antúnez & Mendoza, 1992), but this remains rather speculative. Two related explanatory hypotheses, which differ in the space-time scale, are discussed here: (1) post-glacial range expansion, such as found for many European fauna (Brown & Gibson, 1983; Cox

& Moore, 1993); and (2) formation of a contact zone between two subspecies (Mayr & Ashlock, 1991).

Barbadillo (1987) explains that there are two possible sources of origin for the *P. hispanicus* species as a whole taxon: an Iberian origin from stock related to *P. muralis*, or a Maghrebian origin from stock of an ancient *Podarcis* form. In my opinion, both hypotheses constitute interesting arguments when they are viewed

TABLE 2. Simple normalized Mantel test of matrix correspondence between SPACE distance matrix (i.e. spatial structure) and each environmental distance matrix, after 200 repeated random permutations (* $P < 0.005$, one-tailed Mantel test,).

Environmental matrices	Space matrix	
	<i>P. h. 1</i>	<i>P. h. 2</i>
<i>n</i>	221	263
altitude	0.29275*	0.18848*
temperature	0.32812*	0.28594*
precipitation	0.27666*	0.33382*
frost I	0.23776*	-
climate	-	0.46456*

TABLE 3. Pearson product-moment correlation between pair(s) of environmental variables: positive values means that both variables tend to increase together; negative values that one variable tends to decrease while the other increases. * $P < 0.005$.

	altitude	temp.	precipitation	climate
altitude	-	-0.689*	0.394*	0.407*
temperature	-0.738	-	-0.609*	-0.679*
precipitation	0.482*	-0.611*	-	0.655*
frost I	0.451*	-0.371*	0.690	-

in different ways: an Iberian origin is postulated for *P. hispanicus* 1 and a Magrebian origin for *P. hispanicus* 2, but both may be related to the last glaciation period. Post-glacial colonization by *Podarcis* of the on-shore islands and islets off Iberia provides indirect evidence. One might therefore expect that only non-flying vertebrates species could pass over island-mainland bridges (MacArthur, 1972). Nowadays, only the wall lizard *P. m. muralis* is present on the Asturian and Cantabrian islets (Northern Spain) and on the adjacent mainland, while *P. hispanicus* (*P. hispanicus* 1) is only found in the warmer corners of the mainland (Barbadillo, 1987; Guillaume, 1987; Mateo, 1990; Pérez-Mellado, 1997b). In NW Galicia (Spain), *P. bocagei* predominates on both the islands (e.g. Sisargas) and the mainland (Galán, 1985, 1986). Below Cape Finisterre, *P. bocagei* and *P. hispanicus* (*P. hispanicus* 1) exist allopatrically on some islands and islets along the west coast of Galicia, though both species exist in sympatry on the mainland (Galán, 1987; Galán & Fernández, 1993; Balado *et al.*, 1995; Pérez-Mellado, 1997a). Along the west coast of Portugal there are few islands, and only *P. bocagei* is present there (e.g. Farilhões UTM 43.7 4.5, Berlengas UTM 43.6 4.5, Peniche tombo UTM 43.5 4.6, Baleal UTM 43.5 4.7 and Pessegueiro UTM 41.8 5.1), though *P. hispanicus* (*P. hispanicus* 2) is widespread on the mainland (Vicente, 1985; Sá-Sousa, 1990, 1995; see Fig. 2). On Sagres islets in the SW Algarve the status of *Podarcis* is unknown. At the southernmost extremities of Iberia, *P. hispanicus* (*P. hispanicus* 2) inhabits the province of Cádiz and the Rock of Gibraltar (an ancient on-shore island), and provides important clues for determining the origins of the Iberian herpetofauna (Busack, 1977, 1986; Cortés, 1982). Other SE Iberian islands were colonized by other *P. hispanicus* forms. The Mediterranean island of Alborán, situated between Spain (83 km) and Morocco (56 km) and separated from them by sea less than 500 m deep, has no reptiles (Mateo, 1990). Finally, in NW Africa only *P. hispanicus vaucheri* is found, and this has colonized the Chafarinas and Alhucemas islets off Morocco (Mateo, 1991; Bons & Geniez, 1996). Further genetic data would be needed to check *P. hispanicus* relationships. Busack (1986) pointed out the close genetic relationships between Andalusian (i.e. from Cádiz prov.) and Moroccan (i.e. from Tétouan prov.) populations of *P. hispanicus vaucheri* (= *P. hispanicus* 2), implicitly assuming that subspecies passed across the Strait of Gibraltar, at least during the last glaciation period. Other authors supported this point of view on the basis of morphological resemblance (Klemmer, 1959; Salvador, 1986; Guillaume, 1987). Conversely, Pérez-Mellado & Galindo (1986) and Pérez-Mellado (1997a) argue that *P. h. vaucheri* is strictly NW African, while *P. h. hispanicus* is the only Iberian mainland subspecies, though being rather polymorphic.

CONTACT ZONE

Mayr & Ashlock (1991) defined four possible kinds of contact zone, explaining that populations that qualify under (I) and (II), if sufficiently different, are nearly always treated as subspecies, and that populations that qualify under (III) and (IV) are often treated as species: (I) A and B intergrade clinally in a (usually fairly wide) zone of contact; (II) A and B interbreed completely in a (usually rather narrow) zone of contact; (III) A and B meet in a zone of contact where occasional hybrids occur; and (IV) A and B meet in a zone of contact but do not interbreed at all. Based on the model contours, one might expect both *P. hispanicus* forms to occur within a large contact zone (type I) in some regions of Portugal e.g. Alto Douro, and Beira Baixa (cf. Figs. 1, 2). However, only *P. hispanicus* 1 was detected in these regions, during thorough fieldwork. In the Beira Baixa there appears to be a distribution gap, but *P. hispanicus* 1 is probably present there, connecting the records of Serra da Gardunha, e.g. UTM 44.2 6.2 and Serra do Ramiro UTM 44.3 6.6, with those to the south around Serra de São Mamede (e.g. Castelo de Vide UTM 43.6 6.3, 500 m; and Marvão UTM 43.6 6.4, 850 m), plus the Spanish locations of Valência de Alcântara UTM 43.6 6.5, 450 m, Aliseda UTM 43.6 6.9, 350 m and Cáceres (not in Fig. 1). Most of the *P. hispanicus* data attributed to Cáceres province (Palomo, 1993) presumably correspond to *P. hispanicus* 1, at least from Cáceres up to the northernmost border of that province, above which appear the *P. hispanicus* 1 populations studied by Pérez-Mellado (1983c) and Pérez-Mellado & Galindo (1986) in Salamanca province and the Sistema Central range. Serra de São Mamede (situated on the 300 m high plains of Alto Alentejo province) is the only Portuguese mountain range south of the river Tejo that exceeds 1000 m, creating an altitudinal intergradation between Atlantic and Mediterranean conditions. These conditions favour both the sympatric occurrence of Atlantic and Mediterranean forms and a high diversity of species. Remarkable is the isolated occurrence of three Iberoatlantic endemic species with their Mediterranean congeneric species: the midwife-toads *Alytes obstetricans*/*A. cisternasii*, the frogs *Rana iberica* /*R. perezi* and the green lizards *Lacerta schreiberi*/*L. lepida* (Malkmus, 1997b). Both *P. hispanicus* 1 and *P. hispanicus* 2 are widespread in Serra de São Mamede though they do not occur syntopically. This case illustrates the situation often occurring in Portugal. However, the field records for *P. hispanicus* 1 and *P. hispanicus* 2 are not clear enough to show the nature of their contact zone in Portugal. Some features of the zone of contact suggest type III: (1) the two forms do not coexist spatially or temporally; (2) categorical spatial exclusion seems to predominate between *P. hispanicus* 1 and *P. hispanicus* 2 forms and occurs over small distances (km) and/or changes in altitude (e.g. Carregosa /Oliveira de Azeméis UTM 45.2 5.4 in the

Serra do Arestal; Corga / Bolfiar UTM 44.9 5.5 in the Serra do Caramulo; Castelo de Vide / Carreiras UTM 43.6 6.3 in the Serra de São Mamede); (3) permanent morphological and ecological distinctness is maintained by both *P. hispanicus* 1 and *P. hispanicus* 2 throughout their ranges; and (4) only one example from Marvão showed an intermediate pattern between *P. hispanicus* 1 and *P. hispanicus* 2.

CONCLUSION

Future research should aim at improving the model by incorporating other relevant variables, such as descriptors of habitat quality. The results could also be improved either by changing the scale to a more precise one or by using different modelling approaches e.g. trend surface models and Bayesian integrated statistical inference (Pereira & Itami, 1991). The probability maps also give some useful clues for further surveys on the distribution gaps of this species. It would also be interesting to study (at a fine scale) the contact zone between *P. hispanicus* 1 and *P. hispanicus* 2, examining possible clinal separation or more categorical spatial exclusion, as the first data suggested. For example, García-París, Martín, Dorda & Esteban (1989) found in the Autonomous Community of Madrid (Spain) that either the morphological features, the ecological preferences or the distribution ranges of *P. hispanicus* seem to be related to different geographical areas of that region. Both *P. hispanicus* 1 and *P. hispanicus* 2 morphotypes, and their preferential habitats are described by these authors. It is possible that other potential contact zones, similar to that observed in Portugal, occur elsewhere in Iberia.

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REFERENCES

- Albuquerque, J. P. M. (1954). *Carta ecológica de Portugal*. Lisboa: Direcção Geral Serviços Agrícolas, Ministério da Economia.
- Antúñez, A. & Mendonza, M. (1992). Factores que determinan el área de distribución geográfica de las especies: conceptos, modelos y métodos de análisis. In *Objetivos y métodos biogeográficos. Aplicaciones en Herpetología*, 51-72. Vargas, J.M., Real, R., and Antúñez, A. (Eds). Monogr. Herpet. 2. Valencia: Asociación Herpetológica Española.
- Arnold, E. N. & Burton, J. A. (1978). *A field guide to the reptiles and amphibians of Britain and Europe*. London: W. Collins Sons & Co. Ltd.
- Augustin, N. H., Muggleston, M. A. & Buckland, S. T. (1996). An autologistic model for spatial distribution of wildlife. *J. Appl. Ecol.* **33**, 339-347.
- Austin, G. E., Thomas, C. J., Houston, D. C. & Thompson, D. B. A. (1996). Predicting the spatial distribution of buzzard *Buteo buteo* nesting areas using a Geographical Information System and remote sensing. *J. Appl. Ecol.* **33**, 1541-1550.
- Balado, R. F., Bas-López, S. & Galán, P. (1995). Anfíbios e réptiles. In *Atlas de Vertebrados de Galicia*. vol. I, 65-170. Soc. Galega Hist. Nat., Cons. Cult. Galega (Eds). Santiago de Compostela: Agencia Gráfica.
- Barbadillo, L. J. (1987). *La guía de Incafo de los anfibios y reptiles de la Península Iberica, islas Baleares y Canarias*. Madrid: Incafo S. A..
- Bons, J. & Géniez, Ph. (1996). *Amphibians and reptiles of Morocco (including Western Sahara)*. Biogeographical Atlas [english title]. Barcelona: Asociación Herpetológica Española. [trilingual book: Spanish, French and English]
- Boulenger, G. A. (1905). A contribution to our knowledge of the varieties of the wall lizard (*Lacerta muralis*) in Western Europe and North Africa. *Trans. Zool. Soc. London* **17**, 351-436.
- Bray, R. J. & Curtis, J. T. (1957). An ordination of the upland forest communities in Southern Wisconsin. *Ecological Monographs* **27**, 325-349.
- Brito, J. C., Brito e Abreu, F. Paulo, O. S., Rosa, H. D. & Crespo, E. G. (1996). Distribution of Schreiber's Green lizard (*Lacerta schreiberi*) in Portugal: a predictive model. *Herpetological J.* **6**, 43-47.
- Brown, J. H. & Gibson, A. C. (1983). *Biogeography*. St. Louis, USA: C. V. Mosby Co.
- Busack, S. D. (1977). Zoogeography of amphibians and reptiles in Cádiz province, Spain. *Nat. Geogr. Research* **2**, 17-36.
- Busack, S. D. (1986). Biogeographic analysis of the herpetofauna separated by the formation of the Strait of Gibraltar. *Annals of Carnegie Mus. nat. Hist.* **46**, 285-315.
- CNA (1983). *Atlas do Ambiente*. Lisboa: Comissão Nacional do Ambiente (CNA), Direcção Geral do Ambiente, Ministério do Ambiente e dos Recursos Naturais. (85 environmental charts).
- CNA (1984a). *Atlas do Ambiente: notícia explicativa I.2 - Temperatura*. Lisboa: Comissão Nacional do Ambiente (CNA), Direcção Geral do Ambiente, Ministério do Ambiente e dos Recursos Naturais.
- CNA (1984b). *Atlas do Ambiente: notícia explicativa I.4.1 e I.4.2 - Precipitação*. Lisboa: Comissão Nacional do Ambiente (CNA), Direcção Geral do Ambiente, Ministério do Ambiente e dos Recursos Naturais.
- Cortés, J. E. (1982). The herpetofauna of Gibraltar: status, recent history and current research. *Brit. J. Herp.* **6**, 273-275.

- Cox, C. B. & Moore, P. D. (1993). *Biogeography - an ecological and evolutionary approach*. Oxford: Blackwell Scientific Publications.
- Crespo, E. G. & Oliveira, M. E. (1989). *Atlas da distribuição dos anfíbios e répteis de Portugal Continental*. Lisboa: SNPRCN.
- Dutilleul, P. (1993). Spatial heterogeneity and the design of ecological field experiments. *Ecology* **74**, 1646-1658.
- Eastman, J. R. (1988). *Idrisi for Windows user's guide v. 1.0*. Clark Labs for Cartographic Technology and Geographic analysis. Massachusetts, USA: Clark University Press.
- EGRET (1991). *EGRET - Statistical analysis package*. Statistics and Epidemiological Research Corporation, Seattle, WA 98105, USA.
- Ferrand de Almeida, F. (1991). A criação da "Reserva Natural do Paúl de Arzila" e nova contribuição para o conhecimento da sua fauna. *Ciênc. Biol. Ecol. Syst. (Portugal)* **11**, 47-58.
- Fretey, J. (1986). *Les reptiles de France: métropolitaine et des îles satellites- tortues et lézards*. Paris: Hatier.
- Galán, P. (1985). Morfología de las *Podarcis bocagei* (Seoane, 1884) (Sauria, Lacertidae) de dos islas atlánticas: Sisargas y Berlengas. *Trab. Compost. Biol.* **12**, 121-139.
- Galán, P. (1986). Morfología y distribución del género *Podarcis* Wagler, 1830 (Sauria, Lacertidae) en el noroeste de la Península Ibérica. *Rev. Esp. Herp.* **1**, 87-142.
- Galán, P. (1987). Notas preliminares sobre la herpetofauna de las islas Cíes y Ons. *Mustela* **3**, 64-69.
- Galán, P. & Fernández, G. (1993). *Anfíbios e réptiles de Galicia*. Vigo: Ed. Xerais de Galicia.
- García-París, M., Martín, C., Dorda, J. & Esteban, M. (1989). *Los Anfíbios y Reptiles de Madrid*. Madrid: Ministerio del Agricultura, Pesca y Alimentación de Madrid.
- Gates, S., Gibbons, D. W. Lack., P. C. & Fuller. R. J. (1996). Declining farmland bird species: modelling geographical patterns of abundance in Britain. In *Large-scale ecology and conservation biology*, 111-128. Edwards, P. J., May, R. M. and Webb N. R. (Eds.). London: Blackwell Scientific Publications.
- González de la Vega, J. P. (1989). *Anfíbios y reptiles de la provincia de Huelva*. Huelva: Imprenta Jiménez, S.L..
- Guillaume, Cl. P. (1987). *Les petits lacertidés du Bassin Méditerranéen Occidental (genera Podarcis et Archaeolacerta essentiellement)*. Ph.D. thesis. Montpellier: Univ. Sciences et Techniques du Languedoc.
- Guillaume, Cl. P. (1997). *Podarcis hispanica* (Steindachner, 1870). In *Atlas of amphibians and reptiles in Europe*, 278-279. Gasc, J. P., Cabela, A., Crnobrnja-Isailovic, J., Dolmen, D., Grossenbacher, K., Haffner, P., Lescure, J., Martens, H., Martínez-Rica, J.P., Maurin, H., Oliveira, M. E., Sofianidou, T. S., Veith, M. and Zuiderwijk, A. (Eds). Paris: Mus. Nat. Hist. Nat. Paris and Societas Europaea Herpetologica (SEH).
- Hosmer, D. W. Jr. & Lemeshow, S. (1989). *Applied logistic regression*. New York: John Wiley & Sons.
- Klemmer, K. (1959). Systematische Stellung und Rassengliederung der Spanischen Mauereidechse *Lacerta hispanica*. *Senckenb. Biol.* **40**, 245-250.
- Legendre, P. (1990). Quantitative methods and biogeographic analysis. In *Evolutionary biogeography of the marine algae of the North Atlantic*, 9-34. Garbary, D. J. and South, G. R. (Eds). NATO ASI Series, volume G 22. Berlin: Springer-Verlag.
- Legendre, P. (1993). Spatial autocorrelation: trouble or new paradigm? *Ecology* **74**, 1659-1673.
- MacArthur, R. H. (1972). *Geographic ecology: patterns in the distribution of species*. New York: Harper & Row, Publ.
- Malkmus, R. (1981). Os anfíbios e répteis nas serras de Portugal. *Arq. Mus. Boc. (sér. B)* **9**, 97-122.
- Malkmus, R. (1984a). Herpetologische Ausflüge un die Serra da Malcata, Portugal. *Herpetofauna* **6**, 6-11.
- Malkmus, R. (1984b). Die Serra da Arrábida (Portugal) und ihre Herpetofauna (Amphibia, Reptilia). *Nachr. Naturw. Mus. Aschaffenburg* **92**, 85-148.
- Malkmus, R. (1985). Über die Herpetofauna im Fátima-Karst Portugals. *Natur und Museum (Frankfurt-am-Main)* **115**, 174-184.
- Malkmus, R. (1987). Herpetologische Untersuchungen bei Lissabon. *Arq. Mus. Boc. (sér. B)* **22**, 263-287.
- Malkmus, R. (1990a). Reptilien und Amphibien aus der Serra de Montemuro, Portugal. *Herpetofauna* **12**, 15-20.
- Malkmus, R. (1990b). Herpetofaunistische Daten aus Nordostportugal. *Salamandra* **26**, 165-176.
- Malkmus, R. (1991). Naturkundliche Ausflüge um Mértola, Südportugal. *Natur und Museum (Frankfurt-am-Main)* **121**, 37-49.
- Malkmus, R. (1992). Zur Herpetofauna der Algarvischen Gebirge. *Nachr. Naturw. Mus. Aschaffenburg* **99**, 61-117.
- Malkmus, R. (1993a). Zur Herpetofauna der Serra do Reboredo. *Nachr. Naturw. Mus. Aschaffenburg* **100**, 73-90.
- Malkmus, R. (1993b). Die Serra de Monchique - eine Klima-Insel im Süden Portugals. *Natur und Museum (Frankfurt-am-Main)* **123**, 171-182.
- Malkmus, R. (1995). *Die Amphibien und Reptilien Portugals, Madeiras und der Azoren*. Magdeburg: Westarp Wissenschaften.
- Malkmus, R. (1997a). Beitrag zur Verbreitung der Amphibien und Reptilien des Transgadianalandes (Portugal) (Amphibia et Reptilia). *Faun. Abh. Staat. Mus. Tier. Dresden* **21**, 115-129.
- Malkmus, R. (1997b). Die Verbreitung der Amphibien und Reptilien in der Serra de São Mamede, Portugal. *Zeitsch. für Feldherpetologie* **4**, 63-92.

