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EGG RETENTION IN LACERTID LIZARDS: RELATIONSHIPS WITH REPRODUCTIVE ECOLOGY AND THE EVOLUTION OF VIVIPARITY

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ABSTRACT: We examined stages of embryonic development at the time of oviposition in 10 populations of seven species of lacertids from northern Spain, including one of the few species of lizards that exhibits reproductive bimodality (*Lacerta vivipara*). In the species studied, embryonic development at the time of oviposition ranges, as a whole, from stage 22–34 in the classification of Dufaure and Hubert, showing highly significant differences between populations. *Lacerta vivipara* (two populations; stages from 30–34) and *L. monticola* (28–31) are the species with a more advanced intrauterine embryogenesis, while at the opposite end one can find *Podarcis bocagei* (22–26) and *P. hispanica* (two subspecies: stages from 24–27). *Lacerta viridis, L. schreiberi* and *P. muralis* are in an intermediate situation (stages 25–29), without appreciable differences among species. Our data show that species with more advanced egg retention reach the highest elevations in the study area, and there also seems to exist a relationship between the egg retention level and the northern distribution limit for oviparous lizards in Europe. However, there is no evidence of intraspecific variability in that regard. No significant correlations were found between developmental stage at oviposition and female size, clutch size, or egg mass, but relative clutch mass (RCM) was significantly larger in species with a more advanced embryonic development at oviposition. This difference in RCM was mainly due to an increase in clutch size (adjusted for female size) and not to an increase in the mass of individual eggs, which tended to be lower in relation to female mass in those species with a more prolonged egg retention.

Key words: Lacertidae; *Lacerta*; *Podarcis*; Egg retention; Viviparity; Reproductive ecology

NEARLY one fifth of the extant species of Squamata are viviparous (live-bearing). This reproductive mode is widespread in many phylogenetic lineages, occurring even in many families and genera where oviparous species also exist. This implies a large number of independent origins of live-bearing within the Squamata, if one assumes that oviparity is the primitive condition from which viviparity irreversibly arises (Blackburn, 1982, 1985; Fitch, 1970; Shine, 1984, 1985).

Current models of the evolution of viviparity in reptiles assume that it arises by means of a progressively longer egg retention in the uterus while embryogenesis continues. This leads to an increasing degree of development before oviposition and therefore to a reduction of the subsequent incubation period (Shine, 1983*a*, 1984).

Until a few years ago, most reviews on the evolution of viviparity in reptiles accepted that prolonged egg retention is a relatively exceptional trait (Packard et al., 1977; Shine and Bull, 1979; Tinkle and Gibbons, 1977). Nevertheless, Shine (1983*b*) showed that intrauterine embryogenesis in many oviparous squamates continues until about half the length of the development period (around stage 30 according to Dufaure and Hubert, 1961). This important finding, which substantially details and enlarges some former statements (e.g., Bons, 1967; Shine and Bull, 1979), forces one to reexamine many of the previous data and hypotheses about the gradation of reproductive modes in reptiles. It also focuses on the need for additional data about the level of pre-laying embryonic development in different groups of Squamata, and the relationship of uterine retention with other parameters of reproductive ecology.

We here present a study of reproductive characteristics in a group of closely related species of Lacertidae, including one of the few species of lizards that exhibits reproductive bimodality (*Lacerta vivipara*; Braña, 1986). Our aims are twofold: (1) to describe the stages of embryonic development at oviposition in adjacent populations, and (2) to examine some of the preadaptations and constraints that have been suggested to influence the evolution of viviparity.

MATERIALS AND METHODS

Females with follicles in terminal phases of vitellogenesis or with oviductal eggs (first clutches) were collected in Asturias and the Basque Country (north of the Iberian Peninsula) during the reproductive season of 1988 from nine populations of seven species of lacertids (genera *Lacerta* and *Podarcis*: Table 1). We included previously published data from a population of *L. vivipara* from Asturias (Braña, 1986). The specimens were housed in cages with facilities for egg laying, subject to a 10L:14D photoperiod and supplied with a heat source creating a temperature gradient ranging from ambient temperature (15–19 C) up to 40 C, so that the animals could regulate their body temperatures within their voluntary range during the light hours.