- Mann, W., Dorn, P. & Brandl, R. (1991). Local distribution of amphibians: the importance of habitat fragmentation. *Global Ecol. Biog. Letters* **1**, 36-41.
- Mantel, N. (1967). The detection of disease clustering and a generalized regression approach. *Cancer Research* **27**, 209-220.
- Mateo, J. A. (1990). Aspectos biogeográficos de la fauna reptiliana en las islas españolas. *Rev. Esp. Herp.* **4**, 33-44.
- Mateo, J. A. (1991). Los anfibios y reptiles de Ceuta, Melilla, Chafarinas, Peñón de Vélez de la Gomera, Peñón de Alhucemas e islotes. *Rev. Esp. Herp.* **5**, 37-41.
- Mayr, E. & Ashlock, P. D. (1991). *Principles of systematic zoology*. Singapore: McGraw-Hill Inc.
- Meek, R. (1983). Observations on the amphibians and reptiles of the Algarve, Portugal. *Brit. Herp. Soc. Bull.* **7**, 57-63.
- Palomo, J. A. (1993). Atlas provisional de los anfibios y reptiles de Extremadura. *Aegyptus* **11**, 7-20.
- Pavignano, I., Giacomini, C. & Castellano, S. (1990). A multivariate analysis of amphibian habitat determinants in North Western Italy. *Amphibia-Reptilia* **11**, 311-324.
- Pereira, J. M. C. & Itami, R. M. (1991). GIS-based habitat modeling using logistic multiple regression: a study of the Mt. Graham red squirrel. *Photogrammetric Engineering & Remote Sensing* **57**, 1475-1486.
- Pérez-Mellado, V. (1981). Nuevos datos sobre la sistemática y distribución de *Podarcis bocagei* (Seoane, 1884) (Sauria, Lacertidae) en la Península Ibérica. *Amphibia-Reptilia* **2**, 259-265.
- Pérez-Mellado, V. (1983a). Activity and thermoregulation patterns in two species of Lacertidae: *Podarcis hispanica* (Steindachner, 1870) and *Podarcis bocagei* (Seoane, 1884). *Ciênc. Biol. Ecol. Syst. (Portugal)* **5**, 5-12.
- Pérez-Mellado, V. (1983b). Alimentación de dos especies simpátricas de saurios en el Sistema Central, *Podarcis hispanica* (Steindachner, 1870) y *Podarcis bocagei* (Seoane, 1884) (Sauria, Lacertidae). *Studia Oecologica* **4**, 89-114.
- Pérez-Mellado, V. (1983c). La herpetofauna de Salamanca: un análisis biogeográfico y ecológico. *Salamanca, Rev. Provincial Estudios* **9-10**, 9-78.
- Pérez-Mellado, V. (1984). Sobre los anfibios y reptiles de la Sierra de la Estrela (Beira Alta, Portugal). *Bull. Soc. Cat. Ictio. Herp.* **8**, 13-20.
- Pérez-Mellado, V. (1997a). *Podarcis hispanica* (Steindachner, 1870) - lagartija ibérica, lagartixa-ibérica. In *Distribución y biogeografía de los anfibios y reptiles en España y Portugal*, 240-242. Pleguezuelos, J. M. (Ed). Monográfica Tierras del Sur. Granada: Univ. Granada and Asociación Herpetológica Española.
- Pérez-Mellado, V. (1997b). *Podarcis muralis* (Laurenti, 1768) - lagartija roquera, lagartixa dos muros. In *Distribución y biogeografía de los anfibios y reptiles en España y Portugal*, 243-245. Pleguezuelos, J. M. (Ed). Monográfica Tierras del Sur. Granada: Univ. Granada and Asociación Herpetológica Española.
- Pérez-Mellado, V. & Galindo, M. P. (1986). *Sistemática de Podarcis (Sauria, Lacertidae) ibéricas y norteafricanas mediante técnicas multidimensionales*. Sér. Manuales Universitários. Salamanca: Univ. Salamanca.
- Pérez-Quintero, J.C. (1990). Atlas provisional de los anfibios y reptiles de la provincia de Huelva. *Rev. Esp. Herp.* **4**, 17-31.
- Press, S. J. & Wilson, S. (1978). Choosing between logistic regression and discriminant analysis. *J. American Statistical Association* **73**, 695-705.
- Ribeiro, O. (1987). *Portugal, o Mediterrâneo e o Atlântico*. Lisboa: Livraria Sá da Costa.
- Romero, J. & Real, R. (1996). Macroenvironmental factors as ultimate determinants of distribution of common toad and natterjack toad in the south of Spain. *Ecography* **19**, 305-312.
- Sá-Sousa, P. (1990). *Notas sobre a biologia evolutiva de Podarcis bocagei (Seoane, 1884) (Sauria, Lacertidae)*. Relatório de Estágio FCUL [Degree thesis], Lisboa: Univ. Lisboa (unpublished).
- Sá-Sousa, P. (1995). Distinção das lagartixas do género *Podarcis* em Portugal. *Folha Herpetológica*, **5**, 4-6.
- Salvador, A. (1986). *Podarcis hispanica* (Steindachner, 1870) - Iberische Mauereidechse. In *Handbuch der Amphibien und Reptilien Europas - 2/II Sauria* (3), 71-82. Böhme, W. (Ed) Wiesbaden: Aula-Verlag.
- Schwarzer, U. (1998). Acerca das lagartixas *Podarcis* no Sudoeste de Portugal. *Folha Herpetológica*, **11**, 3-4.
- Vicente, L. A. (1985). Description d'une nouvelle sous-espèce de *Podarcis bocagei* Seoane, 1884 (Sauria, Lacertidae) de l'île de Berlenga, *Podarcis bocagei berlenensis*. *Bull. Mus. Natn. Hist. Nat., Paris, 4^{ème} sér.* **7A**, 267-274.
- Walker, P. A. (1990). Modelling wildlife distribution using a geographic information system: kangaroos in relation to climate. *Journal of Biogeography* **17**, 279-289.
- Wiens, J. A. (1989). *The ecology of bird communities: I. Foundations and patterns*. Cambridge, New York: Cambridge Univ. Press.

APPENDIX 1

Classes of the five environmental variables used in the final logistic regression equations. Type of climate is a qualitative variable assessed as composition and intergradation (*) of greater climate domains: M, Mediterranean; A, Atlantic; \tilde{A} , Atlantic or Macronesian; I, Iberian or continental. S and O refer to the prefixes sub- and oro- respectively, indicating altitudinal effects on climate. *Climate* was extrapolated from the type of climate using the correspondence values (original values emboldened), see Albuquerque (1954) for more details.

class	altitude (m)	temperature (oC)	frost I (days/yr)	rainfall (mm/yr)	climate	
					type	$\Sigma A\%$
1	<100	<7.5	<1	<400	M	1
2	100-200	7.5-10.0	1-5	400-500	IM*M	7
3	200-300	10.0-12.5	5-10	500-600	IM	13
4	300-400	12.5-15.0	10-20	600-700	SM*IM	17
5	400-500	15.0-16.0	20-30	700-800	SM	20
6	500-600	16.0-17.5	30-40	800-1000	AM*SM	30
7	600-700	>17.5	40-50	1000-1200	$\tilde{A}M*SM$	32
8	700-800		50-60	1200-1400	SA*SM*IM	34
9	800-900		60-70	1400-1600	$\tilde{A}M$	37
10	900-1000		70-80	1600-2000	AM	40
11	1000-1100		>80	2000-2400	SA*I	45
12	1100-1200			2400-2800	MA*AM	50
13	1200-1300			>2800	SA*SM	54
14	1300-1400				MA	60
15	1400-1500				SA*AM	65
16	1500-1600				$\tilde{S}\tilde{A}*SM$	66
17	1600-1700				SA*MA*AM	67
18	1700-1800				SA*MA	69
19	>1800				A*MA	70
20					SA*A*MA	71
21					SA	73
22					$\tilde{S}\tilde{A}$	75
23					A*SA	80
24					OA*SA or OA	85

EMBRYONIC USE OF ENERGY AND POST-HATCHING YOLK IN THE GRAY RAT SNAKE, *PTYAS KORROS* (COLUBRIDAE)

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Female *Ptyas korros* from a population on Dinghai, Zhoushan Islands, in eastern China, produced one clutch per breeding season. Clutch size varied from 7 to 14, and was positively correlated with female SVL. The duration of incubation at 30 ± 0.5 °C averaged 54.7 days. Dried shells from freshly laid eggs averaged 30.0% of the entire egg dry mass. Egg contents of the freshly laid egg contained higher quantities of dry material, non-polar lipids and energy than did newly hatched hatchlings. Shells from freshly laid eggs contained higher quantities of ash than did those from hatched eggs. During incubation, approximately 77% of dry material, 54% of non-polar lipids and 69% of energy in the egg contents of freshly laid eggs were transferred to the hatchling. There were inverse relationships between carcass dry mass, post-hatching yolk dry mass and fat body dry mass for hatchlings sampled immediately after hatching. Post-hatching yolk could be used to support subsequent growth of newly emerged young, as indicated by significant increases in the carcass dry mass and SVL of hatchlings during their first days of life, following the depletion of post-hatching yolk.

Key words: Colubridae, *Ptyas korros*, incubation, egg, hatchling, post-hatching

INTRODUCTION

It is a common pattern in oviparous reptiles that the nutrient provision in eggs exceeds the needs for producing a complete hatchling. While developing within eggs, embryos use yolk as the source of all organic and most inorganic nutrients, and eggshell as the additional source of some minerals (e.g. calcium). A portion of yolk, namely post-hatching yolk, may remain unutilized until the time of hatching. Post-hatching yolk may be used for maintenance metabolism and probably for soft tissue growth in some hatchling reptiles (e.g. Kraemer & Bennett, 1981; Congdon *et al.*, 1983*a,b*; Troyer, 1983, 1987; Wilhoft, 1986; Congdon, 1989; Congdon & Gibbons, 1989; Fischer *et al.*, 1991). The relative quantity of post-hatching reserves may vary considerably among reptiles that share this characteristic and, for a given species, it appears to be related to energy requirements during the first days or weeks of life (Kraemer & Bennett, 1981; Troyer, 1987). Post-hatching yolk is not a conceptually new term, but further studies are still needed to show its exact function. In several species of snake, e.g. *Elaphe carinata* (Ji *et al.*, 1997*a*), *Elaphe taeniura* (Ji *et al.*, 1999*a*) and *Dinodon rufozonatum* (Ji *et al.*, 1999*b*), we have found that nutrients in the post-hatching yolk can be transformed into the carcass of newly emerged young. As the consequence of this transformation, hatchlings increase in size (snout-vent length and tail length) during their first days of life.

Here, we present data on the gray rat snake, *Ptyas korros* (Colubridae), that is widely distributed in the

southern provinces of China (Zhao & Adler, 1993) and locally very abundant in the Zhoushan Islands (29° 32' - 31° 04' N, 121° 30' - 123° 25' E), Zhejiang, eastern China. We address the three topics: (1) the composition of freshly laid eggs and newly hatched hatchlings, (2) energy and material budgets during incubation and (3) post-hatching yolk and its contribution to the early growth of hatchlings.

MATERIALS AND METHODS

Fourteen gravid *P. korros* were collected from various localities on Dinghai, Zhoushan Islands, in late June of 1994 and 1995; five gravid females were collected from Dinghai in mid-June 1998 to increase sample size. The snout-vent length (SVL) ranged from 735 to 1000 mm, and the post-partum body mass from 98.8 to 280.9 g. The snakes were transported to our laboratory at Hangzhou Normal College and were housed individually in 80 x 80 x 80 cm wire cages until oviposition. Oviposition occurred between 22 June and 15 July. All post-partum snakes were released into the field where they were collected.

We collected, measured and weighed eggs promptly so as to avoid any uncertainty about the initial mass due to gain or loss of water, and then numbered them. Relative clutch mass was expressed as the ratio of clutch mass to the total body mass of females, including the clutch (Seigel & Ford, 1986). Sixteen eggs were considered to be abnormal because they had either a less developed shell or a condensed yolk.

In 1994 and 1995, a total of 39 freshly laid eggs (1-4 from each clutch) were opened at laying. Each dissected freshly laid egg contained a small embryo which was too small and fragile to be separated and therefore was included with the yolk. Egg contents (embryo plus yolk) of the dissected freshly laid eggs were removed

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and weighed. Shells were rinsed briefly in distilled water, dried by blotting with a paper towel and weighed. Egg contents and shells were then dried to constant mass in an oven at 65 °C, weighed and stored frozen at -15 °C until they could be processed for determining composition. None of the eggs collected in 1998 was opened at laying.

We incubated 129 eggs in covered plastic containers that were placed in an incubator inside which the temperature was set at 30±0.8 °C. The containers contained known amounts of vermiculite and distilled water to produce approximately -12 kPa (2 g water/1 g vermiculite) water potential (Lin & Ji, 1998). Eggs were one-third buried in the substrate. We moved containers daily between shelves in the incubator according to a predetermined schedule to minimize any effects of thermal gradients inside the incubator. Incubation temperatures in close proximity to the eggs were monitored twice daily using a digital thermometer. We weighed containers every other day and, if necessary, mixed distilled water evenly into the substrate to compensate for water absorbed by the eggs and for the small losses due to evaporation. We weighed incubating eggs at weekly intervals before day 42 and at daily intervals thereafter. The duration of incubation was defined as the time elapsed from egg laying to hatchling emergence.

Upon emergence, each hatchling was measured and weighed. Body measurements included snout-vent length (SVL), tail length (TL) and body mass. Shells from hatched eggs were processed following the procedures described above for those from freshly laid eggs. Deformed hatchlings were excluded from further analyses.

Thirty-seven hatchlings (1-3 from each clutch; hereafter 0-day hatchlings) were sacrificed on the day of hatching, 30 (1-3 from each clutch; hereafter 7-day hatchlings) 7 days after hatching, and 28 (0-2 from each clutch; hereafter 14-day hatchlings) 14 days after hatching. Both 7- and 14-day hatchlings were fasted at room temperatures (24-36 °C) before they were sacrificed. The hatchlings were dissected and separated into carcass, yolk sac (if present) and fat bodies. The three components of the hatchling were oven dried to constant mass at 65 °C, weighed and then ground with a mortar and pestle.

We extracted non-polar lipids from dried samples of egg contents, carcass, post-hatching yolk and fat bodies in a Soxhlet apparatus for a minimum of 5.5 hr using absolute ether. The amount of lipids in a sample was determined by subtracting the lipid-free dry mass from the total sample dry mass. We determined the energy density of egg contents, carcass, post-hatching yolk and fat bodies using a GR-3500 adiabatic bomb calorimeter (Changsha Instruments). We determined the ash content of eggshells by burning samples in a muffle furnace at 600 °C for a minimum of 12 hr and weighing the remaining ash.

To avoid pseudoreplication, data from a single clutch were blocked prior to further statistical analysis and then were tested for normality using the Kolmogorov-Smirnov test, and for homogeneity of variance using Bartlett's test. Log_e transformation was performed when necessary to achieve normality. We compared the measured variables of dissected freshly laid eggs and hatched eggs using analysis of covariance (ANCOVA) with total egg wet mass at oviposition as the covariate. We tested for differences in carcass dry mass, SVL and TL among 0-day, 7-day, and 14-day hatchlings using ANCOVA with total egg wet mass at oviposition as the covariate. The homogeneity of slopes was checked prior to testing for differences in the adjusted means. A four-factor (dry masses of hatchling, carcass, post-hatching yolk and fat body entered as factors) partial correlation analysis was performed on 0-day hatchlings to test the relationships between these variables. Descriptive statistics are presented as mean ± 1 standard error.

RESULTS

Female *P. korros* laid pliable-shelled eggs. Clutch size in our sample averaged 10.2±0.4 (range 5-14, $N=19$), and was positively correlated with maternal SVL ($r^2=0.49$, $F_{1,17}=16.01$, $P<0.001$). Relative clutch mass averaged 0.317±0.011 (range 0.23-0.440, $N=19$). Clutch means ($N=19$) for the wet mass and length and width of freshly laid eggs averaged 9.0±0.3 (range 6.6-10.9) g, 38.1±0.7 (range 33.5-43.5) mm and 19.0±0.3 (range 16.6-20.9) mm, respectively. Dried shells from freshly laid eggs averaged 30.0% of the entire egg dry mass (Table 1).

Eggs gained mass over the course of incubation due to absorption of water and, one day prior to hatching, weighed approximately 133% (107-195%) of egg mass at oviposition. Fourteen eggs failed to hatch following incubation. Hence, the hatching success was 87% (112/129). The clutch mean for duration of incubation averaged 54.7±0.6 (range 50.5-57.2, $N=19$) days. Three hatchlings were abnormal. The clutch means ($N=19$) for wet body mass, SVL and TL of newly emerged hatchlings averaged 6.36±0.19 g (range=4.55 -7.32), 224.7 ± 1.9 mm (range 205.7-249.5) and 94.4±1.1 mm (range 82.7-101.5), respectively.

Egg contents of the dissected freshly laid eggs contained higher quantities of dry material, non-polar lipids and energy than did 0-day hatchlings (Table 1). Shells from freshly laid eggs contained higher quantities of ash than did those from hatched eggs (Table 1). During incubation, approximately 77% of dry mass, 54% of non-polar lipids and 69% of energy in egg contents of the freshly laid egg were transferred to the hatchling (Table 1).

The hatchlings sampled on 7 days after hatching had significantly larger carcasses than did 0-day (ANCOVA; $F_{1,35}=6.05$, $P<0.02$) and 14-day hatchlings (ANCOVA; $F_{1,33}=4.49$, $P<0.04$) (Table 2). We did not

TABLE 1. Composition and F values of ANCOVA for *Ptyas korros* freshly laid and hatched eggs. Data from a single clutch are blocked and are expressed as adjusted means \pm 1 standard error, with total egg wet mass as the covariate. $N=14$ (clutches). All mass units are in g, and energy units KJ. Symbols immediately after F values represent significance levels: NS $P>0.05$, * $P<0.05$, *** $P<0.001$.

	Freshly laid egg	Hatched egg	$F_{1,25}$
	Egg contents	Total hatchling	
Wet mass	6.95 \pm 0.04	6.04 \pm 0.09	69.41 ***
Dry mass	2.06 \pm 0.03	1.59 \pm 0.03	92.78 ***
Water	4.89 \pm 0.06	4.54 \pm 0.15	3.73 NS
Non-polar lipids	0.61 \pm 0.01	0.33 \pm 0.01	230.95 ***
Energy	49.5 \pm 0.8	34.4 \pm 0.7	199.61 ***
	Eggshell	Eggshell	
Dry mass	0.88 \pm 0.02	0.84 \pm 0.01	3.08 NS
Organic mass	0.69 \pm 0.02	0.66 \pm 0.01	1.41 NS
Ash mass	0.195 \pm 0.005	0.178 \pm 0.005	6.22 *

find a significant difference in the mean carcass dry mass between 0- and 14-day hatchlings (ANCOVA; $F_{1,33}=0.09$, $P=0.767$; Table 2). A partial correlation analysis on 0-day hatchlings showed inverse relationships between carcass dry mass, post-hatching yolk dry mass and fat body dry mass (carcass vs post-hatching yolk: $r=-0.97$; carcass vs fat bodies: $r=-0.80$; post-hatching yolk vs fat bodies: $r=-0.74$; all $P<0.001$).

The hatchlings sampled on 7 (ANCOVA; $F_{1,35}=30.01$, $P<0.0001$) and 14 days (ANCOVA; $F_{1,33}=48.97$, $P<0.0001$) after hatching had significantly larger SVLs than did 0-day hatchlings (Table 2). There was no significant difference in the mean SVL between 7- and 14-day hatchlings (ANCOVA; $F_{1,33}=1.64$, $P=0.210$; Table 2).

DISCUSSION

Numerous studies have indicated that conversion of nutrients and energy from egg to hatchling during the course of incubation or embryogenesis vary amongst reptiles (e.g. Ewert, 1979; Congdon *et al.*, 1983a,b; Wilhoft, 1986; Fischer *et al.*, 1991; Ji *et al.*, 1996, 1997a,b; Zhao *et al.*, 1997). However, inter-specific comparisons should be made with caution, because incubation conditions may influence material and energy budgets during incubation, and different methods by which investigators use to incubate eggs might make data uncomparable. Our experience with incubating eggs of squamate reptiles is that the conversion efficiencies of dry material, non-polar lipids and energy during incubation vary among species whose eggs

TABLE 2. Size, mass and components of *Ptyas korros* hatchlings sacrificed immediately after hatching ($N=19$ clutches) and on 7 ($N=19$ clutches) and 14 days ($N=17$ clutches) after hatching. Data from a single clutch are blocked and are expressed as means \pm 1 standard error. All mass units are in g, and length units mm.

	0-day hatchling	7-day hatchling	14-day hatchling
<i>Initial egg mass</i>	8.8 \pm 0.3	8.3 \pm 0.3	8.1 \pm 0.3
<i>Hatchling wet mass</i>			
- at hatching	6.3 \pm 0.2	5.9 \pm 0.3	6.0 \pm 0.3
- 7 or 14 days after hatching	-	5.6 \pm 0.3	5.4 \pm 0.2
<i>Hatchling SVL</i>			
- at hatchling	223.3 \pm 3.0	212.9 \pm 2.9	210.6 \pm 1.9
- 7 or 14 days after hatching	-	237.0 \pm 2.8	238.4 \pm 3.0
<i>Hatchling TL</i>			
- at hatching	93.3 \pm 1.6	90.8 \pm 2.0	89.6 \pm 1.9
- 7 or 14 days after hatching	-	91.4 \pm 2.8	92.4 \pm 2.4
<i>Hatchling dry mass</i>	1.63 \pm 0.07	1.35 \pm 0.06	1.18 \pm 0.0
- carcass	1.18 \pm 0.04	1.21 \pm 0.05	1.10 \pm 0.05
- yolk sac	0.22 \pm 0.03	0.004 \pm 0.001	0
- fat bodies	0.23 \pm 0.02	0.13 \pm 0.01	0.08 \pm 0.01
<i>% water of hatchling</i>	74.3 \pm 0.6	75.5 \pm 0.8	76.6 \pm 0.4

TABLE 3. A comparison of the conversion efficiencies of dry mass, non-polar lipids and energy between *Ptyas korros* and other squamate reptiles whose eggs were incubated under similar conditions to those described in this paper.

Species	Conversion efficiency (%)			Duration of incubation (days)	Data sources
	Dry mass	Non-polar lipids	Energy		
Scincidae					
<i>Eumeces chinensis</i>	66	44	62	22.6	Ji <i>et al.</i> (1996)
Colubridae					
<i>Ptyas korros</i>	77	54	69	54.7	This study
<i>Elaphe carinata</i>	81	64	72	50.5	Ji <i>et al.</i> (1997a)
<i>Elaphe taeniura</i>	85	75	81	54.9	Ji <i>et al.</i> (1999a)
<i>Dinodon rufozonatum</i>	81	70	79	45.8	Ji <i>et al.</i> (1999b)
<i>Rhabdophis tigrinus lateralis</i>	70	37	61	29.3	Zhao <i>et al.</i> (1997)
<i>Zaocys dhumnade</i>	76	63	70	48.3	Ji (unpubl. data)
Elapidae					
<i>Naja naja atra</i>	75	64	69	50.7	Ji <i>et al.</i> (1997b)

are incubated under similar conditions to those described in this paper (Table 3). The variations could, of course, be partly due to inter-specific differences in costs of embryonic development and incubation length (Dmi'el, 1970; Vleck & Hoyt, 1991). For example, a species having higher costs of embryonic development and longer incubation length can be expected to have a lower conversion efficiency of energy. However, the differences in the measured conversion efficiencies can also be greatly dependent on egg and hatchling characteristics that may differ considerably among species.