Terraria were inspected at least five times every day for the presence of clutches, and more frequently when there was evidence of imminent egg laying, so that the eggs were usually collected within a few minutes after oviposition. For each female (post-oviposition), we measured snout–vent length and mass, clutch size, clutch mass, and individual egg mass (to the nearest 0.001 g). A variable number of eggs from each clutch was dissected to establish the stage of development of the embryo at the time of oviposition, according to the table of Dufaure and Hubert (1961); any further reference to embryonic development stages refers to this classification. The shells of the dissected eggs, pooled for each female, were cleaned in distilled water, dried at 60 C until a constant mass was reached and then incinerated in a muffle furnace at 500 C for 12 h and weighed to the nearest 0.0001 g, in order to assess their inorganic ash content.

Relative clutch mass (RCM) refers to the fresh clutch mass/female mass (without eggs) ratio, and all the data were obtained for freshly laid eggs by females that were kept in captivity for a few days or weeks.

Nonparametric analyses were performed on every test involving embryonic development stages because of the not truly numerical condition of such stages. For nonparametric correlations, populations were rank-ordered according to mean values of frequency distributions of development stages. Mean values for every population have been used to investigate parametric correlations between variables; data were log transformed when necessary to achieve normality.

RESULTS

General Characteristics of Females and Clutches

Female size as well as clutch characteristics in the 10 populations studied are shown in Table 1. Among populations (Table 2), we found significant positive correlations between female size (SVL) and clutch size, egg mass, and clutch mass (*P*

TABLE 1.—Female size and clutch characteristics for different populations of Lacertidae from Northern Spain.

	SVL (mm)				Female mass (g)				Clutch size			
	$\bar{x}$	1 SD	Range	n	$\bar{x}$	1 SD	Range	n	$\bar{x}$	1 SD	Range	n
Lacerta vivipara												
Basque Country	55.5	2.9	50.0–60.5	10	3.3	0.6	2.3–3.9	9	6.5	1.2	5–8	10
Asturias*	52.2	3.7	44.5–58.2	14	2.6	0.5	1.7–3.1	14	5.3	1.7	2–8	14
L. monticola	69.6	2.0	66.8–72.2	12	5.0	0.4	4.4–5.9	12	8.6	1.4	6–12	12
L. schreiberi	118.6	—	—	1	30.4	—	—	1	11	—	—	1
L. viridis	112.5	5.9	106.1–122.0	6	30.9	5.9	21.2–41.0	6	12.0	2.1	9–14	6
Podarcis muralis												
Basque Country	60.0	6.0	52.3–68.5	9	3.3	0.9	2.1–4.7	9	4.9	1.5	3–7	9
Asturias	59.8	1.7	57.7–62.5	8	3.2	0.2	2.9–3.5	8	5.6	0.9	4–7	8
P. h. hispanica	51.8	3.7	47.6–57.3	8	2.2	0.3	1.9–2.6	8	2.3	0.7	1–3	8
P. h. sebastiani	61.6	4.6	57.0–67.7	4	3.5	0.6	2.8–4.2	4	4.0	0.8	3–5	4
P. bocagei	55.4	2.3	51.2–58.1	9	2.6	0.4	2.1–3.2	9	3.3	0.5	3–4	9

* Data from Braña (1986).

< 0.001 in all cases). Clutch size, average egg mass, and total clutch mass were, in turn, closely interrelated ($P < 0.01$–0.001). The RCM showed no significant correlation with female size (SVL) or with any of the clutch characteristics. However, relative egg mass (average egg mass/female mass) exhibited a significant negative correlation with SVL ($r = -0.849$, $P < 0.01$).

At the intrapopulation level, relationships between reproductive variables and female size are weaker and cannot be applied to all populations. This may be due in part to a very limited size range and to the small sample size in many of them. In general, the variable most highly correlated with female size was clutch mass, which was significantly correlated with female SVL in *Lacerta monticola* ($r = 0.57$, $P < 0.05$), in both populations of *Podarcis muralis* (Asturias: $r = 0.72$, $P < 0.05$; Basque Country: $r = 0.87$, $P < 0.01$) and in the population of *L. vivipara* from Asturias ($r = 0.73$, $P < 0.01$). Clutch size was significantly correlated with the female SVL in the populations of *L. vivipara* from Asturias ($r = 0.66$, $P < 0.01$) and *P. muralis* from the Basque Country ($r = 0.88$, $P < 0.01$). The average egg mass was correlated with SVL in *L. monticola* ($r = 0.58$, $P < 0.05$) and in the population of *P. muralis* from the Basque Country ($r = 0.72$, $P < 0.05$). RCM was not correlated with female size in any of the populations studied.

The ash content of the eggshells (ash mass/shell dry mass: Table 1) varied between 0.25 (*P. h. sebastiani*) and 0.38 (*L. viridis*), showing significant differences among populations (ANOVA: $F = 493$, df 7,55, $P < 0.001$). The significant differences in this comparison were for *P. h. sebastiani* and *P. muralis* from Asturias versus *P. bocagei*, *L. monticola*, and *L. viridis* (Student-Newman-Keuls test: $P < 0.05$). No significant correlations were found with any of the clutch characteristics, although the highest correlation coefficients for the eggshell ash content correspond to variables related to SVL (Table 2). The intrapopulation variability in eggshell ash content is larger in *L. vivipara* (coefficient of variation: 31.7%) than in the other populations (c.v. from 6.1%–16.0%; average = 10.5%).

Embryo Development at the Time of Oviposition

Some authors have reported that unsuitable maintenance conditions could cause irregularly long retention periods during which embryogenesis progresses (Cuellar, 1984; Shine, 1983*b*; Stamps, 1976). This is unlikely to be a problem in the present study for three reasons. First, some females oviposited a few days after being captured in the field, and their eggs contained embryos whose degree of development did not differ from that of females that oviposited after a longer period of captivity; by comparing the develop-

TABLE 1.—Continued.

Relative clutch mass				Mean egg mass (g)				Eggshell Ash mass/dry mass			
$\bar{x}$	1 SD	Range	n	$\bar{x}$	1 SD	Range	n	$\bar{x}$	1 SD	Range	n
48.8	5.9	39.8–59.7	8	0.24	0.03	0.18–0.32	50	0.32	0.10	0.21–0.52	9
45.2	9.9	32.4–59.9	12	0.22	0.02	0.17–0.27	12	NO DATA AVAILABLE			
56.1	4.9	46.0–66.6	12	0.33	0.03	0.27–0.38	103	0.35	0.02	0.32–0.40	12
35.4	—	—	1	0.98	—	—	11	0.36	—	—	1
37.3	5.8	29.1–43.7	6	0.95	0.11	0.73–1.21	72	0.38	0.04	0.33–0.43	6
40.3	9.0	25.6–49.0	8	0.28	0.04	0.22–0.35	39	0.31	0.05	0.25–0.39	8
47.4	6.2	35.6–53.9	8	0.27	0.03	0.22–0.35	45	0.27	0.04	0.24–0.36	8
30.2	9.7	15.1–48.7	8	0.30	0.04	0.20–0.35	18	0.31	0.02	0.29–0.34	8
37.0	2.7	34.3–39.7	4	0.33	0.03	0.25–0.38	15	0.25	0.03	0.23–0.28	4
33.4	5.9	26.3–43.2	9	0.26	0.03	0.23–0.31	25	0.36	0.04	0.32–0.42	9

ment stages in the clutches laid during the first week after capture with the ones made later, no significant differences were found in *P. hispanica* (Wilcoxon rank-sum test for two groups: $P = 0.324$) nor in the population of *P. muralis* from the Basque Country ($P = 0.210$), while in *L. viridis* the first ovipositions had embryos in more advanced stages than the later ones ($P = 0.015$). Second, in some species, we have found oviductal eggs in females collected in the field that had embryos whose developmental stages fall within the range obtained for eggs laid in the cages (*P. bocagei*, stage 25; *P. muralis*, stage 27; *L. monticola*, stage 29; *L. vivipara*, stage 31). Third, synchronization of the first oviposition in the laboratory and in the field has been verified in some populations (*P. bocagei*, *P. h. hispanica*, *L. monticola*, *L. viridis*).