The inverse relationships between post-hatching yolk dry mass, carcass dry mass and fat body dry mass in 0-day hatchlings suggest trade-offs among the three hatchling components. The increase in body size (SVL) during the first post-hatching week represents growth due mainly to the transformation of nutrients in the post-hatching yolk into the carcass. This conclusion is supported by the fact that newly emerged young increase in carcass mass following the depletion of post-hatching yolks. The same pattern has been found in other snakes, e.g. *Elaphe carinata* (Ji *et al.*, 1997a), *Elaphe taeniura* (Ji *et al.*, 1999a) and *Dinodon rufozonatum* (Ji *et al.*, 1999b), indicating that post-hatching yolk can be used for tissue growth in these snakes. The apparently greater carcass dry mass of 7-day hatchlings and the similarity in the mean carcass dry mass between 0- and 14-day hatchlings suggest a pattern of carcass dry mass increasing during the first week and decreasing thereafter. Such a pattern is more evident in *E. carinata* (Ji *et al.* 1997a) and *E. taeniura* (Ji *et al.*, 1999a), whose post-hatching yolks are relatively larger and are not completely exhausted one week after hatching.

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REFERENCES

- Congdon, J. D. (1989). Proximate and evolutionary constraints on energy relations of reptiles. *Physiol. Zool.* **62**, 356-373.
- Congdon, J. D. & Gibbons, J. W. (1989). Posthatching yolk reserves in hatchling American alligator. *Herpetologica* **45**, 305-309.
- Congdon, J. D., Gibbons, J. W. & Greene, J. L. (1983a). Parental investment in the chicken turtle (*Deirochelys reticularia*). *Ecology* **64**, 419-425.
- Congdon, J. D., Tinkle, D. & Rosen, R. (1983b). Egg components and utilization during development in aquatic turtles. *Copeia* **1983**, 264-268.
- Dmi'el, R. (1970). Growth and metabolism in snake embryos. *J. Embryol. Exp. Morph.* **23**, 761-772.
- Ewert, M. A. (1979). The embryo and its eggs: development and natural history, In *Turtles: Perspectives and Research*, p.333-413. Harless M., Morlock H. (Eds.). John Wiley and Sons, New York.
- Fischer, R. U., Mazzotti, F. J., Congdon, J. D. & Gatten, R. E. Jr. (1991). Post-hatching yolk reserves: parental investment in American alligators from Louisiana. *J. Herpetol.* **25**, 253-256.
- Ji, X., Fu, S.-Y., Zhang, H.-S. & Sun, P.-Y. (1996). Material and energy budget during incubation in a

- Chinese skink, *Eumeces chinensis*. *Amphibia-Reptilia* **17**, 209-216.
- Ji, X., Sun, P.-Y., Fu, S.-Y. & Zhang, H.-S. (1997a). Utilization of energy and nutrients in incubating eggs and post-hatching yolk in a colubrid snake, *Elaphe carinata*. *Herpetol. J.* **7**, 7-12.
- Ji, X., Sun, P.-Y., Fu, S.-Y. & Zhang, H.-S. (1997b). Incubation and utilization of energy and material during embryonic development in the cobra *Naja naja atra*. *J. Herpetol.* **31**, 302-306.
- Ji, X., Sun, P.-Y., Fu, S.-Y. & Zhang, H.-S. (1999a). Utilization of egg energy and material during incubation and post-hatching yolk in a colubrid snake, *Elaphe taeniura*. *Asiatic Herpetol. Res.* **8**, 342-346.
- Ji, X., Xu, X.-F. & Lin, Z.-H. (1999b). Influence of incubation temperature on characteristics of *Dinodon rufozonatum* (Reptilia: Colubridae) hatchlings, with comments on the function of residual yolk. *Zool. Res.* **20**, 342-346.
- Kraemer, J. E. & Bennett, S. H. (1981). Utilization of posthatching yolk in loggerhead turtle, *Caretta caretta*. *Copeia* **1981**, 406-411.
- Lin, Z. H. & Ji, X. (1988). The effects of thermal and hydric environments on incubating eggs and hatchlings of the grass lizard, *Takydromus septentrionalis*. *Zool. Res.* **19**, 439-445.
- Seigel, R. A. & Ford, N. B. (1986). Variation in relative clutch mass in snakes among and within species. *Herpetologica* **42**, 179-185.
- Troyer, K. (1983). Posthatching yolk energy in a lizard: utilization pattern and interclutch variation. *Oecologia (Berl.)* **58**, 340-344.
- Troyer, K. (1987). Posthatching yolk in a lizard: internalization and contribution to growth. *J. Herpetol.* **21**, 102-106.
- Vleck, C. M. & Hoyt, D. F. (1991). Metabolism and energetics of reptilian and avian embryos. In *Egg Incubation, its Effect in Embryonic Development in Birds and Reptiles*, pp. 285-306. Deeming, D. C., Ferguson, M. W. J. (Eds.). Cambridge University Press, Cambridge.
- Wilhoft, D. C. (1986). Egg and hatchling components of the snapping turtle (*Chelydra serpentina*). *Comp. Biochem. Physiol.* **84A**, 483-486.
- Zhao, E.-M. & Adler, K. (1993). *Herpetology of China*. Society for the Study of Amphibians and Reptiles, Oxford, Ohio, USA, 521pp.
- Zhao, Q., Zhang, J.-Q., Huang, H.-Y. & Ji, X. (1997). Utilization of egg energy and material by *Rhabdophis tigrinus lateralis* embryos during incubation. *J. Hangzhou Normal Coll.* **97**, 60-64.

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DIFFERENTIAL GROWTH AND LONGEVITY IN LOW AND HIGH ALTITUDE *RANA IBERICA* (ANURA, RANIDAE)

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Age, body size and histological bone growth were analysed in two populations of *Rana iberica* that were genetically similar and which represented the altitudinal extremes of the species range. In spite of having a much longer hibernation, mountain frogs were significantly bigger (snout-vent lengths) for all ages, with the exception of the pre-maturity period. Mountain frogs were longer-lived (oldest females 6 years, males 5 years, one male outlier 9 years) than lowland frogs, where at most only one individual of each sex attained the age of 4 years. The minimum age at sexual maturity was 2 years for both sexes and populations. For both sexes, and using different assumptions about the duration of the period of seasonal activity, the relative contribution of the growth rate component seems slightly higher (46-75 % for females, 60-82 % for males) than differences in life span (i.e. total days of activity: 25-54 % for females, 18-40 %) in accounting for the overall size differences found between populations.

Key words: age, altitude, Anura, growth, skeletochronology

INTRODUCTION

The Iberian brown frog *Rana iberica* Boulenger, 1879, is an endangered endemic species from the Iberian Peninsula. This species is one of the few non-Mediterranean Spanish anurans, distributed in the Atlantic Eurosiberian realm throughout north-western Spain, north and central Portugal and the Sistema Central, a mountain range which crosses the Iberian Peninsula from ENE to WSW (Crespo, 1997; Esteban, 1997; Fig. 1). A few relict populations of the species

have also been found in the Basque Country (Esteban, 1997). The distribution of *Rana iberica* shows a wide altitudinal range (Pleguezuelos & Villafranca, 1997), although the habitat it uses across this range is similar. *Rana iberica* is found in the humid northern regions, even at sea level (Galán, 1982, 1989), whereas in drier areas, such as central Spain, this species is only a mountain form, found at over 2000 m (Esteban, 1997; Pleguezuelos & Villafranca, 1997). The very different winter climatic conditions under which these populations are found causes drastic variations in their seasonal period of activity (Esteban, 1990).

Some morphological studies show that a large variation in body size occurs among different populations of this species (Lizana, Pérez-Mellado & Ciudad, 1987; Galán, 1989). This variation is present despite the fact that this species shows very low genetic differentiation, as inferred from allozyme electrophoretic studies, throughout its range (Herrero, Arano & Esteban, 1990; Arano, Esteban & Herrero, 1993). In ectothermic animals with continuous growth, such as amphibians, differences in size among populations may be the result of differential growth rates, sexual maturity onset, yearly activity period (total days of annual activity), and longevity (total years lived). Thus, there are plastic phenotypic responses to local environmental conditions that alter individual growth time and/or energy budget constraints (Berven, 1982; Hemelaar, 1988).

Skeletochronology and bone histology have proved to be excellent tools in evaluating the physiological activity induced in amphibians by seasonal changes. Such changes lead to the formation of bone growth marks, such as 'zones', i.e. thicker layers of bone laid down during periods of fast osteogenesis, and 'lines of arrested growth' (LAGs) formed in periods when osteogenesis is very slow or non-existent (Castanet,

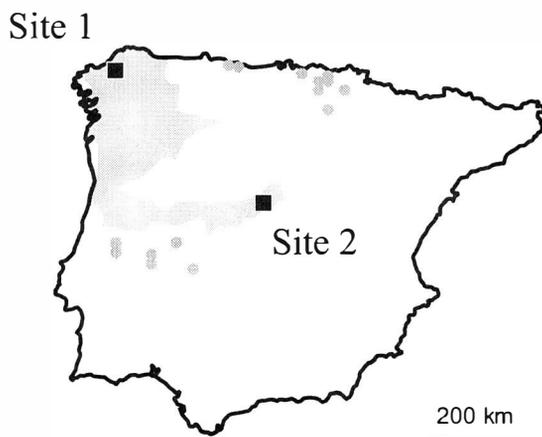


FIG. 1. Distribution range of *Rana iberica*, with indications of the sites studied. Range of *R. iberica* in grey. Site 1: lowland population of Monfero. Site 2: high mountain population of El Espinar.

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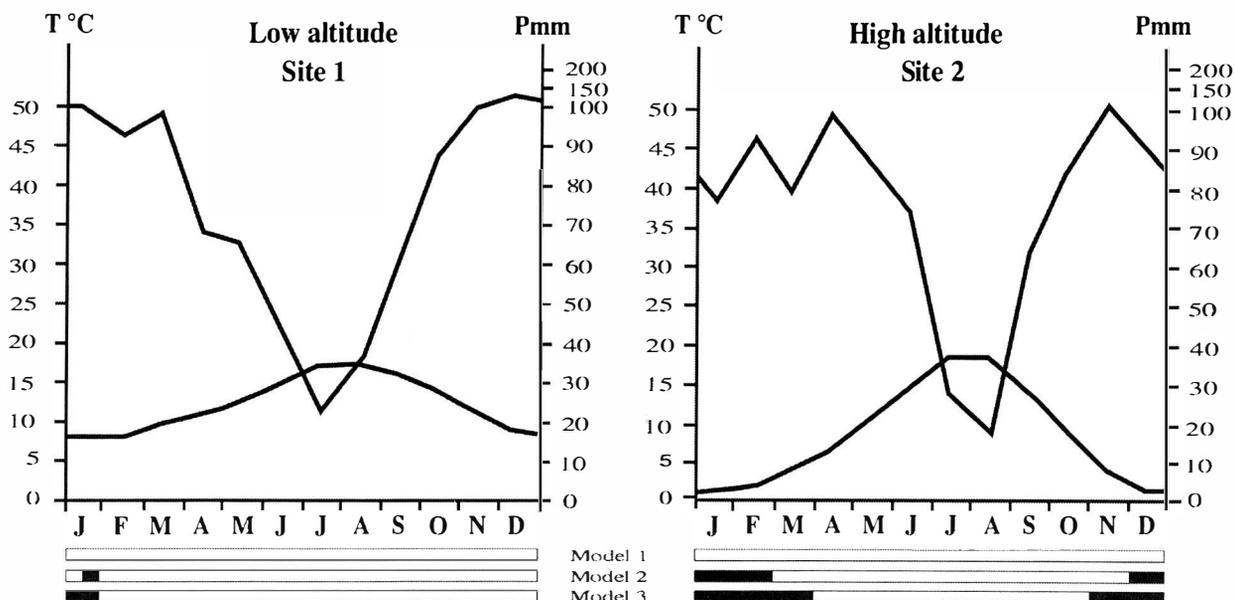


FIG. 2. Climatic diagrams and phenological assumptions for the populations of low altitude (Site 1) and high altitude (Site 2). T°C: temperature in degrees Celsius. Pmm: precipitation in cubic mm per m². For models, black lines indicate periods of hibernation (see Table 3).

Francillon-Vieillot, Meunier & de Ricqlès, 1993). A zone followed by a LAG corresponds to a single annual cycle of activity in cold or temperate regions. The number of growth marks and their histological structure have been used in a large number of amphibian species to estimate individual age (Smirina, 1994), and they also enable us to trace the history of growth year by year.

In this article we study the relationships between age, size and histological bone growth in two selected populations of *Rana iberica*. These populations represent the altitudinal extremes of the species range (Fig. 1). Taking advantage of the genetic similarity between the populations at the isozyme level (Nei genetic distance 0.019; Arano *et al.*, 1993), this study will analyse the degree to which body size is related to longevity, growth rates and duration of the annual activity period.

MATERIALS AND METHODS

Histological samples of 113 specimens of *Rana iberica*, collected in different years from two areas in Spain (Fig. 1) were studied. One sample (Site 1) comes from the north-western Iberian region, in the neighbourhood of Monfero (43° 20' N, 8° 20' W; province of Coruña), and is composed of 49 adults (27 males and 22 females). This area is situated at an altitude of between 100 and 200 m. The relevant climatic conditions at the site have been inferred from the meteorological station in the nearby town of Betanzos, where an annual rainfall of 900-1000 mm and a mean air temperature range of 13-14 °C was recorded over 37 years (Fig. 2; León-Llamazares, 1988). The second sample (Site 2) is composed of 64 adults (26 males and 38 females) from the Sistema Central mountains at altitudes from 1600 to

1700 m, the majority collected in the area between El Espinar and La Granja de San Ildefonso (40° 45' N, 4° 10' W; province of Segovia). Our meteorological data for this region comes from the station at La Granja de San Ildefonso. The climate here is characterized by a cold winter, with an annual precipitation of around 1200 mm, and an average yearly temperature between 7 and 9 °C over 41 years. The climatic diagram for site 2 is presented in Fig. 2, based on León-Llamazares (1987).

Esteban (1990) presents general data on the seasonal phenology of the populations analysed here. Nevertheless, on account of the high interannual phenological variation expected, we have used three working assumptions that will cover all the relevant possibilities about the duration of the activity period. The first, admittedly unrealistic, assumes that frogs are active all year in both populations. The second projects a hibernation period of 15 days (350 active per year) for the lowland population. This is a minimum estimation, deduced from the fact that lines of arrested growth (LAGs) are present in the population, and each of these marks require from 15 days to 5 weeks to develop (Smirina, Klevezal & Berger, 1986). Therefore, we think that LAGs are formed in Monfero during the coldest month, which has a mean temperature of 7.8 °C. The corresponding situation in the high mountains would be 275 days of activity, a figure that assumes that the majority of the frog population is not active in months with a mean temperature below 5 °C. This result is precisely equivalent for Site 2 to a hibernating period during the months in which the mean of the minimal temperatures is below 0°. The third assumption assigns a hibernation period of one month to the

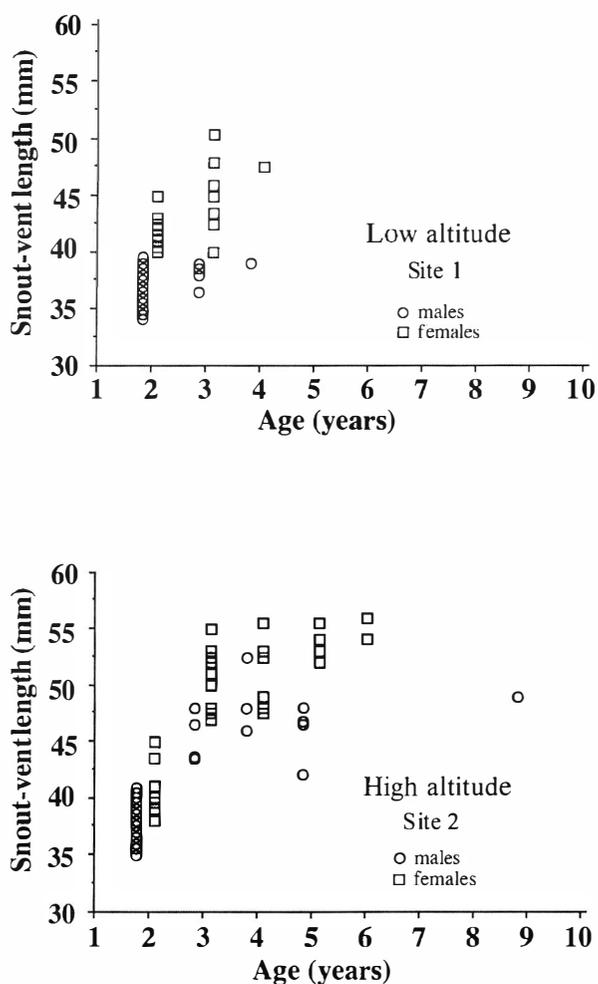


FIG. 3. Plot of age (LAG number) versus SVL for low (Site 1) and high (Site 2) altitude populations of *Rana iberica*.

lowland region and five months to the mountain region, with a monthly mean temperature of 8 °C for activity as the common threshold. Nevertheless, a mountain hibernation of five months is a non-realistic maximum, because we have frequently observed active frogs during most of both November and March.

The osteological material and the data about sex and snout-vent lengths (SVL) for the specimens come from the herpetological collection of the Museo Nacional de Ciencias Naturales (Madrid, Spain). This material was previously used in other studies about the genetic variability (Herrero *et al.*, 1990; Arano *et al.*, 1993) and morphology (Galán, 1982, 1989) of this threatened endemic species, and no additional specimens have been collected for our study.

Skeletochronological preparations were made, with slight modifications, according to the Smirina (1972) protocol. A tibiofibula of each specimen was decalcified in nitric acid 3% for 5 hrs and washed overnight in running tap water. Sections of the diaphysis of frozen bones were cut using a cryostat microtome. Sections were 20 μ m thick, stained for 15 minutes at room temperature with Ehrlich hamatoxylin and mounted in aqueous synthetic resin (Aquamount) after being rinsed

for at least 5 minutes in tap water. The analysis and interpretation of growth marks was done under an ordinary light microscope, followed by photomicrography. On each photograph, a curvimeter was used to measure the perimeters of the marrow cavity, the outer margin of the tibiofibula, and each line of arrested growth (LAG). In all tibiofibular cross-sections, one or more stained LAGs were clearly distinct and easy to count. We accept the assumption that each LAG represents the end of a one year cycle, as demonstrated for several ranids in cold and temperate climates (Smirina, 1972; Gibbons & McCarthy, 1983; Patón, Juarranz, Sequeros, Pérez-Campo, López-Torres & Barja de Quiroga, 1991).

The software packages Mathematica 3.0 (Wolfram, 1996) and Statview IV were used for the calculations. Interpolation in the developmental trajectories were obtained by fitting low-order polynomial curves between the data points. We have used step-wise interpolation functions generated by the Mathematica standard interpolation facilities. These curves used are not intended to have any biological meaning, and their equations are not given; they only provide the best possible accuracy for interpolation and further estimation of the two relative components (growth rate and total days of activity) of final size.

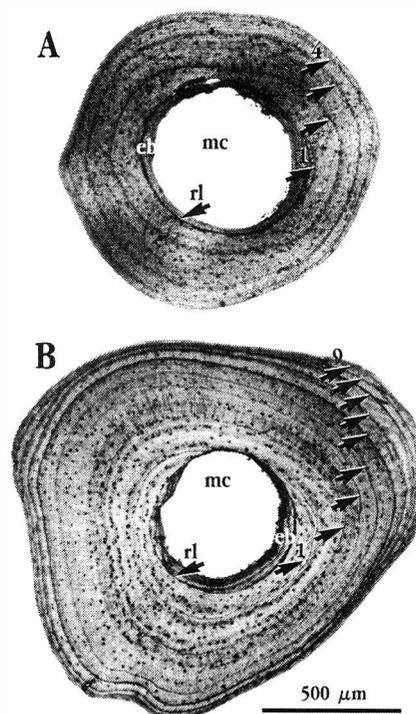


FIG. 4. Cross sections taken at the middle of the tibiofibular diaphysis of *Rana iberica*. A: female from Site 1 (SVL= 49 mm), showing four LAGs. B: male from Site 2 (SVL= 50 mm), with nine LAGs. eb: endosteal bone; mc: medullar cavity; rl: resorption line.

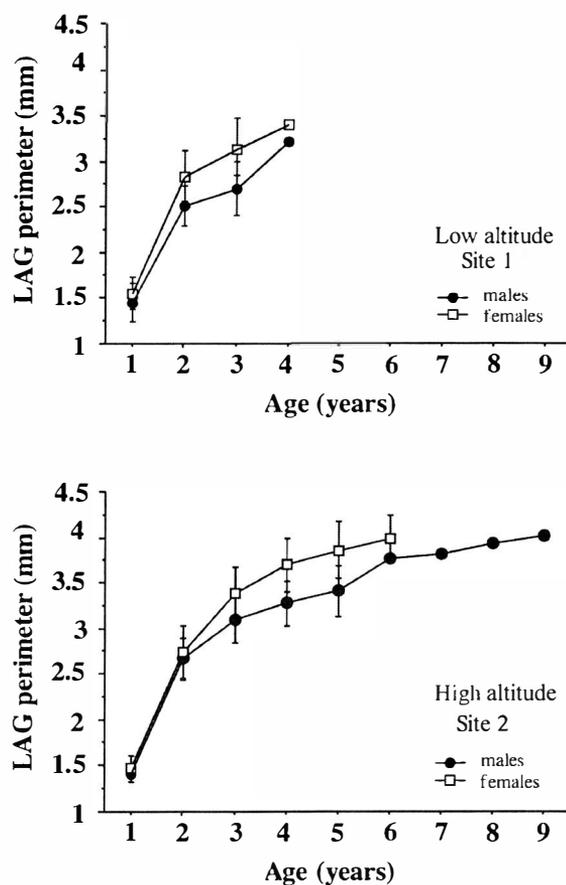


FIG. 5. Mean tibiofibular annual growth in low (Site 1) and high (Site 2) altitude populations of *Rana iberica*. Male perimeters at 5-8 years (Site 2) are based on one 9 year-old individual. Age (in years) is not biologically equivalent in both sites because their annual activity periods are different (see text). Black dots: males. Open squares: females. Vertical bars represent standard deviation.