The developmental stage of the embryos at the time of oviposition in the 10 populations studied ranges from stages 22–34. The differences between populations were highly significant (Kruskal-Wallis test; $H = 239.7$, $P < 0.0001$; Fig. 1). Every population shows a fairly limited spectrum, up to four or five stages when sample size was adequately large. Even in these populations, two or three consecutive stages were largely dominant, so that the three more frequent stages comprised, on average, 92.33% of all cases.

The least embryonic development at oviposition was shown by *Podarcis bocagei* (stages 22–26) and the two subspecies of *P. hispanica* (24–27), while at the other extreme were *Lacerta monticola* (28–31) and the two populations of *L. vivipara* (30–34). *Lacerta viridis*, *L. schreiberi*, and the two populations of *P. muralis* were intermediate in the stages represented at oviposition (25–29), and there were no significant differences between these species. In the three pairs of conspecific popula-

TABLE 2.—Correlation matrix for variables defining female size and clutch characteristics. Mean values for each population were used in computations. Abbreviations are: CS = clutch size, RCM = relative clutch mass, EM = egg mass, CM = clutch mass, EA = eggshell ash.

	SVL	CS	RCM	EM	CM	EA
SVL	1.000					
CS	0.906***	1.000				
RCM	−0.137	0.241	1.000			
EM	0.974***	0.819**	−0.320	1.000		
CM	0.924***	0.973***	0.044	0.921***	1.000	
EA	0.566	0.611	−0.072	0.554	0.577	1.000

** $P < 0.01$.
*** $P < 0.001$.

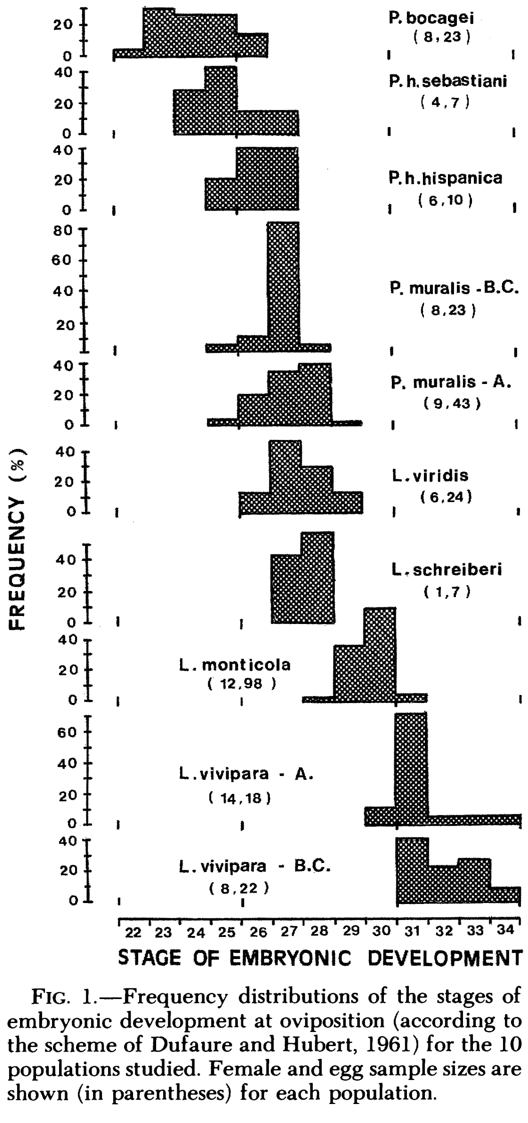

FIG. 1.—Frequency distributions of the stages of embryonic development at oviposition (according to the scheme of Dufaure and Hubert, 1961) for the 10 populations studied. Female and egg sample sizes are shown (in parentheses) for each population.

tions, the ranges of embryonic development stages at oviposition were very similar, but there were some differences in their relative frequencies (Wilcoxon rank-sum test for two groups: *P. muralis*, $P = 0.06$; *P. hispanica*, $P < 0.05$; *L. vivipara*, $P < 0.01$).

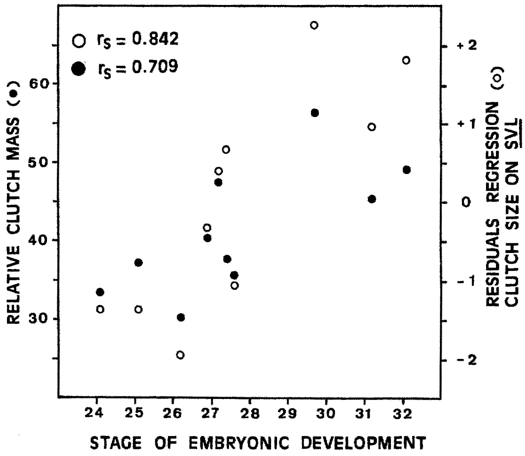

FIG. 2.—Plot of relative clutch mass and residuals of the regression of clutch size on SVL, versus stages of embryonic development at the time of oviposition in different populations.

Egg Retention Relationships

An interspecific comparison did not reveal any significant correlations between the developmental stage at the time of oviposition and female size, clutch size, or egg mass. Yet the correlation with RCM was significant (Spearman's rank correlation; $r_s = 0.709$, $P < 0.05$; Fig. 2). This correlation did not arise from an increase in egg mass due to water inflow as the "in utero" development of the embryos progressed (Cuellar, 1984; Packard et al., 1977), because the mean egg mass relative to female mass was significantly lower in populations with more advanced stages at oviposition ($r_s = -0.685$, $P < 0.05$). On the other hand, the SVL-adjusted clutch size (residuals of regression of clutch-size on SVL; Fig. 2) increased as the degree of development of the embryos at oviposition increased ($r_s = 0.842$, $P < 0.01$).

The degree of intrauterine embryogenesis was lower in the populations of *Podarcis* than in those of *Lacerta* (Wilcoxon rank-sum test, $P < 0.01$; Fig. 1). The populations studied represent species both of wide and restricted geographic distribution, including relict mountain species (Arnold, 1973); this makes difficult analyzing a possible relation between their latitudinal limits and the level of egg retention. With respect to their altitudinal distribution in the study area, *L. monticola* and *L. vivipara* are the species that reach the highest altitudes (1900–2000 m a.s.l.); *P. muralis*, *L. schreiberi* and *L. viridis* have their altitudinal limit between 1350 and 1500 m, and *P. bocagei* (1300 m) together with *P. hispanica* (1100 m) are the species with the lowest altitudinal threshold

(Braña, 1984). The upper limit of the altitudinal distribution, considered at a specific level because there is no detailed information for every population, is significantly related with the embryo development stage at oviposition ($r_s = 0.821$, $P < 0.05$).

No significant relationship has been found between the level of intrauterine embryogenesis and the ash content of the eggshells ($P > 0.05$).

DISCUSSION

The embryonic development at the time of oviposition in the populations studied ranged from stages 22–34, representing a considerable degree of egg retention. Hence, lacertids resemble some other families of Sauria previously examined (Shine, 1983*b*).

If progressive egg retention is a necessary intermediate stage for the evolution of viviparity in reptiles, it is reasonable to expect a higher frequency of species with advanced stages of embryonic development at oviposition in those taxonomic groups with closely related viviparous species (Blackburn, 1982). This applies especially to those oviparous populations belonging to species that exhibit reproductive bimodality (i.e., species with oviparous and viviparous populations). For different oviparous populations of *L. vivipara*, a species in which bimodality has been confirmed recently, the level of intrauterine development ranged between stages 30–34 (Braña, 1986; Braña and Bea, 1987; Heulin, 1988), higher than the other lacertids studied. This situation is similar to that reported for *Sceloporus aeneus*, an oviparous species considered until recently as belonging to a species with reproductive bimodality (Guillette, 1981; Guillette and Smith, 1985), whose intrauterine embryogenesis progresses as far as stage 35 (Guillette and Lara, 1986). Other species with reproductive bimodality seem to exhibit a similar pattern (Shine, 1985). These developmental stages are only slightly more advanced than those mentioned by Shine (1983*b*) for many species of oviparous Sauria, although the highest levels of retention were recorded in some taxonomic groups, such as the *Scincidae* and *Iguanidae*, where the largest number of independent origins of viviparity among the Sauria have been reported (Blackburn, 1982; Shine, 1985).