TABLE 1. Number of individuals (N), mean size in mm (SVL), standard deviation and range, for each sex in both populations. U -test: probabilities in the Mann-Whitney U -test for differences between sexes and sites.

	Site 1	Site 2	U -test (sites)
<i>Males</i>			
N	27	26	
Mean \pm SD	36.93 \pm 1.62	41.33 \pm 4.66	$P<0.001$
Range	34.0-39.5	35.0-49.0	
<i>Females</i>			
N	19	38	
Mean \pm SD	43.53 \pm 2.99	48.75 \pm 5.28	$P<0.001$
Range	40.0-50.5	38.0-56.0	
U -test (sexes)	$P<0.001$	$P<0.001$	

RESULTS

Osseous remodelling was detected in the centre of the cross section of 24.5% and 28% of the individuals in the populations of Site 1 and Site 2 respectively. In most cases this endosteal resorption was slightly asymmetrical and did not completely destroy the first LAG. However, we suspect that LAG 1 was removed in 4 and 3 specimens from Site 1 and Site 2 respectively, because the mean perimeter of the medullar cavity for these individuals (Site 1: 1.66 mm, SD=0.10; Site 2: 1.76 mm, SD=0.24) was significantly larger ($P<0.01$ for both sites in Mann-Whitney U -tests) than the LAG 1 perimeters in the subsample that did not show complete resorption (Site 1: 1.48 mm, SD=0.20; Site 2: 1.44 mm, SD=0.12). Likewise, the innermost LAG of the individuals sus-

TABLE 2. Mean and standard deviation of LAG perimeter for males and females in both populations. U -test: Mann-Whitney U -test for differences between sites.

LAG	Site 1		Site 2		U -test
	N	Perimeter (mm)	N	Perimeter (mm)	
<i>Males</i>					
1	18	1.43 \pm 0.21	21	1.41 \pm 0.09	$P=0.370$
2	27	2.49 \pm 0.22	26	2.68 \pm 0.22	$P=0.003$
3	6	2.67 \pm 0.30	11	3.11 \pm 0.23	$P=0.010$
4	1	3.02	7	3.27 \pm 0.25	—
5	—	—	5	3.41 \pm 0.28	—
6	—	—	1	3.78	—
7	—	—	1	3.80	—
8	—	—	1	3.83	—
9	—	—	1	3.87	—
<i>Females</i>					
1	16	1.53 \pm 0.18	25	1.47 \pm 0.14	$P=0.522$
2	19	2.81 \pm 0.28	38	2.73 \pm 0.29	$P=0.441$
3	9	3.21 \pm 0.40	28	3.41 \pm 0.29	$P=0.041$
4	1	3.45	15	3.70 \pm 0.29	—
5	—	—	7	3.87 \pm 0.32	—
6	—	—	2	3.98 \pm 0.26	—

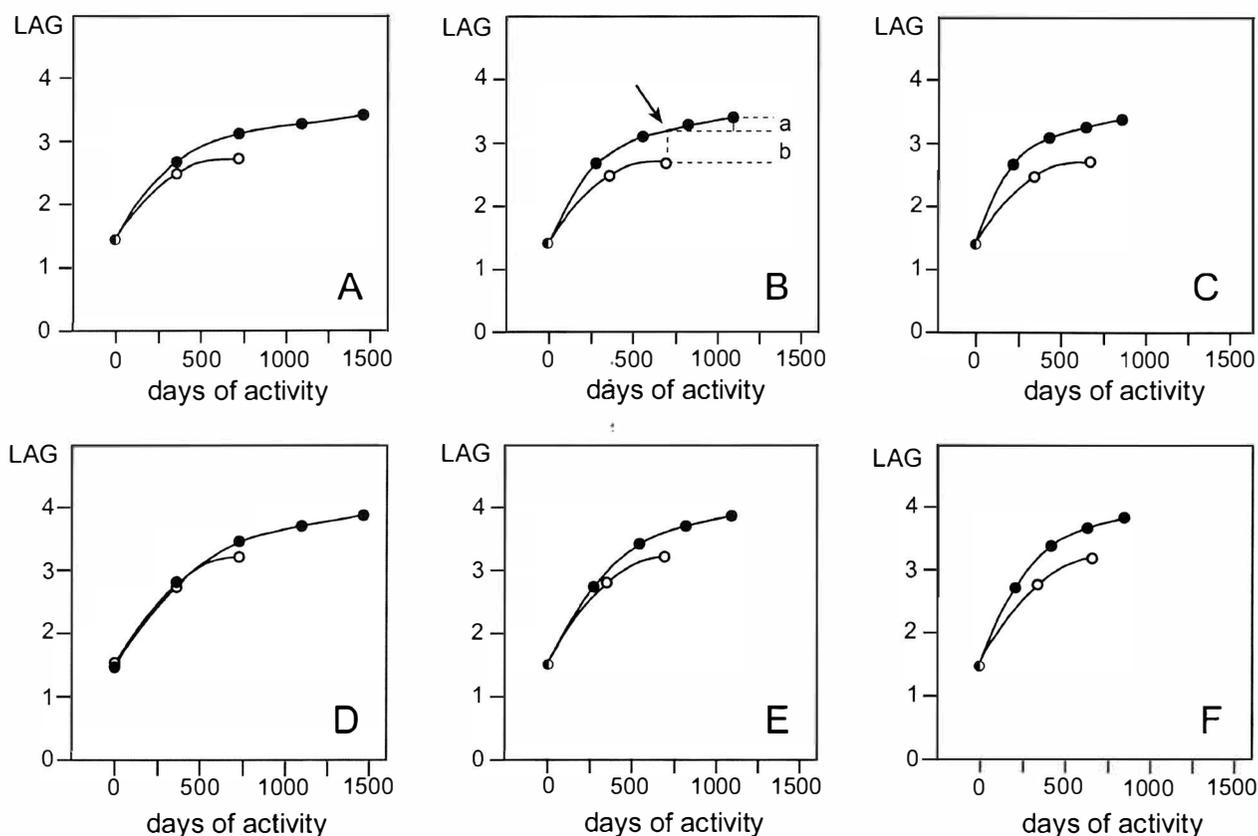


FIG. 6. Growth of the central tibiofibular perimeter (LAG, in mm) for different phenological assumptions. The history of growth has been inferred directly from maximum LAG perimeters in samples >5 (see text). A-C: males. D-F: females. A,D: 365 days of activity. B, E: 350 (Site 1) and 275 (Site 2) days of activity. C, F: 335 (Site 1) and 215 (Site 2) days of activity. Upper curves (black dots) correspond to the high altitude Site 2. Arrow: interpolation point on Site 2 of the maximum age on Site 1. Final size on Site 2 caused by a differential life span component (a) or by differences in growth rate (b).

pected of complete resorption (Site 1: 2.67 mm, $SD=0.26$; Site 2: 2.54 mm, $SD=0.22$) was within the range of the LAG 2 for the specimens which preserved LAG 1 (Site 1: 2.27-3.32 mm; Site 2: 2.30-3.25 mm). We conclude that LAG have been completely lost in the above mentioned specimen, and we have therefore added one to the number of counted LAGs. This remodelling process is mainly produced when the growth rate is highest, before the onset of sexual maturity (Leclair, 1990), and has been reported in other *Rana* species (Leclair & Castanet, 1987; Esteban, 1990; Esteban, García-París & Castanet, 1996; Sagor, Ouellet, Barten & Green, 1998).

As indicated in Table 1, females were on average larger than males in both populations. For both sexes, the population of Site 2 was significantly larger (Table 1). Galán (1982, 1989) finds similar sizes to our Site 1 in populations from La Coruña (SVL males 29.2-38.6 mm; females 36.6-51.0 mm), although in our sample we found a slightly smaller minimum size.

The age structure of the populations, determined by LAG counts, is shown in Fig. 3 in relation to SVL. In Site 1, males had a mean age of 2.26 years ($SD=0.53$), while the mean age for females was 2.53 ($SD=0.61$). The male subsample from Site 2 had a mean age of 3.04 ($SD=11.66$) and the female value was 3.37 yrs

($SD=1.17$). Significant sexual differences occur in age in both populations (Mann-Whitney U -test $P>0.05$), but both sexes from Site 2 were older than their counterparts from Site 1 ($P<0.01$). The modal values for ages were 2 yrs in the males of both populations and in the females at Site 1, and 3 yrs for females at Site 2.

The skeletochronological pattern allows us to infer the age at which sexual maturity is attained (Castanet *et al.*, 1993). The minimum age for maturity observed here was 2 yrs in both sexes and populations, and no significant differences in body size at maturity was found between populations ($P>0.05$).

The oldest individuals were found in the highland population, where the oldest females were 6 yrs old and the males 5 yrs old, with the exception of a single male (SVL 50 mm) which had lived for 9 yrs (Fig. 4B). In comparison, the members of the lowland population were younger, and only one individual of each sex attained the age of 4 yrs (Fig. 4A).

An analysis of growth patterns in terms of age and size throughout each individual's life, as preserved in the histological bone marks, has been carried out. LAG perimeters, which represent the bone perimeter at the end of each growth season, are well known measures which can be adopted as reliable indicators of past size and growth (Hemelaar, 1988). Correlation between

TABLE 3. Comparison of tibiofibular growth for each sex and population. Annual percentage (%) and daily (μm) increase in mean perimeter for each age. M1: model of 365 days of annual activity in both populations. M2: model of 350 days of activity for Site 1 and 275 days for Site 2. M3: model of 335 days of activity for Site 1 population and 215 days for Site 2.

Years of life	Site 1				Site 2			
	%	M1	M2	M3	%	M1	M2	M3
Males								
1 st	100				100			
2 nd	174	203	211	221	190	247	327	419
3 rd	186	33	34	36	221	85	113	144
4 th	—	—	—	—	232	30	40	51
5 th	—	—	—	—	242	27	36	47
Females								
1 st	100				100			
2 nd	183	227	237	248	186	235	312	399
3 rd	209	71	74	78	232	127	168	215
4 th	—	—	—	—	252	54	72	92
5 th	—	—	—	—	263	232	42	54

SVL and tibiofibula perimeter, for each population and sex, was found to be significant in our study (Site 1: males $r=0.56$, females $r=0.81$, Site 2: males $r=0.89$, females $r=0.85$; $P<0.05$). Fig. 5 shows the tibiofibular growth for both populations. The regression analysis of tibiofibular perimeter on age showed a highly significant correlation for both sexes and populations ($P<0.01$), although the tibiofibular perimeters vary substantially within most age groups, and the largest individuals were not always the oldest ones. As expected, immature individuals grew much faster in both populations (Table 3). Growth rates were higher for females than for males ($P<0.05$).

The specimens from Site 2 attained significantly greater sizes in tibiofibular perimeter than those from Site 1, at the age of 2 yrs and 3 yrs (males) and 3 yrs (females), in Mann-Whitney U -tests ($P<0.005$). This size difference is indicative of a faster bone growth in highland individuals after maturity, for all possible assumptions about periods of hibernation (Table 3, Fig. 6).

Fig. 6 shows the overall histological growth trajectories for each population, sex and annual activity assumption. These diagrams give a general view of the relative contributions of growth rates and longevity in accounting for the final size differences between populations. The difference in ordinates (LAG perimeter) in Fig. 6 between the final points of both trajectories indicates the total size difference. The difference in ordinates between the final point of the shortest lived trajectory (Site 1) and their corresponding interpolation (i.e., with the same numbers of days of activity) in the trajectory of Site 2, indicates the contribution of differential growth rates to the overall size comparison. Any growth increase after this point in Site 2 is exclusively caused by a differential longevity factor (Fig. 6B). The results were slightly different for

males and females, but in both sexes the growth rate played a more important role than the age, with percentages around 60%, 79%, and 82% for males, and 46%, 70%, and 75% for females under hibernating assumptions A to C respectively.

DISCUSSION

Several of the results that we have found agree with similar studies done on other populations of brown frogs (Sagor, Ouellet, Barten & Green, 1998). The positive relationship between increasing body size and altitude is a frequent observation. Our samples from almost the lowest and highest elevations can be compared with the intermediate sizes (maximal SVL 42.0 mm for males and 50.7 for females) present in another *Rana iberica* population at medium altitude (around 850 m) from the western Sistema Central (Lizana *et al.*, 1987). The increase in longevity in amphibian populations living in mountain conditions has already been cited in other European brown frogs (Guarino, Angelini, Giacoma & Cavallotto, 1995; Ryser, 1996) and in numerous other amphibians (see review in Smirina, 1994). This phenomenon has been related to a delay in the onset of sexual maturity for populations living at lower temperatures (Stearns, 1989; Charnov, 1990; Charnov & Berrigan, 1990), and to different rates of predation derived from the shorter duration of the annual activity period (Licht, 1976; Ryser, 1996). Nevertheless, no delayed maturity exists in any of our populations, and Guarino *et al.* (1995) have found similar ages for maturity in two populations of *Rana italica*, a similar European brown frog species.

Our results should be taken as preliminary until more detailed ecological and life cycle studies are available for the populations examined. Nevertheless, the results do not completely conform with current life-history theory for ectotherms, as summarized by the

'developmental temperature-size rule' (Atkinson & Sibly, 1997). Size differences are not found at the end of the juvenile period - they increase during the adult growth period. According to the most realistic phenological assumption, we have estimated that growth rates account for no less than 46-75% (females), and up to 60-82% (males), of the total size differences between populations (Fig. 6). These facts can be explained in several ways. On the one hand, we could suppose that growth rate, as a complex life history trait, has been subject to selection, and that this genetic differentiation is not reflected in the neutral loci sampled on allozymes (Latta, 1998). On the other hand, if genetic differentiation is negligible at all levels, as both environments (and presumably food supplies) are quite similar during the common activity period of frogs, then an environmentally induced factor (temperature) would account for the size differences recorded (Partridge & French, 1996; Atkinson & Sibly, 1997). Both explanations cannot fully explain the lack of size differences at the time of the first LAG, unless growth metabolic inductors were drastically different, or some biased compensatory growth occurred in late autumn. Therefore, it seems possible that resource allocation differences may be involved. The metabolic adult rate in the highland population, as observed in the male skeletochronology sections, may perhaps not necessarily be associated with first reproduction, which may have occurred during the third year in a fraction of the highland population. In this way, a considerable energetic cost would have been avoided by the two year-old males. Furthermore, undetected differences may exist in tadpole size and time of metamorphosis.

The histological data sets here compiled show that growth rate plays a more important role than longevity (i.e. total years lived) or activity period (total days of activity lived) in explaining the size differences observed between lowland and highland populations. Further research is necessary for a more detailed quantitative description of the differential ontogenetic size trends and their causal basis.

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REFERENCES

- Arano, B., Esteban, M. & Herrero, P. (1993). Evolutionary divergence of the Iberian brown frogs. *Annales des Sciences. Naturelles, Zoologie* **11**, 2101-204.
- Atkinson, D. & Sibly, R. M. (1997). Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. *Trends in Ecology and Evolution* **12**, 235-239.
- Berven, K. A. (1982). The genetic basis of altitudinal variation in the wood frog *Rana sylvatica*: an experimental analysis of life-history traits. *Evolution* **36**, 962-983.
- Castanet, J., Francillon-Vieillot, H., Meunier, F. & Ricqlès, A. de. (1993). Bone and individual aging. In *Bone. Vol 7. Bone Growth-B*, 245-283. B. K. Hall (Ed.). Boca Raton, Florida: CRC Press.
- Charnov, E. L. (1990). On evolution of age of maturity and the adult lifespan. *Journal Evolutionary Biology* **3**, 139-144.
- Charnov, E. L. & Berrigan, D. (1990). Dimensionless numbers and life history evolution: age of maturity versus the adult lifespan. *Evolutionary Ecology* **4**, 273-275.
- Crespo, E. (1997). *Rana iberica* Boulenger, 1879. In *Atlas of amphibians and reptiles in Europe*, 142-143. Gasc, J.P. et al. (Eds.). Paris: Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle (IEGB/SPN).
- Esteban, M. (1990). Environmental influences on the skeletochronological record among recent and fossil frogs. *Annales des Sciences. Naturelles, Zoologie* **11**, 201-204.
- Esteban, M. (1997). *Rana iberica*. In *Distribución y Biogeografía de los Anfibios y Reptiles en España y Portugal*, 161-163. J. M. Pleguezuelos (Ed.). Granada: Asociación Herpetológica Española and Universidad de Granada Press.
- Esteban, M., García-París, M. & Castanet, J. (1996). Use of bone histology in estimating the age of frogs (*Rana perezi*) from a warm temperate climate area. *Canadian Journal of Zoology* **74**, 1914-1921.
- Galán, P. (1982). Biología de la reproducción de *Rana iberica* en zonas simpátricas con *Rana temporaria*. *Doñana Acta Vertebrata* **9**, 85-98.
- Galán, P. (1989). Diferenciación morfológica y selección de hábitats en las ranas pardas del noroeste ibérico: *Rana iberica* Boulenger, 1879 y *Rana temporaria* Seoane, 1885. *Treballs Societat Catalana Ictiologia i Herpetologia* **2**, 193-209.
- Gibbons, M. M. & McCarthy, T. K. (1983). Age determination of frogs and toads (Amphibia, Anura) from north-western Europe. *Zoologica Scripta* **12**, 145-151.
- Guarino, F. M., Angelini, F., Giacoma, C. & Cavallotto, L. (1995). Age determination by skeletochronology in low- and high-elevation populations of *Rana italica*. In *Scientia Herpetologica*, 187-191. G. A. Llorente, A. Montori, X. Santos & M. A. Carretero (Eds.). Barcelona: Asociación Herpetológica Española.
- Hemelaar, A. M. S. (1988). Age, growth and other population characteristics of *Bufo bufo* from different latitudes and altitudes. *Journal of Herpetology* **22**, 369-388.

- Herrero, P., Arano, B. & Esteban, M. (1990). Karyotypic characterization of brown frogs from the Iberian Peninsula (Ranidae: *Rana*). In *Cytogenetics of Amphibia and Reptilia*, 135-140. E. Olmo (Ed.). Basel: Birkhauser.
- Latta, R. G. (1998). Differentiation of allelic frequencies at quantitative trait loci affecting locally adaptive traits. *American Naturalist* **151**, 283-292.
- Leclair, R. (1990). Relationships between relative mass of the skeleton, endosteal resorption, habitat and precision of age determination in ranid amphibians. *Annales des Sciences. Naturelles, Zoologie*, **11**, 205-208.
- Leclair, R. & Castanet, J. (1987). A skeletochronological assessment of age and growth in the frog *Rana pipiens* Schreber (Amphibia, Anura) from southwestern Quebec. *Copeia* **1987**, 361-369.
- León-Llamazares, A. (1987). *Caracterización agroclimática de la provincia de Segovia*. Madrid: Ministerio de Agricultura.
- León-Llamazares, A. (1988). *Caracterización agroclimática de la provincia de La Coruña*. Madrid: Ministerio de Agricultura.
- Licht, L. E. (1976). Sexual selection in toads (*Bufo americanus*). *Canadian Journal of Zoology* **54**, 1177-1284.
- Lizana, M., Pérez-Mellado, V. & Ciudad, M. J. (1987). Biometry and relation with the ecology of *Rana iberica* and *Rana perezi* in the Sistema Central (Spain). In *Proceedings of the 4th Ordinary General Meeting of the Societas Europaea Herpetologica*, 253-258. Van Gelder, J. J., Strijbosch, H. & Bergers, P.J.M (Eds.). Nijmegen: Societas Europaea Herpetologica.
- Partridge, L. & French, V. (1996). Thermal evolution of ectotherm body size: why get big in the cold? In *Animals and Temperature*, 265-292. Johnston, I. A. & Bennett A. F. (Eds.). Cambridge: Cambridge University Press.
- Patón, D., Juarranz, A., Sequeros, E., Pérez-Campo, R., López-Torres, M. & Barja de Quiroga, G. (1991). Seasonal age and sex structure of *Rana perezi* assessed by skeletochronology. *Journal of Herpetology* **25**, 389-394.
- Pleguezuelos, J.M. & Villafranca, C. (1997). Distribución altitudinal de la herpetofauna ibérica. In *Distribución y biogeografía de los anfibios y reptiles en España y Portugal*, 321-341. J. M. Pleguezuelos (Ed.). Granada: Asociación Herpetológica Española and Universidad de Granada Press.
- Ryser, J. (1996). Comparative life histories of a low- and high-elevation population of the common frog *Rana temporaria*. *Amphibia-Reptilia* **17**, 183-195.
- Sagor, W. S., Ouellet, M., Barten, E. & Green, D. M. (1998). Skeletochronology and geographic variation in age structure in the Wood Frog, *Rana sylvatica*. *Journal of Herpetology* **32**, 469-474.
- Smirina, E. M. (1972). Annual layers in bones of *Rana temporaria*. *Zoologicheskii Zhurnal*. **51**, 1529-1534.
- Smirina, E. M. (1994). Age determination and longevity in amphibians. *Gerontology* **40**, 133-146.
- Smirina, E. M., Klevezal, G. A. & Berger, L. (1986). Experimental investigation of the annual layer formation in bone of Amphibians. *Zoological Journal* **65**, 1526-1534.
- Stearns, S. C. (1989). *The evolution of life histories*. Oxford: Oxford University Press.
- Wolfram, S. S. (1996). *The Mathematica Book* (3rd ed.). Cambridge: Cambridge University Press.

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STATE-DEPENDENT AND RISK-SENSITIVE ESCAPE DECISIONS IN A FOSSORIAL REPTILE, THE AMPHISBAENIAN *BLANUS CINEREUS*

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Morphological adaptations of amphisbaenians to fossorial life may affect their anti-predator behaviour and escape decisions. Amphisbaenians exposed on the soil surface by a predator may decide to escape either by burrowing immediately or by using alternative defensive behaviours. This decision may depend on the internal state (body temperature and associated burrowing performance) but, because anti-predator behaviours may be costly, an optimal response should also be sensitive to risk and vary according to the threat of predator attack. In a laboratory experiment we simulated predatory attack on individual amphisbaenians of the species *Blanus cinereus*, and specifically examined the effects of temperature (warm vs. cold) and predation threat (low vs. high) on escape decisions. Amphisbaenians showed significantly longer episodes of an alternative anti-predator behaviour on the soil surface (coiling) when the predation threat was high and when the temperature was low. The time to burrow until half of the body was buried was significantly longer when the temperature was low and was significantly shorter when the threat was high. The variations observed in anti-predator behaviours may reflect the choice of the optimal response under each circumstance, taking into account the estimated predation risk, which is dependent on the characteristics of the initial attack, and potential burrowing performance, which is dependent on body temperature.

Key words: predation, escape behaviour, fossorial reptile, *Blanus cinereus*

INTRODUCTION

Variation in external ecological conditions and in the internal state of animals may affect the costs and benefits associated with different behaviours. Avoiding predation is crucial for the survival of any organism (Lima & Dill, 1990). An animal that detects an approaching predator needs to decide whether to retreat to a safer location and, if so, when and how to escape. This is a clear example of a decision involving several costs and benefits (Ydenberg & Dill, 1986). Under these circumstances, trade-offs and decision rules (Bouskila & Blumstein, 1992), which are sensitive to internal and external conditions, are likely to be involved.

In surface-dwelling reptiles this cost-benefit analysis, and consequently the escape decisions, may be influenced by several factors such as distance to shelter (Cooper, 1997a), microhabitat (Martín & López, 1995b; Smith, 1996), age (Martín & López, 1995a), sex and reproductive state (Smith, 1996). The effect of body temperature has also been frequently analysed in reptiles because it has important implications for many aspects of their physiology such as, for example, their locomotory performance (reviewed in Huey, 1982). As a result, the ability of reptiles to escape is also affected by their internal thermal state (e.g., Rand, 1964; Hertz, Huey & Nevo, 1982; Arnold & Bennett, 1984; Passek & Gillingham, 1997). In addition, lizards (Burger &

Gochfeld, 1990, 1992; Martín & López 1996; Cooper, 1997b), snakes (Bowers, Bledsoe & Burghardt, 1993) and other animals (e.g., Burger & Gochfeld, 1981) may react differentially to the approach of a predator as a function of the perceived threat of attack. Approaching predators do not always pose an immediate threat, and thus animals should tend to optimize the magnitude of their escape and anti-predatory responses accordingly, saving time and energy.

Amphisbaenians are a group of reptiles morphologically and functionally adapted to a fossorial life (Gans, 1978). Morphological adaptations to burrowing include trunk elongation, modification of the head size and skull, reduced vision and loss of limbs (Gans, 1978). These adaptations constrain amphisbaenians to solve their ecological demands with a suite of original responses different from those of other, surface-dwelling reptiles (Martín, López & Salvador, 1990, 1991; López & Martín, 1994; López & Salvador 1992; López, Martín & Salvador 1991; López, Salvador & Martín, 1998). Adaptations to fossorial life might also affect their anti-predator behaviour and escape decisions. Although predation pressure is apparently lower in the underground environment, there are some specialized predators, such as the wild boar and the Egyptian mongoose, which habitually dig extensive areas of soil or lift stones looking for prey and can leave amphisbaenians exposed on the soil surface (Busack, 1978; Martín & López, 1990). In these circumstances, amphisbaenians can escape either by burrowing immediately or by using alternative defensive behaviours on the soil surface, such as being immobile and cryptic or

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showing saltatory coiling behaviour (review in Greene, 1988). This decision may depend on the internal state (body temperature) and associated burrowing performance, but an optimal response should also be risk-sensitive and vary according to the level of threat of predator attack.

We hypothesized that if the burrowing performance of amphisbaenians is better under favourable thermal conditions (i.e. optimal body temperature), amphisbaenians will tend to use alternative anti-predator behaviours to escape when thermal conditions are unfavourable. Additionally, because anti-predator behaviours and burrowing may be costly, the magnitude and characteristics of the escape response should be optimized according to the predation threat level by balancing the fitness effects of avoiding predators and saving energy.

In order to understand the reactions of fossorial reptiles to predation risk, we studied in the laboratory the burrowing escape behaviour of the amphisbaenian *Blanus cinereus*, using a multi-factor experimental approach. We aimed to identify the effects of variations in internal thermal state and in predation risk levels on amphisbaenians' escape decisions.

MATERIAL AND METHODS

The amphisbaenian *B. cinereus* is a fairly abundant fossorial species widespread in Spain. It lives in areas with sandy soils or abundant leaf litter, where it is usually found under rocks (Martín *et al.*, 1990, 1991). During March and April 1997, we captured adult *B. cinereus* (snout-vent length, SVL, males: mean \pm SE = 203 \pm 4 mm, $n=12$; females: 194 \pm 4 mm, $n=13$) by lifting stones in an oak forest near Navacerrada (Madrid Province, Central Spain). Amphisbaenians were kept individually in outdoor 5 litre cages with sand substrate from the capture area at "El Ventorrillo" field station (5 km from capture site). Amphisbaenians were fed mealworm pupae (*Tenebrio molitor*) and adult ants (*Pheidole pallidula*) twice weekly. Humidity was enhanced daily with a water spray. The photoperiod and the ambient temperature were those of the surrounding region. Amphisbaenians were held in captivity for at least one month before testing to allow acclimatization to laboratory conditions. All the animals were healthy during the trials and were returned to their exact capture site at the end of the experiments.

We measured anti-predator behaviour and burrowing escape performance of individuals by simulating a predatory attack on a buried individual that was extracted from the soil, handled and left exposed on the surface. Tests were performed in an experimental terrarium (100 x 50 x 40 cm) filled with a sand substrate from the capture area, under two different internal thermal states (i.e. cold vs. warm body) and two different levels of predation risk (i.e. threat of attack). Each individual was tested in all conditions under a randomized sequence, but it was used only once in each trial to

avoid stress; the escape trials were spaced sufficiently (at least one day) that fatigue resulting from one test would not have affected subsequent tests.

To obtain differences in temperature conditions, amphisbaenians - buried in sand in their cages - were preheated or precooled by placing them in a constant temperature cabinet, together with the experimental terraria. We monitored substrate temperature (T_s) during the escape trials to ensure that thermal conditions did not vary during a test. The substrate temperatures of the cages were on average 31.1 \pm 0.1 °C in the warm condition and 16.9 \pm 0.2 °C in the cold condition. During preliminary tests we recorded body temperatures (T_b) of amphisbaenians and compared them with T_s . Body temperatures were highly correlated with associated T_s ($r=0.97$; $P<0.001$). On average, however, T_b was about 0.5°C higher than T_s , suggesting that amphisbaenians may achieve some limited physiological control over their T_b (Martín *et al.*, 1990; López *et al.*, 1998). This relationship was also similar to that found in free ranging *B. cinereus*, whose mean field body temperature was 22.2°C (Martín *et al.*, 1990).

Amphisbaenians were observed individually. To begin a trial, we took one buried individual amphisbaenian from its cage, simulating a predatory attack (e.g. a wild boar, that would have captured an amphisbaenian by digging the soil where it was buried). Because amphisbaenians have very reduced vision, we assumed that they assess threat level as a function of duration and intensity of tactile contact. Thus, we either handled an amphisbaenian once, briefly and gently, and then released it (low predation threat level), or we handled it for a few seconds and, after an initial release, we simulated five more attempts at capture by tapping the amphisbaenian's body with the hand (high predation threat level). We finally left the amphisbaenian on the soil surface in the middle of the experimental terrarium and recorded its behaviour without further handling. Experiments were recorded from above on videotape (Hi-8 format, 40 ms per frame) using a video-camera aligned perpendicularly to the terrarium. Timing and characteristics of the defensive and burrowing escape responses were accurately measured with a frame-by-frame analysis of the videotapes.

The repertoire of defensive displays of amphisbaenians has been qualitatively described elsewhere (Kenneweg, 1956; Van den Elzen, 1980; Malkmus, 1982; Greene, 1988). When released on the substrate, an amphisbaenian typically exhibits the following sequence of defensive behaviours, with variable duration: (1) it forms with the body a spiral, circular or sometimes a "pretzel-shaped" coil, then uncoils and reforms the coil ('Coiling'); (2) it remains still, apparently cryptic but not rigid or unresponsive, and occasionally forms a knot around a stick, or covers the head with a coil ('Still'); (3) the amphisbaenian uncoils the body, adopts a normal posture and moves slowly on the soil surface with undulate concertina movements of

TABLE 1. Results (F values) from independent two-way repeated-measures ANOVAs examining effects of temperature (cold vs. warm), predation threat (low vs. high) and temperature \times threat interaction, on defensive and burrowing times of amphisbaenians. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; $df = 1, 23$ for all tests.

	Temperature	Predation threat	Interaction
<i>Defensive:</i>			
Coiling	10.99**	20.79***	2.93
Still	8.07**	0.42	0.33
Search	4.94*	0.08	0.62
<i>Burrowing:</i>			
Half-body	15.17***	5.30*	0.53
All but tail	18.15***	1.37	1.03

the body while, apparently, searching for a place to burrow ('Search'). After a period of searching, the amphisbaenian switches to burrowing at the chosen location. We noted the occurrence of these behaviours and measured the time amphisbaenians spent in each to the nearest second. We also measured the burrowing time, which we divided into three partial burrowing times: (1) time from initiation of burrowing until half of the amphisbaenian's body was buried under the soil surface, (2) time until all the body except the tail was buried and (3) time until the total length of the body was buried. Because amphisbaenians often stopped burrowing for long periods when part of their short tail

(tail length: mean \pm SE = 22.5 \pm 2 mm) was still on the surface, we used only the first two partial times in our analyses.

Previous analyses showed no differences between sexes in defensive and burrowing performance, so we considered males and females together. We used repeated-measures two-way analyses of variance (ANOVAs) (Sokal & Rohlf, 1995) to test for differences in each of the defensive and burrowing times of the same individuals in each condition of temperature (cold vs. warm) and predation threat (low vs. high) (within-subjects factors). We included the interaction between temperature and threat to determine whether responses to different threats changed under different thermal conditions.

RESULTS

Amphisbaenians showed significantly longer episodes of coiling behaviour when the predation threat was high and when the temperature was cold (Fig. 1, Table 1). Temperature did not significantly affect how coiling behaviour varied in response to different threats, as shown by the non-significant interaction term. Still and searching behaviours were of significantly longer duration at cold temperatures, but were not affected by predation threat.

Burrowing times were significantly longer at the lower temperature than at the higher temperature (Fig. 2, Table 1). The predation threat significantly affected only the time that an amphisbaenian spent burrowing until half of its body was buried in the substrate;

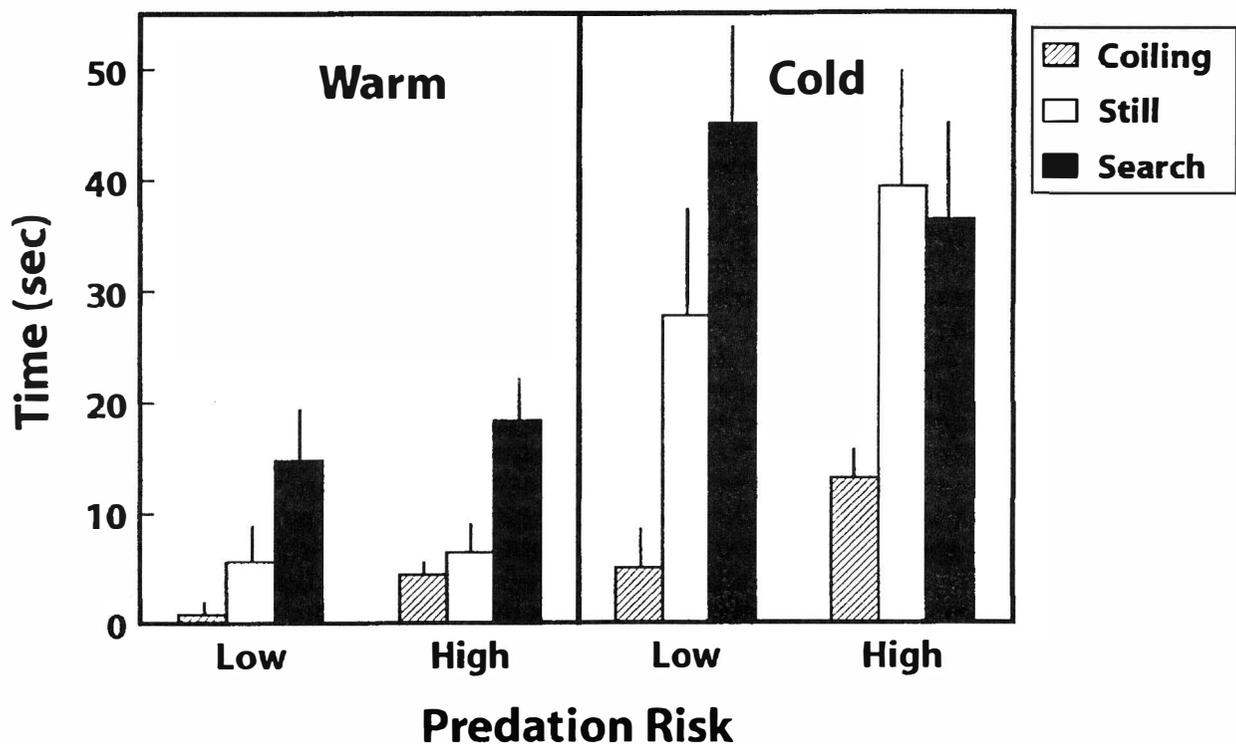


FIG. 1. Time (mean \pm 1 SE) spent performing each of two consecutive defensive behaviours (coiling and still) and in searching on the soil surface, by the amphisbaenian *Blanus cinereus* under two temperature conditions (warm vs. cold) and two different levels of predation threat (low vs. high).

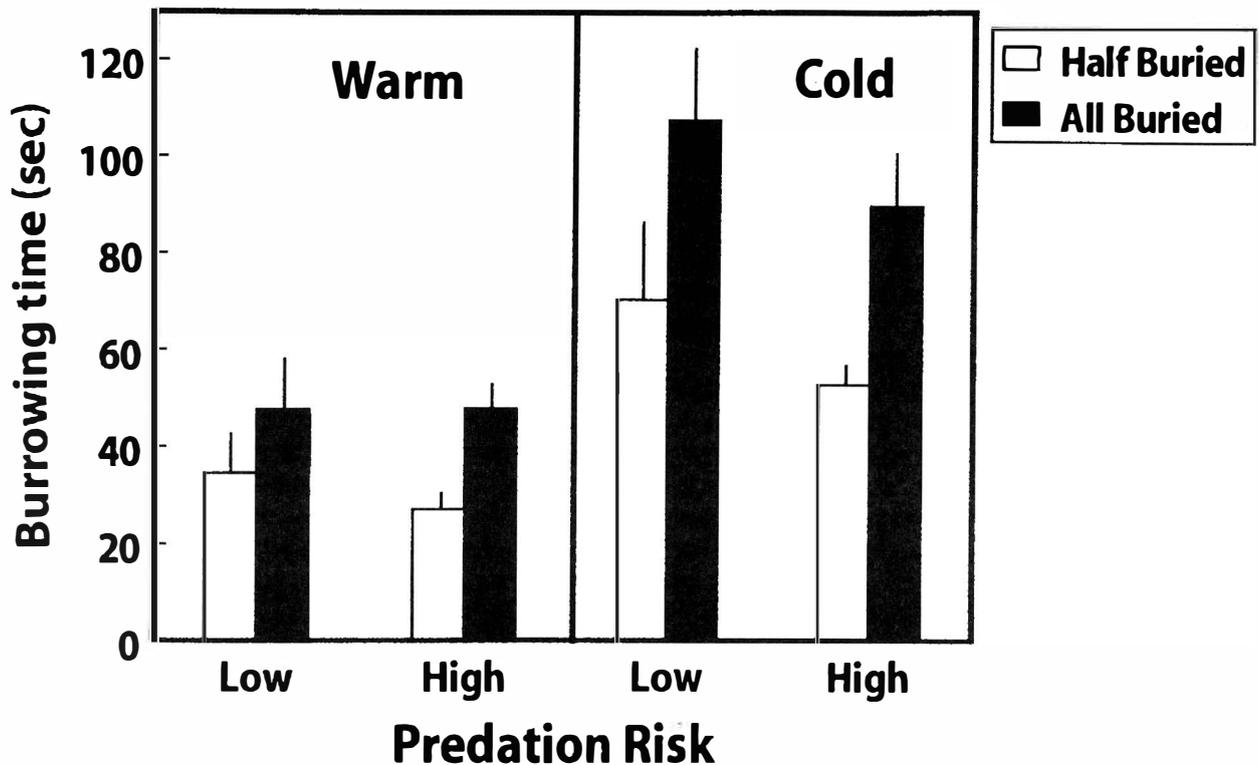


FIG. 2. Time (mean + 1 SE) from initiation of burrowing until half of the amphisbaenian's body was buried under the soil surface, and time until all the body except the tail was buried, under two temperature conditions (warm vs. cold) and two different levels of predation threat (low vs. high).

amphisbaenians burrowed significantly faster when the predation threat was high. The time spent burrowing until only the tail was left out of the substrate was also significantly longer at the lower temperature, but it was not affected by predation threat.

Of the 25 amphisbaenians tested under warm conditions, most of them burrowed until only the tail was left on the surface and then continued until all the body was entirely buried in the substrate (24 and 25 for low and high threat respectively). Under colder conditions, although most individuals also burrowed until only the tail was left on the surface (23 and 21 for low and high threat, respectively), only 17 and 18 (for low and high threat, respectively) completed the burrowing sequence during the experimental period.

DISCUSSION

The results of our experiment show that the anti-predatory response of the amphisbaenian *B. cinereus* is affected by the internal thermal state and that it is also sensitive to predation risk levels. The variations observed in anti-predator behaviours may reflect the choice of the optimal response under each circumstance, taking into account factors such as the perceived predation risk, which is dependent on the characteristics of the initial attack, and potential burrowing performance, which is dependent on body temperature.

The amphisbaenians responded to an increase in predation threat by spending more time in coiling behaviour. They also increased the magnitude of this

response (i.e. a faster and more vigorous formation of the coil). Coiling is a behavioural response of many limbless reptiles to attempted predation (e.g. Gans, 1974; Bauer, 1986; Greene, 1988), and appears to be a mechanism for startling or disorientating potential predators and eliciting misdirected strikes, rather than just a way to escape and move to safety. Because, in the high threat situation, we simulated repeated predation attempts, an amphisbaenian might perceive that the potential predator was trying to capture it directly rather than just touching it casually (i.e. low threat situation). Thus, an amphisbaenian should exhibit behaviours that would allow it to avoid an immediate capture. In contrast, escape by burrowing would not be as effective when a direct attack has already been launched, because it requires more time and because an amphisbaenian burrowing in a fixed place would be easier to capture. Similarly, coiling and other defensive behaviours were more often shown under cold conditions, when burrowing performance was lower. Nevertheless, although temperature was probably the main factor affecting burrowing speed, amphisbaenians that had faced a higher predation threat subsequently also burrowed faster, at least until half of their body was buried.

Temperature clearly affected burrowing performance of amphisbaenians, and this may help to explain the differences observed in defensive behaviours. Many lizards (Rand, 1964; Hertz *et al.*, 1982; Crowley & Pietruszka, 1983) and snakes (Arnold & Bennett,

1984; Hailey & Davies, 1986; Passek & Gillingham, 1997) have different defensive behaviours depending on their body temperature. Warmer animals tend to flee from a potential predator, whereas colder animals will tend to remain and perform a more static defensive behaviour. The movement that a cold ectotherm is capable of may not be sufficient to escape from a predator, and so it should put its energy into alternative static behaviours that may serve to avoid capture (Passek & Gillingham, 1997). Thus, immobility may be an optimal alternative defensive behaviour for amphisbaenians when burrowing performance is low and costly (Kamel & Gatten, 1983). Immobility may benefit amphisbaenians by increasing their ability to avoid detection by predators, or by reducing the severity of the attack once detection has occurred (Brodie, Johnson, & Dodd, 1974; Greene, 1988). In addition, immobile amphisbaenians often form a knot in some part of the body around some stick or grass-stem (see photographs in Van den Elzen, 1980; Malkmus, 1982). This defensive strategy, which is followed by body rigidity, using axial bending when grasped, and by pressing the sharp tip of the tail against the predator, simulating a counter-attack, makes capture and consumption by a potential predator more difficult.

In conclusion, when thermal conditions were unfavourable or the predation threat was high, amphisbaenians employed alternative defensive behaviours before escaping by burrowing. These variations in anti-predator behaviours may reflect the choice of the optimal response under each circumstance.