Previous data about intrauterine embryogenesis in lacertids are fairly scattered. Bons (1967) found embryos with 25–30 somites at oviposition, which would correspond to stage 26, in Moroccan populations of *Psammodromus algirus*, in three species of the genus *Acanthodactylus*, and in *Eremias olivieri*; Dhouailly and Saxod (1974) indicate stage 26 for *Podarcis muralis* and *Lacerta viridis*; Shine (1983*b*) ascribes an embryo of *P. sicula* to stage 25 (represented as *Lacerta sicula* by Senn, 1979); Rollinat (1934) describes embryos with pigmented eyes in freshly laid eggs of *L. agilis*, that could be attributed at least to stage 30, and Bosch (1989) reported the same stage for *L. mosorensis*. These data satisfactorily fit the geographic and taxonomic outline drawn for the level of egg retention in the lacertids of northern Spain; the species of *Podarcis* and those with a thermophilic character and a mainly Mediterranean distribution (Arnold, 1973) show a lower level of intrauterine embryogenesis compared to the species of *Lacerta*. Among the latter, an egg retention level close to that of *L. monticola* and of the oviparous populations of *L. vivipara* can be seen in *L. agilis*, the most northerly distributed oviparous lizard in Europe. In addition, Rykena (1987) pointed out that the incubation time after oviposition is, at any temperature between 18 and 30 C, slightly shorter in *L. agilis* than in other "green lizards" (*Lacerta* s. str.). Moreover, an inverse relationship seems to exist between the incubation time and the northern limit of the distribution area in the species of this group, although there are some exceptions that could be explained by historical reasons or by competitive interactions (Rykena, 1987). Assuming that reduction of incubation time is related to a higher proportion of embryogenesis occurring in utero, then the species with a longer retention would reach the northern latitudes.

Among the lacertids that we studied, there was a relationship between the degree of intrauterine embryogenesis and the elevational limit reached by the species. This is consistent with the latitudinal relationship previously examined, because cold weather associated with high latitudes or elevations is one of the agents most often proposed as a selective force that favors egg retention and the transition to viviparity (Blackburn, 1982; Shine, 1984, 1985; Shine and Bull, 1979).

However, a relationship between egg retention level and the geographic distribution limits can only indicate that those species with a longer retention have a higher capacity of colonization or a competitive advantage in areas with cool climate (Blackburn, 1982). In fact, lacertids with a higher retention level show wider distributions in their latitude (*L. agilis*, from 43° North up to 62° North) or elevation (*L. monticola* and the oviparous populations of *L. vivipara* in northern Spain, with an almost continuous presence from sea level to 2000 m). Geographic differences in retention level within these species have, however, not been found. The incubation times obtained by Rykena (1987) for populations of *L. agilis* from the southern end of the distributional area are comparable to those obtained by Jensen (1982) for populations close to the northern end. Intrauterine embryogenesis of *P. muralis* and *L. viridis* near Grenoble (Dhouailly and Saxod, 1974) are similar to those found in northern Spain. In *L. monticola*, oviductal eggs with stage 29 embryos have been found in females collected at 100 m, corresponding to a standard stage in eggs from high-elevation females. Also, there is no evidence of elevational variation in the embryonic development at oviposition among the different oviparous populations of *L. vivipara* (Braña, 1986; Heulin, 1988; Heulin et al., 1989; this work plus unpublished data). Huey (1977) described an elevational cline in retention level among lizards of the genus *Anolis*, but his results are not at all conclusive, because they are based upon the examination of oviductal eggs whose gestation time is unknown. Therefore, there is no direct evidence that the more advanced stages of egg retention in lacertids have had their origin in areas of cold weather, but they favor colonization and survival in such regions. Once the populations with a fairly advanced retention degree settle in cold areas, selection could favor progressively increasing retention times, as suggested by Shine and Bull (1979).