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REFERENCES

- Arnold, S. J. & Bennett, A. F. (1984). Behavioural variation in natural populations. III: Antipredator displays in the garter snake *Thamnophis radix*. *Anim. Behav.* **32**, 1108-1118.
- Bauer, A. M. (1986). Saltation in the pygopodid lizard, *Delma tinctoria*. *J. Herp.* **20**, 462-463.
- Bouskila, A. & Blumstein, D. T. (1992). Rules of thumb for predation hazard assessment: predictions from a dynamic model. *Am. Nat.* **139**, 161-176.
- Bowers, B. B., Bledsoe, A. E. & Burghardt, G. M. (1993). Responses to escalating predatory threat in garter and ribbon snakes (*Thamnophis*). *J. Comp. Psychol.* **107**, 25-33.
- Brodie Jr., E. D., Johnson, J. A. & Dodd Jr., C. K. (1974). Immobility as a defensive behavior in salamanders. *Herpetologica* **30**, 79-85.
- Burger, J. & Gochfeld, M. (1981). Discrimination of the threat of direct versus tangential approach to the nest by incubating herring and great black-backed gulls. *J. Comp. Physiol. Psychol.* **95**, 676-684.
- Burger, J. & Gochfeld, M. (1990). Risk discrimination of direct versus tangential approach by basking black iguanas (*Ctenosaura similis*): variation as a function of human exposure. *J. Comp. Psychol.* **104**, 388-394.
- Burger, J. & Gochfeld, M. (1992). Risk discrimination of eye contact and directness of approach in black iguanas (*Ctenosaura similis*). *J. Comp. Psychol.* **106**, 97-101.
- Busack, S. D. (1978). Diurnal surface activity in the amphisbaenian, *Blanus cinereus* (Vandelli) 1797 (Reptilia, Lacertilia, Amphisbaenidae). *J. Herp.* **12**, 428.
- Cooper Jr., W. E. (1997a). Escape by a refuging prey, the broad-headed skink (*Eumeces laticeps*). *Can. J. Zool.* **75**, 943-947.
- Cooper Jr., W. E. (1997b). Threat factors affecting antipredator behavior in the broad-headed skink (*Eumeces laticeps*): repeated approach, change in predator path, and predator's field of view. *Copeia* **1997**, 613-619.
- Crowley, S. R. & Pietruszka, R. D. (1983). Aggressiveness and vocalization in the leopard lizard (*Gambelia wislizenii*): the influence of temperature. *Anim. Behav.* **31**, 1055-1060.
- Gans, C. (1974). *Biomechanics: An Approach to Vertebrate Biology*. Philadelphia: Lippincott.
- Gans, C. (1978). The characteristics and affinities of the Amphisbaenia. *Trans. Zool. Soc. London* **34**, 347-416.
- Greene, H. W. (1988). Antipredator mechanisms in reptiles. In *Biology of the Reptilia. Vol. 16*, 1-152. Gans, C. & Huey, R. B. (Eds.). New York: John Wiley and Sons.
- Hailey, A. & Davies, P. M. C. (1986). Effects of size, sex, temperature and condition on activity metabolism and defence behaviour of the viperine snake, *Natrix maura*. *J. Zool., Lond.* **208**, 541-558.
- Hertz, P. E., Huey, R. B. & Nevo, E. (1982). Fight versus flight: body temperature influences defensive responses of lizards. *Anim. Behav.* **30**, 676-679.
- Huey, R. B. 1982. Temperature, physiology and ecology of reptiles. In *Biology of the Reptilia. Vol. 12*, 25-91. Gans, C. & Pough, F. H. (Eds.). New York: Academic Press.
- Kamel, S. & Gatten, R. E. (1983). Aerobic and anaerobic activity metabolism of limbless and fossorial reptiles. *Physiol. Zool.* **56**, 419-429.
- Kenneweg, F. H. (1956). Meine beobachtungen an der netzwühle, *Blanus cinereus* Vand. *Aquar. Terrar. Z.* **9**, 77-78.

- Lima, S. L. & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* **68**, 619-640.
- López, P. & Martín, J. (1994). Responses by the amphisbaenian *Blanus cinereus* to chemicals from prey or potentially harmful ant species. *J. Chem. Ecol.* **20**, 1113-1119.
- López, P., Martín, J. & Salvador, A. (1991). Diet selection by the amphisbaenian *Blanus cinereus*. *Herpetologica* **47**, 210-218.
- López, P. & Salvador, A. (1992). The role of chemosensory cues in discrimination of prey odors by the amphisbaenian *Blanus cinereus*. *J. Chem. Ecol.* **18**, 87-93.
- López, P., Salvador, A. & Martín, J. (1998). Soil temperatures, rock selection and the thermal ecology of the amphisbaenian reptile *Blanus cinereus*. *Can. J. Zool.* **76**, 673-679
- Malkmus, R. (1982). Einige bemerkungen zur abwehrreaktion bei *Blanus cinereus* sowie zur verbreitung dieser art in Portugal. *Salamandra* **18**, 71-77.
- Martín, J. & López, P. (1990). Amphibians and reptiles as prey of birds in southwestern Europe. *Smithsonian Herp. Inf. Serv.* **82**, 1-43.
- Martín, J. & López, P. (1995a). Escape behaviour of juvenile *Psammotromus algirus* lizards: constraint of or compensation for limitations in body size? *Behaviour* **132**, 181-192.
- Martín, J. & López, P. (1995b). Influence of habitat structure on escape tactics of *Psammotromus algirus* lizards. *Can. J. Zool.* **73**, 129-132.
- Martín, J. & López, P. (1996). The escape response of juvenile *Psammotromus algirus* lizards. *J. Comp. Psychol.* **110**, 187-192.
- Martín, J., López, P. & Salvador, A. (1990). Field body temperatures of the amphisbaenid lizard *Blanus cinereus*. *Amphibia-Reptilia* **11**, 87-96.
- Martín, J., López, P. & Salvador, A. (1991). Microhabitat selection of the amphisbaenian *Blanus cinereus*. *Copeia* **1991**, 1142-1146.
- Passek, K. M. & Gillingham, J. C. (1997). Thermal influence on defensive behaviours of the eastern garter snake, *Thamnophis sirtalis*. *Anim. Behav.* **54**, 629-633.
- Rand, A. S. (1964). Inverse relationship between temperature and shyness in the lizard *Anolis lineatopus*. *Ecology* **45**, 863-864.
- Smith, G. R. (1996). Correlates of approach distance in the striped plateau lizard (*Sceloporus virgatus*). *Herpetol. J.* **6**, 56-58.
- Sokal, R. R. & Rohlf, F. J. (1995). *Biometry, 3rd ed.* New York: W. H. Freeman and Co.
- Van den Elzen, P. (1980). Zur abwehrreaktion von *Blanus trauchi aporus* Werner, 1898 (Reptilia, Sauria, Amphisbaenidae). *Salamandra* **16**, 52-56.
- Ydenberg, R. C. & Dill, L. M. (1986). The economics of fleeing from predators. *Adv. Stud. Behav.* **16**, 229-249.

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BUNCH GRASS LIZARD, *SCELOPORUS SCALARIS*, POPULATION DYNAMICS AT LA MICHILIA BIOSPHERE RESERVE, MEXICO

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We studied the population dynamics of *Sceloporus scalaris* from 1979 to 1982 using mark-recapture methods. The estimated population density was 50 adults per hectare. The sex ratio was approximately 1:1, with females slightly predominating at older ages. Based on morphological data, four well-differentiated age classes were established - juveniles, sub-adults, adults <1yr and adults >1 yr. The mean clutch size was 8.8 eggs per female, but varied widely (5 to 12) in relation to female body size. The estimated number of hatchlings in 10 hectares was 2245 and embryo mortality was 13.89%. After hatching, the average mortality was higher than 76% for all ages and both sexes. The population life table indicates a Slobodkin Type IV survivorship curve, with a net reproductive rate of 1.059. The average generation time for this population was 1.2 years.

Key words: lizard, Mexico, population dynamics, *Sceloporus scalaris*

INTRODUCTION

The bunch grass lizard, *Sceloporus scalaris* Wiegmann, is a very common and abundant Mexican lizard distributed in 22 states in Mexico and the south-western United States of America (USA) (Smith, 1939). Despite its broad distribution in Mexico, most of the studies of this species have been done in the USA (Ballinger & Congdon, 1980, 1981; Bock, Smith & Bock, 1990; Smith, Ballinger & Congdon, 1993; Mathies & Andrews, 1995). Also, most of the previous studies have concerned only taxonomic (Smith & Poglayen, 1958; Stebbins, 1966; Anderson, 1972; Smith & Hall, 1974; Thomas & Dixon, 1976; Van Devender & Lowe 1977; Mink & Sites 1996) and reproductive (Stebbins, 1954; Anderson, 1962; Greene, 1970; Smith & Hall, 1974; Newlin, 1976) aspects of this species. There has been only one previous study dealing with the population dynamics of this species, and it was done in the United States (Ballinger & Congdon, 1981). The lack of recent literature pertaining to *S. scalaris* does not allow us to discuss our results in the light of more up-to-date findings.

The accurate establishment of population attributes, such as age at maturity, age specific fecundity, mortality and survivorship, is a basic requirement for understanding the evolutionary adaptations of any population (Barbault, 1975; Vinegar, 1975; Andrews & Wright, 1994; Smith, 1996). Research has attempted to establish the evolutionary patterns that outline the demographic attributes of populations (Tinkle, 1969; Tinkle, Wilbur & Tilley, 1970; Ballinger, 1973; Parker & Pianka, 1975; Barbault, 1975, 1981). However, to

achieve an accurate evaluation of evolutionary theories in population demography and dynamics, it is necessary to develop much more detailed studies comparing as many populations as possible. The purpose of this work was to study the main attributes and dynamics of one population of this species in north-west Mexico.

MATERIALS AND METHODS

The study site, La Michilía Biosphere Reserve, is in the state of Durango, México, between 104° 20' and 104° 07' W, and 23° 20' and 23° 30' N. The climate is temperate with a mean annual temperature ranging between 17.4 °C and 20.7 °C, and a mean annual precipitation of 567 mm, with most rain occurring during the summer. Vegetation of the zone is typically highly diversified oak-pine forest, with 207 plant species of which 18 are *Quercus* species and 10 are *Pinus* species (Martínez & Saldivar, 1978).

A study plot measuring 500 x 1000 m was marked with stakes every 10 m and censused over 4 years during the following months: October 1979, May 1980, April and September 1982, and every month in 1981. Each of the visits lasted 15 days. Three people walking slowly in parallel looked at the soil and vegetation in the zone, in the search for lizards, for 4 to 7 hr per day. Censuses were made during 50 minute random searches of the plot. Each census started from a different randomized location within the transect, to avoid bias caused by the alteration of lizard activity over the course of the day. For each lizard observed, we recorded its location in relation to distance and bearing from the nearest stake. We then captured the individual by hand. Captured individuals were marked both by toe clipping and by paint code, and the following data were recorded: sex, snout-vent length, tail length and body mass. Body lengths were measured to the nearest 0.1 mm with metal calipers (Scala 222) and body mass was

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measured to the nearest 0.1 g using a Pesola spring balance.

DENSITY

Using only the last three days of capture-recapture data, density was calculated using the Petersen index (Bailey, 1952; Caughley, 1977). Monthly adult density results thus obtained were analysed by month with the Analysis of Variance test (ANOVA; Sokal & Rohlf, 1969) followed by the Tukey-Kramer procedure (Sokal & Rohlf, 1969).

POPULATION STRUCTURE

Lizards were classified by sex and age group from morphological data. Because most of the *S. scalaris* individuals are born over a period of only 15 days, for both clutches, classification by age group can be easily accomplished using the SVL short cohort period data. Differences in secondary sexual morphology between males and females, such as ventral and belly colour patches in males, were evident from a very early age, so the sex ratio was easily determined.

NATALITY

Nativity was determined using the average fecundity estimates for resident females and the estimates of female numbers by age class. To estimate the average fecundity of resident females, we autopsied 120 gravid females from outside the study plot (Ortega & Barbault, 1986). The relationship of clutch size to female body

size for these females was used to estimate clutch size for females in the study plot.

TAIL AUTOTOMY

To calculate the proportion, by age class, of individuals with tail losses, every collected lizard was carefully examined in the search for any indication of tail breakage and regeneration. We did not count individuals whose tail loss was caused by our manipulation.

MORTALITY AND SURVIVORSHIP

Mortality rate was estimated by analysing the recapture data for marked individuals of each age class. After a specific period, we estimated the number of missing individuals. This estimate, determined for each age class, was equated to mortality. Prenatal or embryonic mortality was determined by counting the number of atrophic eggs found in the oviducts of autopsied females, and by contrasting the number of corpora lutea in the ovaries with the total number of eggs found in the oviducts. By integrating the specific fecundity for each sex and age group with age-specific mortality and survival, we generated the *S. scalaris* population life table.

RESULTS

DENSITY

Table 1 shows the average density (per hectare) calculated for each working field visit. The estimated densities for 1981 vary widely from one season to another, and even from month to month. ANOVA results indicate that there are highly significant differences between the months ($F_{11,24}=8.727$; $P<0.001$). The Tukey-Kramer procedure shows there are two well-differentiated groups of months, according to their density values: March, April and May were the months with the highest density ($P<0.01$), and September, November and January were those with the lowest densities ($P<0.01$).

POPULATION STRUCTURE

In accordance with our classification of age class and sex, and using the morphological characteristics of the individuals, we differentiated four age-groups for *Sceloporus scalaris* at La Michilía Biosphere Reserve (Fig. 1). For the first clutch there were: (1) juveniles, younger than 3 months, with SVL <38 mm for males and <31 mm for females; (2) subadults, 3 to 7 months, with SVL 38.1 to 51 mm for males and 31.1 to 46 mm for females; (3) adults I, 7 to 12 months old and reaching sexual maturity, with SVL size 51.1 to 55 mm for males and 46.1 to 54.5 mm for females. The second clutch contained: (1) juveniles, younger than 3 months, with SVL <38 mm for males and <34 mm for females; (2) subadults, 3 to 5.5 months, with SVL 38.1 to 47 mm for males and 34.1 to 45 mm for females; (3) adults I, 5.5 to 12 months old and reaching sexual maturity, with SVL size 47.1 to 51 mm for males and 45.1 to 50.5

TABLE 1. Average density (number of individuals per hectare) of *Sceloporus scalaris* calculated for each visit to the study site. The average corresponds to the density calculated during the last three days of each sampling period \pm SD.

Month	Year	No. adults	No. subadults
October	1979	10 \pm 2	-
May	1980	34 \pm 8	-
January	1981	29 \pm 5	123 \pm 18
February	1981	47 \pm 6	107 \pm 21
March	1981	76 \pm 12	15 \pm 3
April	1981	91 \pm 24	-
May	1981	85 \pm 19	-
June	1981	58 \pm 9	-
July	1981	38 \pm 18	-
August	1981	42 \pm 9	1 \pm 0.4
September	1981	19 \pm 3	4 \pm 1
October	1981	40 \pm 4	222 \pm 26
November	1981	30 \pm 5	195 \pm 21
December	1981	42 \pm 3	180 \pm 14
April	1982	128 \pm 17	-
September	1982	-	-

mm for females. For both clutches, (4) the adults II were older than one year, reaching a maximum size of 62 mm SVL for both males and females. It was not possible to determine from size alone whether the individual was 2, 3 or 4 years old.

Table 2 shows numbers estimated (derived from the density estimates) for each age and sex group for 10 hectares throughout the year. The juveniles appear during late August and their numbers increase rapidly, reaching a maximum in October. The juvenile phase ended in January and was replaced in February by the subadult, which declined during March, being replaced by the adult I group. The adult I group showed a slow decline from March to September. Males and females older than one year reached their maximum density during February and their minimum during September.

Table 2 also makes possible the determination of the sex ratio within each of the different age groups throughout the year. At the younger ages, the ratio is almost 1:1. However, for the older ages there is a tendency for females to be more abundant during the summer months, but this tendency is not statistically significant ($\chi^2= 15.226$; $df =11$; $P<0.05$). Overall, females make up 55.16% of the population.

NATALITY

From the autopsied females (Ortega & Barbault, 1986), it was established that the average clutch size for *S. scalaris* females and for both clutches was 8.79 (SE = 1.96) eggs per female. Clutch size varied widely from female to female, ranging from 5 to 12 eggs, depending on female SVL. There exists a strong relationship between body size and clutch size ($y=0.4281x-14.0325$;

$r=0.822$; $P<0.05$; Ortega & Barbault, 1986). To calculate natality, the female numbers by age class were multiplied by the average clutch size. The estimated number of *S. scalaris* hatched in 10 hectares was 2245 (Table 3). Younger females from the second clutch do not produce a second clutch themselves. This demographic characteristic is significant, because shorter and younger females must wait until their second reproductive season to produce two clutches.

TAIL AUTOTOMY

Tail autotomy rates increase with age. The average values for tail autotomy were: juveniles 9.10%, subadults 11.05%, adults I 39.01% and adults II 50.25%. The minimum average value of caudal autotomy is observed during December, and the maximum during July.

MORTALITY AND SURVIVAL

From the 120 autopsies performed on females during the reproductive seasons, only 25 atrophic eggs were found from a total of 180 oviductal eggs; thus the percentage of embryo failure was relatively low (13.89%), suggesting a low rate of mortality before egg laying (Table 4). The average mortality of individuals estimated by mark-recapture methods over a year was greater than 76% for all age groups and both sexes (Table 4). The minimum mortality occurred amongst juveniles, and the maximum value was for adults II, females.

The *Sceloporus scalaris* population life table (Table 5) indicates a Slobodkin (1962) Type IV survivorship

TABLE 2. Demographic structure for the 1981 population of *S. scalaris* at La Michilia; mean number of individuals (\pm SD) is calculated for 10 hectares.

	Juveniles	Male subadults	Female subadults	Male adults I	Female adults I	Male adults II	Female adults II
Jan	355 \pm 42	402 \pm 82	492 \pm 45	-	-	154 \pm 34	136 \pm 28
Feb	-	568 \pm 75	497 \pm 68	-	-	242 \pm 16	232 \pm 16
Mar	-	73 \pm 23	73 \pm 18	339 \pm 58	339 \pm 123	36 \pm 7	49 \pm 5
Apr	-	-	-	339 \pm 79	310 \pm 42	121 \pm 31	142 \pm 21
May	-	-	-	277 \pm 18	298 \pm 62	158 \pm 123	118 \pm 32
Jun	-	-	-	167 \pm 39	201 \pm 35	36 \pm 5	175 \pm 22
Jul	-	-	-	118 \pm 24	154 \pm 21	26 \pm 6	81 \pm 7
Aug	10 \pm 3	-	-	83 \pm 7	127 \pm 7	127 \pm 13	83 \pm 12
Sep	41 \pm 12	-	-	60 \pm 18	85 \pm 12	10 \pm 25	38 \pm 6
Oct	2216 \pm 270	-	-	-	-	187 \pm 32	213 \pm 15
Nov	1954 \pm 183	-	-	-	-	150 \pm 27	160 \pm 22
Dec	1763 \pm 207	30 \pm 16	20 \pm 7	-	-	171 \pm 32	249 \pm 35
Total	6319	1073	1082	1383	1514	1418	1686

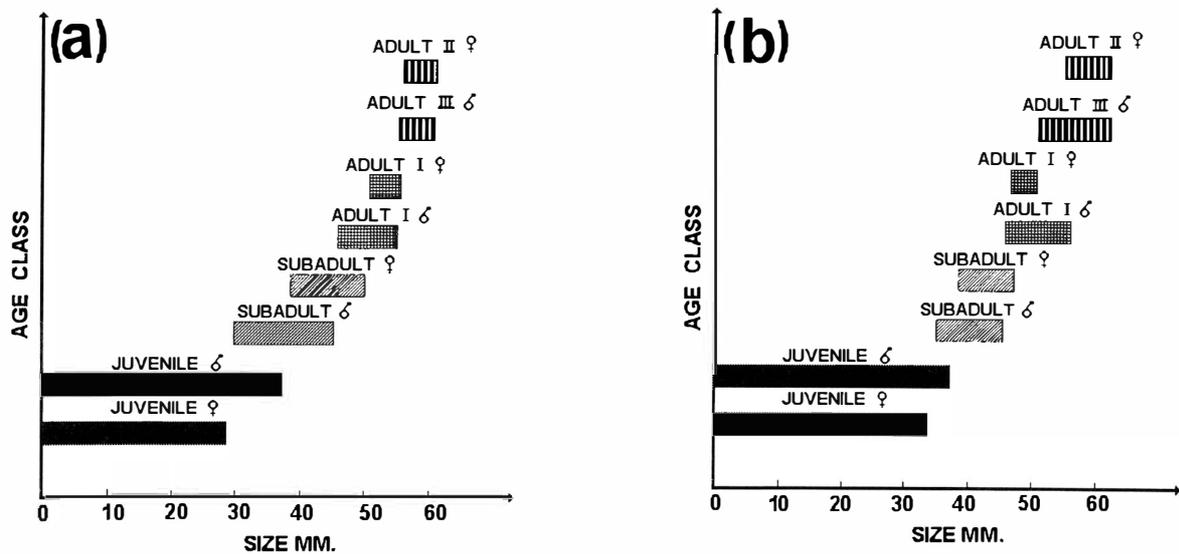


FIG 1. Snout-vent graphs illustrating cohort groupings in La Michilia *S. scalaris* population. (a) First clutch cohort; (b) second clutch cohort.

curve as described by Deevey (1947). The highest mortality occurs in the younger age groups. The population replacement rate (R_0) is 1.059 and the average generation period is 1.19 years.

DISCUSSION

DENSITY

Densities of most common lizard species vary from 10 to 100 adults per hectare (Barbault, 1975) and, according to the calculations of Turner (1977), the average density for lizards is around 51 per hectare. The density for *S. scalaris* at La Michilía (50 per ha) is close to the general average. Ballinger & Congdon (1981), studying a *S. scalaris* population of this species in Arizona, found an adult density of 140 individuals per hectare at the beginning of the summer.

The density found in Arizona is considerably higher than the values found at La Michilía. However, even higher variability occurs in the density figures for different populations of the same lizard species (Darevskij & Terentev, 1967; Grenot, 1976; Pilorge, 1981).

POPULATION STRUCTURE

The age structure of a particular population depends on the length of the hatching period and on the individual's average longevity (Barbault, 1975). *S. scalaris* has a discontinuous, short and well-defined reproductive season (Type II of Barbault, 1975), and it is also relatively short-lived, similar to several temperate and tropical lizard species (Barbault, 1973; 1976). The combination of the two variables, short breeding periods and reduced longevity, determines the age structure observed in the *S. scalaris* population at La Michilía. Age groups were clearly defined, showing the highest density in the groups of juveniles and adults I. In the population studied by Ballinger & Congdon (1981), these authors only provided the composition of the resident individuals for the month of June and only for two age classes, yearlings and adults. The average numbers of individuals per hectare reported by Ballinger and Congdon (1981) were 40 yearling males, 50 yearling females, 20 adult males and 40 adult females. All these numbers are considerably above our estimates for the month of June (Table 2).

TABLE 3. Estimated number of *S. scalaris* hatchlings (mean±SD) produced for both clutches. * = females of the second clutch.

Females	No. in 10 ha	Mean size (mm)	Mean clutch size	Hatchlings produced
Adults I	154±34	47.69±38	6.38±102	983
Adults II	81±7	57.55±5.54	10.60±2.45	859
Adults I*	85±7	46.05±3.07	0	0
Adults II*	38±5	57.55±6.12	10.60±2.07	403

TABLE 4. Mortality and survival percentages of *S. scalaris* individuals.

Class	Mortality	Survival
Embryo	13.89	86.11
Juveniles	76.88	23.12
Male adult	83.82	16.18
Female adult I	82.08	17.92
Male adult II	90.07	9.93
Female adult II	91.29	8.41

The *Sceloporus scalaris* sex ratio at hatching is effectively 1:1, similar to most other lizard species (Barbault, 1975) - with the exception of the very distinctive parthenogenetic species or subspecies (Grassé, 1970). With increasing age, it is common to observe a change in sex ratio, usually in favour of the females (Hirth, 1963; Barbault, 1974), but in some cases favouring the males (Alcala, 1966; Turner, Lannom, Medica & Hoddenbach, 1969). In other cases, numerical equality between males and females (Brooks, 1967; Telford, 1969) remains constant, as is the case with *S. scalaris* at La Michilia (average 54.25% females). In Arizona (Ballinger & Congdon, 1981), females also outnumbered males from slightly up to as much as 2:1.

NATALITY

Comparing the average clutch size of the La Michilia *S. scalaris* population (8.79) with other *S. scalaris* populations, we found that the females of La Michilia are only a little more prolific than those studied in Arizona by Newlin (1976; average clutch size 8.38) and Ballinger & Congdon (1981; average clutch size 8.52). At La Michilia the average size of females (54.82±3.88 mm) is slightly larger than the body size of *S. scalaris* females from Arizona (52.36±4.19 mm, Newlin, 1976; 53.62±4.49 mm, Ballinger & Congdon, 1981). However, there are no significant differences between female sizes in La Michilia and in Arizona ($t=0.43$, $t=0.02$ respectively).

However, the clutch size found at La Michilia is below the clutch size for two *S. scalaris* populations studied by Mathies & Andrews (1995), also in Arizona: 9.4 and 11.2 eggs. In these cases the differences found cannot be explained purely on the basis of female body size; the average female body size for the populations studied by Mathies and Andrews (1995) was smaller than at La Michilia (46.9 and 52.8 mm).

Females of three of the four Arizona *S. scalaris* populations (Newlin, 1976; Ballinger and Congdon, 1981; Mathies and Andrews, 1995) only produce one clutch, whereas 40% of the La Michilia lizard females produce a second clutch (Ortega & Barbault, 1986). An undetermined percentage of females in one of the four Arizona populations also produced a second clutch (Mathies & Andrews, 1995).

MORTALITY AND SURVIVAL

Prenatal mortality varies widely among lizard populations, ranging from less than 5% (Ballinger, 1971) to 90% (Blair, 1960; Barbault, 1973). *Sceloporus scalaris* pre-natal mortality values at La Michilia (13.9%) are similar to the hatchling failure rate found in one Arizona population (12.7%; Ballinger & Congdon, 1981). Pre-natal mortality values at La Michilia are relatively low compared to the most common values found for lizards (40% to 60%; Brooks, 1967; Tinkle, 1969; Barbault, 1974). *S. scalaris* juvenile mortality at La Michilia (76.8%) was close to the values found for the Arizona population (68.7%; Ballinger & Congdon, 1981), and both values were close to the average values found for all lizards (Zweifel & Lowe, 1966; Barbault, 1975). *S. scalaris* adult mortality at La Michilia (86.9%) was greater than the value found in Arizona (74.1%; Ballinger & Congdon, 1981) and close to that of lizard species with high mortality rates (Barbault, 1975).

At La Michilia there were many potential predators of *S. scalaris*, including (Ortega, 1986) 11 bird species, 7 mammal species and 8 reptile species. However, there are no accurate records of the efficiency of these predators in relation to this lizard population. For this

TABLE 5. Life table for the *S. scalaris* population at the Michilia biosphere reserve. x =age in years; l_x = age specific survival proportion; d_x =proportion of the original population death in the age interval; q_x = age specific proportional mortality; m_x =age specific fecundity; $l_x m_x$ = age x individual contribution to the net reproductive rate (R_0). $R_0=1.059$

Age class	x	l_x	d_x	q_x	m_x	$l_x m_x$	$x(l_x m_x)$
Eggs	0	1.0	0.139	0.139	--	--	--
Juveniles	0.17	0.861	0.662	0.769	--	--	--
Adults I	0.67	0.199	0.163	0.820	3.19	0.635	0.425
Adults II	1.67	0.036	0.033	0.916	10.60	0.381	0.637
Adults II	2.67	0.003	0.002	0.916	10.60	0.032	0.085
Adults II	3.67	0.001	0.001	1.000	10.60	0.011	0.039

reason, we cannot accurately discern whether the estimated mortality rates are the result of predator attacks.

The *S. scalaris* population at La Michilía Biosphere Reserve had a replacement rate of 1.059, with an average generation period of 1.19 years. In Arizona, the population studied by Ballinger & Congdon (1981) shows a replacement rate of 1.859, which explained the population increase observed in the area (Ballinger & Congdon, 1981). In Arizona (Ballinger & Congdon, 1981), approximately 44% of the lifetime fertility is the result of the first reproductive year; at La Michilía this value is almost 60%.

This study represents the first contribution, developed in Mexico, to the knowledge of the main population attributes and dynamics of a very common Mexican lizard.

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REFERENCES

- Alcala, A. C. (1966). *Populations of three tropical lizards on Negros islands. Philippines*. Univ. Micr. Inc. Ann-Arbor, Michigan, 269 pp.
- Anderson, D. J. (1962). Egg laying and nesting in *Sceloporus scalaris slevini*. *Herpetologica* **18**, 162-164.
- Anderson, D. J. (1972). Pattern polymorphism in the bunch-grass lizard, *Sceloporus scalaris slevini*. *J. Herpet.* **6**, 80.
- Andrews, R. M. & Wright, S. J. (1994). Long-term population fluctuations of a tropical lizard: a test of causality. In *Lizard ecology: historical and experimental perspectives*, 267-285. Vitt, L.J. and Pianka, E.R. (Eds.). Princeton N. J.: Princeton University Press.
- Bailey, N. T. (1952). Improvements in the interpretation of recapture data. *J. Anim. Ecol.* **2**, 120-127.
- Ballinger, R. E. (1971). Comparative demography of two viviparous lizards (*Sceloporus jarrovi* and *Sceloporus poinsetti*) with considerations of the evolutionary ecology of viviparity in lizards. PhD. Dissertation, Texas A. & M. University. 107 pp.
- Ballinger, R. E. (1973). Comparative demography of two viviparous iguanid lizards (*Sceloporus jarrovi* and *Sceloporus poinsetti*). *Ecology* **54**, 262-238.
- Ballinger, R. E. & Congdon, J. D. (1980). Food resource limitation of body growth rates in *Sceloporus scalaris* (Sauria: Iguanidae). *Copeia* **1980**, 921-923.
- Ballinger, R. E. & Congdon, J. D. (1981). Population ecology and life history of a montane lizard *Sceloporus scalaris slevini* in Southeastern Arizona. *J. Nat. Hist.* **15**, 213-222.
- Barbault, R. (1973). Structure et dynamique d'un peuplement de lézards: les Scincides de la savane de Lamto (Cote D'Ivoire). These de Doctorate Sciences, Univ. Paris VI.
- Barbault, R. (1974). Structure et dynamique d'un peuplement de lézards: les Scincides de la savane de Lamto (Cote D'Ivoire). *La Terre et la Vie* **28**, 352-428.
- Barbault, R. (1975). Dynamique des populations de lézards. *Bull. Soc. Zool. France* **99**, 345-361.
- Barbault, R. (1976). Contribution à la théorie des stratégies démographiques: recherches sur leur déterminisme écologique chez les lézards. *Bull. Soc. Zool. France* **101**, 671-693.
- Barbault, R. (1981). *Ecologie des populations et des peuplements*. Masson Ed. Paris. 220 pp.
- Blair, W. F. (1960). *The rusty lizard, a population study*. Univ. Texas Press. Austin 184 pp.
- Bock, C. E., Smith H. M. & Bock, J. H. (1990). The effect of livestock grazing upon abundance of the lizard *Sceloporus scalaris*, in Southeastern Arizona. *J. Herpet.* **24**, 445-446.
- Brooks, G. R. Jr. (1967). Population ecology of the ground skink *Lygosoma laterale* (Say). *Ecol. Monogr.* **37**, 71-87.
- Caughley, G. (1977). *Analysis of vertebrate populations*. John Willey & Sons Ltd. USA. 434 pp.
- Darevskij, I. S. & Terentev, P. U. (1967). Estimation of energy flow through amphibian and reptile populations, 181-197. In *Secondary productivity of terrestrial ecosystems*, J. Petruszewicz (Ed.). Warsowa, Krakow.
- Deevey, E. S. (1947). Life tables for natural populations of animals. *Quart. Rev. Biol.* **22**, 283-314.
- Grassé, P. P. (1970). La parthénogénèse, 972-977. In *traite de Zoologie, XVI*. Masson. Paris.
- Greene, H. W. (1970). Mode of reproduction in lizards and snakes of the Gómez Fariás region, Tamaulipas México. *Copeia* **1970**, 565-568.
- Grenot, C. (1976). Ecophysiologie du lézard saharien *Uromastix acanthinurus* Bell. 1825 (Agamidae herbivore). *Pub. Lab. Zool. E.N. S.*, **7**, 250 pp.
- Hirth, H. F. (1963). The ecology of two lizards on a tropical beach. *Ecol. Monogr.* **33**, 83-112.
- Martínez, E. & Saldívar, M. (1978). *Unidades de vegetación en la Reserva de la Biósfera de La Michilía en el Estado de Durango*. Publicación No. 4 del Instituto de Ecología. 198 pp.
- Mathies, T. & Andrews, R.M. (1995). Thermal and reproductive biology of high and low elevation populations of the lizard *Sceloporus scalaris*: implications for the evolution of viviparity. *Oecologia* **104**, 101-111.
- Mink, D. G. & Sites, J. W. Jr. (1996). Species limits, phylogenetic relationships and origins of viviparity in the *scalaris* complex of the lizard genus *Sceloporus*

- (Phrynosomatidae: Sauria). *Herpetologica* **52**, 551-571.
- Newlin, M. E. (1976). Reproduction in the bunch grass lizard *Sceloporus scalaris*. *Herpetologica* **32**, 171-184.
- Ortega, A. (1986). *Dinámica y estrategias demográficas de dos poblaciones de iguanidos simpátricos en la reserva de la biosfera la Michilia*. Unpubl. Ph. D. Dissertation. Instituto Politécnico Nacional. México. 329 pp.
- Ortega, A. & Barbault, R. (1986). Reproduction in the high elevation Mexican lizard *Sceloporus scalaris*. *J. Herpetol.* **20**, 111-114.
- Parker, W. S., & Pianka, E. R. (1975). Comparative ecology of populations of the lizard *Uta stansburiana*. *Copeia* **1975**, 615-632.
- Pilorge, T. (1981). *Structure et dynamique d'une population du lézard vivipare*. Pub. Lab. Zool. E.N.S. **18**. 154 pp.
- Slobodkin, L. B. (1962). *Growth and regulation of animal populations*. Holt, Rinehart & Wiston New York, 184 pp.
- Smith, G. R. (1996). Annual life-history variation in the striped plateau lizard, *Sceloporus virgatus*. *Can. J. Zool.* **74**, 2025-2030.
- Smith, G. R., Ballinger, R. E. & Congdon, J. D. (1993). Thermal ecology of the high-altitude bunch grass lizard, *Sceloporus scalaris*. *Can. J. Zool.* **71**, 2152-2155.
- Smith, H. M. (1939). The Mexican and Central American lizards of the genus *Sceloporus*. *Bull. Field Mus. Nat. Hist., Zool. Ser.* 445.
- Smith, H. M. & Hall, W. P. (1974). Contribution to the concepts of reproductive cycles and the systematics of the *scalaris* group of the lizard genus *Sceloporus*. *Great Basin Nat.* **34**, 97-104.
- Smith, H. M. & Poglayen, I. (1958). Noteworthy herptiles from México. *Herpetologica* **14**, 11-15.
- Sokal, B. R., & Rohlf, F. J. (1969). *Biometry*, Freeman Publishing Co., San Francisco. 599 pp.
- Stebbins, R. C. (1954). *Amphibians and reptiles of western North America*. New York, McGraw-Hill. 528 pp.
- Stebbins, R. C. (1966). *A field guide to western reptiles and amphibians*. Boston Houghton Mifflin. XVI. 270 pp.
- Telford, S. R. Jr. (1969). The ovarian cycle, reproductive potential and structure in a population of the Japanese Lacertidea *Tachydromus tachydromoides*. Costa Rica. *Copeia* **1969**, 517-526.
- Thomas, A. R. & Dixon, J. R. (1976). A re-evaluation of the *Sceloporus scalaris* group (Sauria: Iguanidae). *Southwest. Nat.* **20**, 523-525.
- Tinkle, D. W. (1969). The concept of reproductive effort its relation to the evolution of life histories of lizards. *Amer. Natur.* **103**, 501-516.
- Tinkle, D. W., Wilbur, H. M. & Tilley, S. G. (1970). Evolutionary strategies in lizard reproduction. *Evolution* **24**, 55-74.
- Turner, F. B. (1977). The dynamics of squamates, crocodylians and Rhynchocephalians, 157-164. In *Biology of the Reptilia. 7. Ecology and Behavior*. Gans, C. & Tinkle, D.W (Eds.). Acad. Press. New York.
- Turner, F. B., Lannom, J. R., Medica, P. A. & Hoddenbach, G. A. (1969). Density and composition of fenced populations of leopard lizards (*Crotaphytus wislizenii*) in southern Nevada. *Herpetologica* **25**, 247-257.
- Van Devender, W. R. & Lowe, C. H. Jr. (1977). Amphibians and reptiles of Yepómera. Chihuahua, México. *J. Herpet.* **11**, 51-50.
- Vinegar, B. M. (1975). Life history phenomena in two populations of the lizard *Sceloporus undulatus* in southwestern New Mexico. *Amer. Midl. Nat.* **93**, 386-402.
- Zweifel, R. G. & Lowe, C. H. (1966). The ecology of a population of *Xantusia vigilis*, the desert night lizard. *Amer. Mus. Novitat.* **2247**, 1-57.

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SHORT NOTE

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ADVERTISEMENT CALLS OF *BUFO CAMERUNENSIS*, *CHIROMANTIS RUFESCENS*, *DIMORPHOGNATHUS AFRICANUS* AND *PHRYNOBATRACHUS AURITUS*, FROM EQUATORIAL GUINEA (CENTRAL AFRICA)

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The comparison of anuran advertisement calls is a powerful tool for the anuran taxonomist and the call itself is an important characteristic, often omitted in early descriptions of the species. Considerable effort has already been devoted to the description and comparison of anuran calls around the world. In Africa, studies have been completed on northern populations (e.g. Schneider, Tunner & Hodl, 1979; Akef & Schneider, 1993), and with populations from South Africa (e.g. Passmore & Carruthers, 1995). With noted exceptions (Amiet, 1976; Schiøtz, 1999), calls of African species from tropical areas have received much less attention. In particular, the more than fifty species that compose the anuran fauna of Equatorial Guinea have only recently been studied by the scientific community (De la Riva, 1994). As it is, this fauna remains among the least known, especially when compared to those of other countries in West Africa. In this paper we contribute to the knowledge of the anuran fauna of Central Africa by providing a quantitative description of the calls of four species of anurans two of which were previously undescribed.

Recordings were obtained by the second author in 1993, in the vicinity of Moka (01°40' N, 10°17' E), Monte Alén National Park, Centro-Sur province, District of Niefang, Equatorial Guinea. Recording equipment included either a Sony WM D6C or a Sanyo M1120 tape recorder, and a Sennheiser Me 80 directional microphone. We present a characteristic audiospectrogram and oscillogram for a selected 2.5 sec. recording segment for each species. A longer recording (14-73 secs.) from a characteristic single male

of each species was analysed to generate numerical information on the spectral and temporal characteristics of the sounds.

Recordings were processed with a digital signal analysis system based on an Apple Macintosh. The sounds were digitized and edited at a sampling frequency of 44.1 kHz and at 16 bit resolution, with Sound Tools hardware and software. Signalyze software was used to obtain numerical information and to generate audiospectrograms and oscillograms. Frequency information was obtained through fast Fourier transform (FFT; width, 1024 points). The terminology used for the description of the advertisement calls follows Heyer *et al.* (1990). Unless specified, classification and nomenclature of the species follow Frost (1985).

Thirteen different call characteristics were recorded. The variables considered were: call duration, note duration, number of pulses per note, pulse rate (pulses per second), pulse duration/pulse period (T/P), fundamental frequency, dominant frequency, other frequencies with energy (in addition to dominant and fundamental frequencies), frequency range (difference between the highest and lowest frequencies with energy), and change in dominant frequency (dominant frequency at the end of the note minus dominant frequency at the beginning of the note), frequency bandwidth (highest frequency with energy in the call minus lowest frequency with energy), notes per minute (within call), and calls per minute. Collected individuals were deposited in the Centro de Estudios Tropicales, Sevilla, Spain.

The numerical parameters of the calls are shown in Table 1. In all cases, data from a single individual per species are reported.

Bufo camerunensis Parker. This bufonid was relatively common throughout Monte Alén. Advertisement calls were recorded on 2 September 1993. Males called at night from the ground, immediately adjacent to the shores of shallow ponds (less than 0.5 m deep) on the roadside, mixed with a large chorus of *Afrixalus paradorsalis* and *Afrixalus fulvovittatus*. Occasionally, other males could be heard throughout the year forming small choruses on the ground in forest clearings, in the absence of bodies of water. Recordings were obtained on the road between Niefang and Moka, at approximately 600 m.a.s.l. Air temperature near the recording site was 18 °C. The call is a typical *Bufo* call: a long (602-843 ms.) sequence of 25-53 pulses, with increasing pulse rate, emphasized frequencies at 854 Hz and 1658 Hz. (dominant frequency), and a wide frequency band (787-1716 Hz; Fig 1A). Pulse structure was type I after the classification of *Bufo* calls of Martin (1972). The call was repeated at relatively regular intervals (mean calling rate 38.2. calls per minute). Amiet (1976) describes the call of *B. camerunensis* from Ototomo (Cameroun). Although the audiospectrogram published is difficult to read, the only numerical information provided by Amiet (54

TABLE 1. Numerical characteristics of the advertisement calls: mean±SD, and range [in brackets].

	N (no tests)	Call duration (msec.)	Note duration (msec.)	Pulses/ note	Pulses/ second	T/P
<i>Bufo camerunensis</i>	13	718.6±69 [602.8-843.1]	718.6±69 [602.8-843.1]	38.5±6.6 [25-53]	53.4±5.5 [41.5-66.2]	0.008±0.002 [0.006-0.012]
<i>Chiromantis rufescens</i> isolated pulses	17	4644.5±899.9 [4008.2-5280.8]	10.1±1.8 [6.6-13.7]	8.5±3.5 6-11	- -	- -
<i>Chiromantis rufescens</i> pulse train	2	-	312.7±49.4 [277.8-347.6]	11.5±2.1 [10-13]	37±1 [36-37.4]	0.279±0.023 [0.263-0.295]
<i>Dimorphognathus africanus</i>	2	365.2±26.8 [346.2-384.1]	356.2±26.8 [346.2-384.1]	62±4.2 [59-65]	169.8±0.8 [169.2-170.4]	0.639±0.0162 [0.394-0.872]
<i>Phrynobatrachus auritus</i>	6	276.1±29.6 [245.6-322.4]	276.1±29.6 [245.6-322.4]	16.8±2.2 [15-20]	60.4±1.5 [58.3-62]	0.589±0.176 [0.4-0.774]

TABLE 1. (continued...)