However, at the end of the primary differentiation phase (around stage 30), begins a period of exponential growth of the embryo together with a sudden increase in the oxygen demand (Guillette, 1982; Shine, 1983*b*). In addition, increased egg mass and volume due to water inflow at this phase could raise the costs of egg retention (Shine, 1980, 1983*b*). Therefore, from stage 30 onwards, a qualitative change could exist, so that anatomical and physiological modifications may be necessary to surpass extensively such a phase of uterine egg retention.

While the prolonged egg retention could shorten the development time and may enhance offspring survivorship (Shine, 1983*a*), it has the evident shortcomings of a delay between subsequent layings and a reduction in the number of clutches produced during a single reproductive season. For this reason, it is more likely that egg retention progresses in species with only one clutch per season (Shine and Bull, 1979; Tinkle and Gibbons, 1977), or in those areas where the reproductive period is shortened due to climatic factors.

On the other hand, species with a more advanced intrauterine embryogenesis and a lower number of clutches per season could be expected to increase their energetic investment in each of them, as shown by the relationship between egg retention level and RCM in lacertids. It is interesting to recall that the variation in RCM is mainly due to an increase in clutch size and not to an increase in the mass of the individual eggs, which tends to decrease in relation to female mass in species with a more prolonged retention.

Apart that a higher investment in the clutch, achieved by means of increasing clutch size, represents a gain in the number of offspring in those species with prolonged egg retention and a lower number of clutches per season, some of the main determinants of the evolution of oviductal retention might also be of RCM. The same set of specific characteristics related to escape tactics, vulnerability to predation, mobility, and foraging mode can be expected to favor high relative clutch mass and advanced egg retention (e.g., Bauwens and Thoen, 1981; Seigel et al., 1986; Shine, 1980; Vitt and Price, 1982).

One of the changes that should occur during the transition from egg-laying to live-bearing among squamates is the reduction in the degree of calcification of the eggshell (Packard et al., 1977). We did not find any significant trend in this direction among lacertids, although *L. vivipara* shows a great variability in the eggshell ash content. This could be a suitable situation for the simultaneous evolution of a progressively reduced calcification of the eggshell and increased egg retention.

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SONIC COMPLEXITY AND MATE LOCALIZATION IN THE LEAF-FOLDING FROG, *AFRIXALUS DELICATUS*

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ABSTRACT: The accuracy with which females of *Afrixalus delicatus* localized conspecific calls was examined under increasingly complex sonic and structural environments. The complexities characteristic of natural anuran choruses do not appear to influence the precision of female approaches.

Key words: Anura; Accuracy of localization; Environmental complexity; Sonic complexity

IN large, mixed-species choruses of the African tropics, female anurans locate males in a noisy, complex environment. They are confronted with multiple, temporally overlapping sound sources varying in frequency, intensity, and duration. Although female frogs exhibit remarkable precision in localizing a broadcast stimulus under laboratory conditions (Feng et al., 1976; Gerhardt and Rheinlaender, 1980, 1982; Passmore et al., 1984; Rheinlaender et al., 1979), the complexities characteristic of natural breeding sites may impair these abilities.

We examined the accuracy of phonotaxis in the leaf-folding frog under increasingly complex sonic and structural environments. *Afrixalus delicatus* is a small [snout–vent length (SVL) = 15–22 mm; interaural distance = 5.4 mm], nonterritorial, prolonged breeding species. Males produce a functionally partitioned, two-part call: the trill component attracts females and the zip component is used in male-male communication (Backwell, 1987; see Backwell, 1988, for sonogram).

MATERIALS AND METHODS

The accuracy of approaches by females towards male calls were examined under five categories of sonic and environmental complexity during three breeding seasons (October–February 1988–1990). For categories 1–4, the testing arena consisted of a cloth floor (2 × 3 m) on which was drawn a 5 × 5 cm numbered grid. A 60 W red light bulb was suspended 2 m above ground level in the center of the arena. Stimulus tapes were prepared using a single call recorded in the field. A tapeloop was created and rerecorded once to produce the final stimulus. The stimulus covered the