	Fundamental frequency(Hz)	Dominant freq.(Hz)	Other freq.(Hz)	Change in freq.(Hz)	Frequency range(Hz)	Notes/ minute	Calls/ minute
<i>Bufo camerunensis</i>	854±24 [787-868]	1659±49 [1555-1716]	-	152±54 [61-222]	1604±241 [1191-2019]	38.2±4.7 [28.5-47.9]	38.2±4.7 [28.5-47.9]
<i>Chiromantis rufescens</i> isolated pulses	852±180 [167-1010]	852±180 [167-1010]	1777±180 1479-1979	-	545±20 [525-565]	242.8±63.4 [120.2-327.1]	6.9
<i>Chiromantis rufescens</i> pulse train	1484±14 [1474-1494]	1484±14 [1474-1494.2]	-	50±71 [0-101]	838±43 [808-868]	-	-
<i>Dimorphognathus africanus</i>	1151±57 [1111-1191]	2615±71 [2564-2665]	-	30±14 [20-40]	1918±114 [1837-1999]	3.6	3.6
<i>Phrynobatrachus auritus</i>	1622±168 [1494-1959]	1622±168 [1494-1959]	-	84±100 [-101-162]	1595±378 [1050-2100]	51.5±14.1 [32.8-71.5]	51.5±14.1 [32.8-71.5]

pulses per second) coincides with our recordings (range 41-66.2). In addition, most energy from the call of the toads from Cameroun is concentrated slightly below 2000 Hz, which is also true for our recordings. Overall, we can state that there are substantial similarities between the calls which do not suggest potential taxonomic differences.

Chiromantis rufescens (Günther). This racophorid frog was moderately rare in Monte Alén. Males called at night, perched on the vegetation (< 1.5 m high) in primary and secondary forests, during the rainy season (September- November). Recordings were obtained on 30 September 1993. *Afrivalus paradoxalis* and *A. fulvovittatus* could be heard simultaneously. Air temperature near the recording site was 18 °C.

The call includes two parts, a first part in which 6-11 isolated pulses are emitted at regular intervals (calling rate 120-327 calls/min), and a second part which is composed of a relatively longer pulse train (277-347

ms) of 10 to 13 pulses (Fig 1B). The isolated pulses have a low mean dominant frequency of 1484 Hz. and have an additional emphasized frequency at 1777 Hz. The frequency width (range) of the pulse is (525-565 Hz). The resulting sound is similar to a knock on wood. The second part has an emphasized frequency of about 700 Hz and a dominant frequency which increases slightly but gradually towards the end of the call (from 1474 Hz to 1494 Hz). Schiøtz (1967) described the calls of *Chiromantis rufescens* from Iperin, Nigeria. The calls are described as having two motifs. The first motif has similar temporal and spectral characteristics to the isolated pulses in our recordings. The second motif, however, has a similar overall structure to our pulse train, but the reported number of pulses (30 pulses per call in Schiøtz 1967) was substantially higher than ours, and the pulse repetition rate (45 pulses per second, in Schiøtz, 1967) was also higher than in our recordings. Given the overall similarity of the calls,

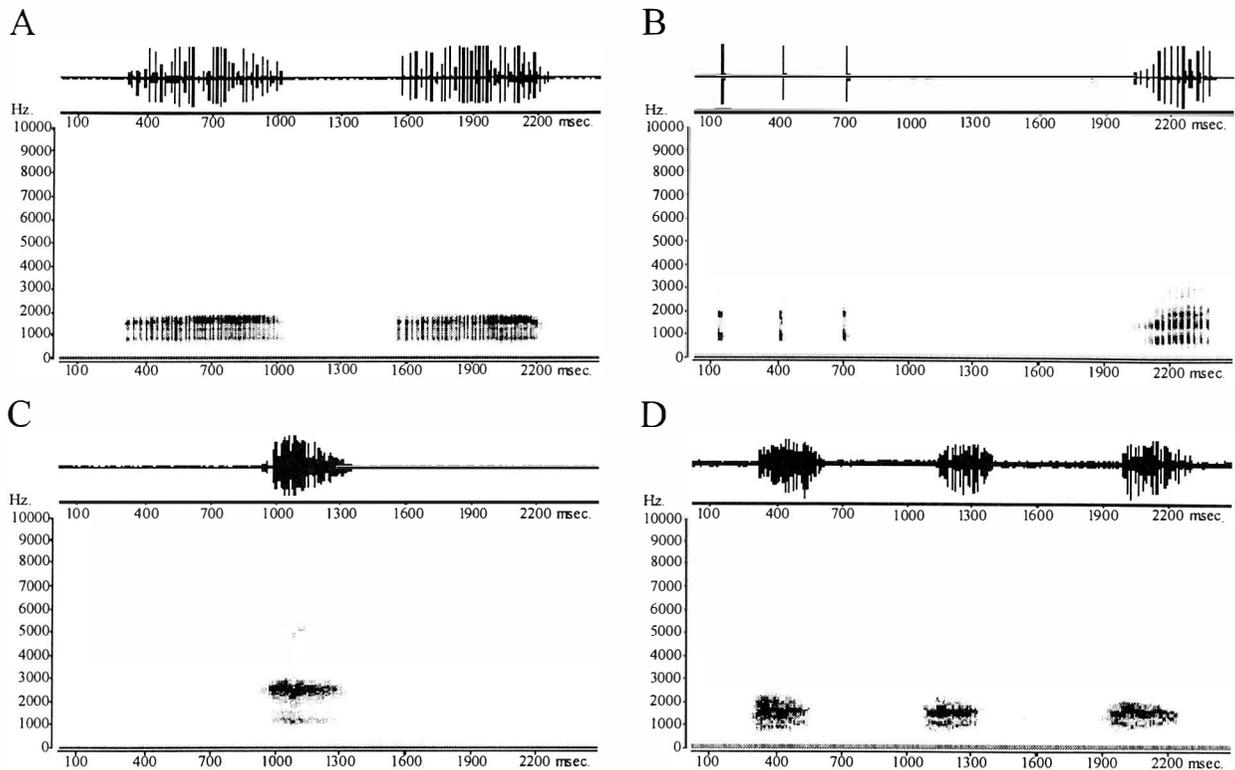


FIG. 1. Characteristic oscillogram (top) and audiospectrogram (bottom) of an advertisement call (A) *Bufo camerunensis*, two calls from two different males; (B) *Chiromantis rufescens*, call showing the last three isolated pulses of a sequence of 11 pulses followed by the pulse train; (C) *Dimorphognathus africanus*; (D) *Phrynobatrachus auritus*.

the differences observed are likely to be a consequence of differences in the recording temperature or motivational state of the males.

Dimorphognathus africanus (Hallowell). This ranid frog was moderately common in Monte Alén. Males called continuously during the day, in the vicinity of streams in the forest, throughout the year. They were secretive, calling from small caves in the bank of the river. Recordings were obtained on 22 October, at an air temperature of approximately 24 °C. No other anuran species could be heard simultaneously. The call is a short trill (346-384 ms.) with an irregular temporal structure (T/P is highly variable) which results in a noisy spectrum (Fig. 1C). The mean dominant frequency is at 2614 Hz, but the emphasized frequency range is wide. The call has a fast raise time and a longer fall time. At the beginning of one of the recorded calls the animal emitted 4-8 isolated pulses (28 ms long) with very low power and with a frequency similar to the rest of the call. To the best of our knowledge there are no previous descriptions of the advertisement call of this species.

Phrynobatrachus auritus Boulenger. This ranid frog was extremely common in Monte Alén. Calls could be heard during the rainy seasons (March to May and September to December). Males called from the ground or

from rocks, at the edges of ponds or calm streams, occasionally in the water. They generally called at night, but they could also be heard during the day, particularly in the morning. They may form large choruses, occasionally with *Bufo gracilipes*. Recordings were obtained on the afternoon of 26 May 1993. Air temperature near the recording site was 20 °C. The call is composed of a sequence of 15-20 pulses emitted at regular intervals (pulse rate: 58-62 pulses/second), forming a raucous trill with a mean dominant frequency of 1622 Hz (Fig 1d). To the best of our knowledge, there have been no previous descriptions of the advertisement call of this species.

ACKNOWLEDGEMENTS

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REFERENCES

- Akef, M. S. A. & Schneider, H. (1993). Reproductive behaviour and mating call pattern in Degen's toad, *Bufo vittatus*, in Egypt (Bufonidae, Amphibia). *J. Afr. Zool.* **107**, 97-104.
- Amiet, J.-L. (1976). Voix d'amphibiens camerounais. V Bufonidae: genres *Bufo*, *Werneria* et *Nectophryne*. *Ann. Faculté des Sciences du Cameroun.* **21/22**, 139-157.
- De La Riva, I. (1994). Anfibios anuros del Parque Nacional de Monte Alén, Río Muni, Guinea Ecuatorial. *Rev. Esp. Herp.* **8**, 123-139.
- Frost, D. R. (1985). *Amphibian species of the world. A taxonomic and geographical reference*. Lawrence, Kansas, U.S.A.: Allen Press Inc. & The Association of Systematics Collections.
- Heyer, W. R., Rand, A. S., Goncalves da Cruz, C. A., Peixoto, O. L. & Nelson, C. E. (1990). Frogs of Boraceia. *Arq. Zool. S. Paulo* **31**, 237-410.
- Martin, W. F. (1972). Evolution of vocalization in the toad genus *Bufo*. In *Evolution in the genus Bufo*, 279-309. Blair, W. F. (Ed). Austin: University of Texas Press.
- Passmore, N. I. & Carruthers, V. C. (1995). *South African frogs. A complete guide*. Southern Book Publishers & Witwatersrand University Press, Johannesburg.
- Schiøtz, A. (1967). The tree frogs (Rhacophoridae) of West Africa. *Spolia Zool. Mus. haun.* **25**, 1-346.
- Schiøtz, A. (1999). *Treefrogs of Africa*. Edition Chimaira. Frankfurt am Main.
- Schneider, H., Tunner, H. G. & Hodl, W. (1979). Beitrag zur kenntnis des paarungsrufes von *Rana lessonae* Camerano, 1882 (Anura Amphibia). *Zool. Anz.* **202**, 20-28.

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BOOK REVIEW

The Diversity of Amphibians and Reptiles. J. L. Cloudsley-Thompson. (1999). VIII + 256 pp., 87 figs. Springer, Berlin. £49.50 (cloth).

No other animals have fired the imaginations of countless generations as much as the dinosaurs. The sheer enormity of their skeletons, carefully reconstructed in natural history museums across the globe, have inspired immeasurable curiosity among the general public, scientists and future biologists. Palaeontologists have painstakingly pieced together aspects of their lives based on tooth formation, bone structure, stomach contents, fossilised vegetation contained within the same geological strata, as well as other clues, to present us with a picture of what the earth might have been like all those millions of years ago. What caused their disappearance is still the subject of heated debate.

Dinosaurs are popular subjects of television documentaries, science fiction films and countless books exploring a history long past. That modern reptiles and amphibians have changed little over millions of years and have much in common with the dinosaurs also makes them fascinating subjects for evolutionary speculation. This book attempts to breathe life into these mysterious fossilised skeletons, and to bridge the gap between the dinosaurs and living reptiles and amphibians.

Professor Cloudsley-Thompson's fascination with dinosaurs and their living relatives is evident within the pages of this book. He describes how modern lizard physiology can be related to fossilised remains, and suggests possible behavioural adaptations based on these similarities. Reptiles and amphibians, having been around for a long time, have evolved a staggering array of mechanisms to exploit nearly every type of habitat on earth. This book reviews the general diversity of these taxa with reference to the ways that they have become adapted to exploiting different niches. Topics covered include locomotion, predator defence, nutrition, reproduction, activity patterns, thermoregulation and physiological aspects of water balance. There is also a chapter reviewing the relationship between herpetofauna and man. This discusses how reptiles and amphibians have shaped mythology and art, and how humans have learned to live alongside and to benefit from their herpetofauna neighbours.

Peppering the pages are pen and ink illustrations by the author of reptiles, amphibians and dinosaurs. Some of the drawings illustrate behaviour, such the ritualised combat between male rattlesnakes (*Crotalus atrox*) and between the *Stegoceras* dinosaurs (reconstructed), while others show bizarre physical adaptations, such as the 'wings' of flying dragons (*Draco volans*) and of the *Kuehneosaurus* (Triassic), *Rhamphorhynchus*

(Jurassic) and *Pteranodon* (Cretaceous). In addition, there are a number of figures depicting daily, seasonal and thermal activity patterns.

This book contains a lot of information, much of it in great detail. For example, some three pages are dedicated to the physiological control of colour change. Herein lies the problem with this book: the level of detail is inconsistent. Although certain topics are given a very thorough treatment, others are glossed over or ignored completely. The author points out that there simply is not enough space within the scope of a book of under 300 pages to cover everything, and he has therefore been selective in his treatment. He does, however, endeavour to point the reader towards other sources of information. He also admits that there was not enough space to contain all the references used to create this book. However, the bibliography is extensive, containing not only the classic literature but also some more obscure works of interest.

Although Professor Cloudsley-Thompson states in the introduction that the book is intended for amateurs and students of herpetology, this is not really a student textbook. One needs a solid background in biology to understand many of the concepts described. A glossary would have been extremely useful, as many of the technical words I encountered were unfamiliar to me, despite my fifteen years as a biologist. Moreover, I was also unable to locate certain words in any of my biological dictionaries. A student starting out in the subject would have a difficult time making sense of the technicalities. It is, however, a great source of detailed information, and I learned a lot from it. In addition, Professor Cloudsley-Thompson's writing reflects his own personal opinions of certain theories, based on his long career in the subject. This adds a personal touch to the narrative and provides an insight into the man himself.

Considering the high price of this book, the editors of the volume did not do their job as thoroughly as one would hope. Typographical errors and misspellings are frequent, and I found one paragraph which was exactly repeated in two separate chapters.

Although this is an extremely informative and ambitious book, it is difficult to recommend it to a wide audience. The price itself is off-putting, and there is a vast choice of dinosaur and herpetological books that are perhaps more readable and certainly more affordable. Equally, the organisation of the book was somewhat confusing and at times difficult to follow. However, I very much liked the comparisons between the extinct and extant, and the book may go some way towards its intended goal of bridging the gap between the large number of popular books on this subject and more advanced texts.

Renata Platenberg
Canterbury Christ Church University College

BOOKS RECEIVED

Das, I. (1998). *The Serpent's Tongue. A Contribution to the Ethnoherpetology of India and adjacent Countries*. Edition Chimaira. Frankfurt am Main.

A compilation of the vernacular names of amphibians and reptiles in the Indian region with a discussion of their origin.

Baran, I. & Atatür, M. K. (1998). *Turkish Herpetofauna (Amphibians and Reptiles)*. Publication Board of the Ministry of Environment, Ankara.

An introduction to the amphibians and reptiles of Turkey, with species descriptions and keys. Illustrated with line drawings and colour photographs (in English).

Demirsoy, A. (1996). *Sürüngenler. Türkiye Omurgalıları*. Çevre Bakanlığı.

Distribution atlas of Turkish reptiles, with species notes and bibliography (in Turkish).

Demirsoy, A. (1996). *Amfibiler. Türkiye Omurgalıları*. Çevre Bakanlığı.

Distribution atlas of Turkish amphibians, with species notes and bibliography (in Turkish).

BOOK ANNOUNCEMENT

A new facsimile reprint from the Society for the Study of Amphibians and Reptiles: George Shaw's *General Zoology*. The first world summary of amphibians and reptiles in English, with a systematic review of Shaw's nomenclature by Hobart M. Smith and Patrick David.

George Shaw (1751-1813), an English naturalist who became Keeper of Zoology at the British Museum, is one of the most familiar names in herpetology. His volume on amphibians and reptiles in his series *General Zoology* comprises the first world review of herpetology in English. Shaw's book, published in 1802, covered 432 species which represent a large fraction of the species known at the time. The text includes scientific and common names, extensive references to previous literature, natural history, and useful historical information. The 141 plates are typical of the era: excellent likenesses at their best, but sometimes amusing, fanciful or even purloined from other works. Taken together, the text and plates represent an authoritative and classic survey at the start of the century during which herpetology became a science.

Pre-publication price to SSAR members US\$60; Institutions and non-members US\$75; shipping cost per book, US address add US\$3, non-US address, add US\$6. Please make cheques payable to 'SSAR'. Overseas orders can be paid by International Money Order; or charged to MasterCard or VISA (Please provide account number and expiry date).

Orders to: Dr Robert D. Aldridge, SSAR Publications Secretary, Dept. of Biology, Saint Louis University, 3507 Laclede Ave., Saint Louis, Missouri 63103-2010, USA (E-mail: ssar@slu.edu).

ANNOUNCEMENTS

1ST INTERNATIONAL SCIENTIFIC MEETING
THE BIOLOGY AND ECOLOGY OF ALPINE
AMPHIBIANS AND REPTILES: 1 - 3
SEPTEMBER 2000

The DPPVN are pleased to invite you to the first scientific meeting on the Biology and ecology of Alpine Amphibians and Reptiles. The meeting dates will be 1-3 September 2000, and the site will be defined in the second announcement (probably by the end of April) that will be mailed only to those who respond to this announcement. The goals of the meeting are: (1) to bring professional and amateur researchers together to exchange ideas and experiences on studies of alpine amphibian and reptiles; (2) to promote amphibian and reptilian research in alpine regions and strengthen the collaboration between amphibian and reptilian specialists; (3) to present results of new research on all aspects of the biology of amphibians and reptiles from alpine habitats, and (4) to present new results of conservation actions focused on these organisms. The official language of the meeting will be English.

Abstracts. Abstract of oral and poster presentation will be published. All abstracts should be submitted in English, and all participants will receive a booklet of abstracts at the start of the meeting. The informative abstracts should not exceed 250 words and should not contain tables and figures. Abstracts should be submitted by e-mail (see below) in Rich-Text Format (rtf) along with your preference for an oral or poster presentation.

Meeting fee: Ca. 60 EURO, which will include the program and abstracts, refreshments and a meeting excursion.

Excursions: There will be meeting excursion arranged free of charge. For those who will wish to stay longer a post-meeting excursions will also be offered.

Registration form: Those intending to participate are kindly asked to send to the organizing committee by 1 April 2000: name, institution, address (including e-mail, fax) and the (general) title of the contribution and the abstract. Travellers advice and information on accommodation (e.g. reservation, meals), which will probably be arranged by the organizers will be sent in the second announcement.

Contact address of the organizing committee:

DPPVN,

Nuša Vogrin,

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Slovenia

Fax: ++386 62 788 30 51

E-mail: milan.vogrin@guest.arnes.si

**The British Herpetological Society,
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<i>Young Herpetologist's Club</i> (9-17 yrs):	
<i>Basic Membership</i> £6; <i>Bulletin Membership</i> , £16.50; <i>Group Membership</i>	£6/£16.50

APPLICATION FOR MEMBERSHIP

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THE HERPETOLOGICAL JOURNAL

INSTRUCTIONS TO AUTHORS

(revised January 1999)

1. The *Herpetological Journal* publishes a range of features concerned with reptile and amphibian biology. These include: *Full Papers* (no length limit); *Reviews* and *Mini-reviews* (generally solicited by a member of the editorial board); *Short Notes*; controversies, under *Forum* (details available from the Editor); and *Book Reviews*. Faunistic lists, letters and results of general surveys are not published unless they shed light on herpetological problems of wider significance. Authors should bear in mind that the *Herpetological Journal* is read by a wide range of herpetologists from different scientific disciplines. The work should therefore appeal to a general herpetological audience and have a solid grounding in natural history.
2. Three copies of all submissions, and illustrations, should be sent to the Scientific Editor. All papers will be subject to peer review by at least two referees. Authors are invited to suggest the names of up to three referees, although the editor may choose alternative referees to those suggested. Papers will be judged on the basis of the reports supplied by referees, scientific rigour, and the degree of general interest in the subject matter. The Editor's decision will be final.
3. Authors should consult a recent issue of the Journal regarding style. Papers should be concise with the minimum number of tables and illustrations. They should be written in English and spelling should be that of the *Oxford English Dictionary*. Papers should be typed or produced on a good-quality printer (at least near-letter quality, avoid worn ribbons), and double-spaced with wide margins all round. The journal is typeset direct from the author's computer diskette, so all manuscripts should be prepared using a wordprocessor (preferably on a PC-compatible microcomputer). It is not necessary to submit a computer diskette with the initial manuscript, but this will be required in the event of the manuscript being accepted for publication.
4. For all papers the title page should contain only the following: title of paper; name(s) of the author(s); address of the Institution where the work was done; a running title of five words or less, and the name and address of the corresponding author with (if available) an email address. The text of the paper should begin on page 2 and be produced in the following order: Abstract, Keywords, Text, Acknowledgements, References, Appendices. Full papers and reviews should have the main text divided into sections. The first subhead will be centred in capitals, the second shouldered in lower case, and the third run on in italics. Footnotes are not permitted. *Short Notes* (generally less than six manuscript pages and accompanied by a single data set) should be produced as continuous text. A sans serif font (e.g. Universe or Helvetica) is preferred.
5. The usual rules of zoological nomenclature apply.
6. Tables are numbered in arabic numerals, e.g. TABLE 1; they should be typed double spaced on separate sheets with a title/short explanatory paragraph above the table. Horizontal and vertical lines should be avoided.
7. Line drawings and photographs are numbered in sequence in arabic numerals, e.g. FIG. 1. Colour photographs can only 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. Illustrations produced using other types of computer printer are not usually of suitable quality. 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. Articles 'submitted' or 'in prep' may not be cited in the text or reference list. 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, illustrations and computer diskette 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 Managing Editor by return of post. Alterations should be kept to the correction of errors; more extensive alterations will be charged to the author.
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