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Weak expression of reproductive seasonality in a dwarf gecko (*Lygodactylus verticillatus*) from arid south–western Madagascar

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Abstract

The reproductive cycle of *Lygodactylus verticillatus*, a small diurnal lizard of the family Gekkonidae, was studied using a large preserved sample from Lake Ihotry in a very arid and seasonal environment in Madagascar. Ovigerous females and small juveniles were found in all seasons. In males, no significant seasonal differences in testis size were found. However, the percentage of ovigerous females was distinctly lower in the dry, cool season (April–October). This indicates reproductive activity in *L. verticillatus* during the whole year, with a rather weakly marked seasonality that results in lower incidence of reproduction during the dry season. Most females dissected had two eggs or follicles of similar size in their oviducts, and only in 5% of the specimens did one oviduct contain a mature egg or a follicle of distinctly larger size than the other oviduct. A clutch size of two eggs therefore seems to prevail in this species, despite its small size (the range of adult female snout-vent lengths was 20–27 mm). According to the available literature data, continuous or weakly seasonal reproduction seems to be more common in geckos than in other lizards, which might be related to the constraint of their low clutch size (1–2 eggs).
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1. Introduction

Animal reproductive cycles usually are strongly correlated to yearly climatic cycles, mostly coinciding with warm and/or wet seasons. In reptiles, this is obvious in species occurring in arid seasonal environments (e.g. Daniel, 1960; Perry and Dmi'el, 1994; Heideman, 1995; Al-Johany et al., 1996), but also seems to be the prevailing pattern in the tropics (Fitch, 1982). Although rainforests were once thought to provide relatively constant conditions year-round, they often are characterized by pronounced dry and wet seasons, and reproduction of most vertebrates starts with the onset of the rainy period (e.g. Fitch, 1982; Wikelski et al., 2000).

Among the wealth of reproductive strategies in lizards, most species of the family Gekkonidae are exceptional in their limitation to laying two eggs, which furthermore are characterized by a calcareous shell (Tinkle et al., 1970; Vitt and Seigel, 1985; Werner, 1989; Doughty, 1997; Clobert et al., 1998). This is true for species included in the subfamily Gekkoninae, while species of the Eublepharinae and Diplodacty-linae lay soft-shelled eggs. Bearing in mind the ongoing discussion of gekkonid classification (e.g. Röll and Henkel, 2002), in the present paper we will use the term "geckos" in a restricted sense to refer to species of the Gekkoninae only. With currently about 900 species, this is a highly successful group, especially in the tropics. Most species are nocturnal, but some lineages secondarily became adapted to diurnality (Röll and Henkel, 2002). A further fascinating aspect of gekkonine evolution is miniaturization; a species of the Neotropical genus *Sphaerodactylus* is the smallest amniote species of the world, with adult snout-vent lengths (SVL) of sometimes <15 mm (Hedges and Thomas, 2001). Some small geckos show a reproductive shift, almost certainly as response to body size reduction, to laying a single egg instead of two (Werner, 1989; Avery, 1996; Doughty, 1996). However, there is no strict link between body size and egg number in this group, as exemplified by the dwarf geckos of the genus *Lygodactylus* Gray 1864, which are known to usually lay two eggs (e.g. Glaw and Vences, 1994; Branch, 1998).

Several geckos are known to reproduce continuously in tropical environments (e.g. Church, 1962; Vitt, 1990), although others show distinct reproductive cycles (e.g. Sanyal and Prasad, 1967; Ota, 1994; Meshaka, 1995). In Madagascar, reproduction of most reptiles is clearly linked to the rainy season that also coincides with higher temperatures (Glaw and Vences, 1996). However, the two montane gecko species *Lygodactylus mirabilis* (Pasteur, 1965) and *Phelsuma barbouri* Loveridge 1942 stand out as exceptions in reproducing during the wet as well as the dry season (Vences et al., 2002). This indicates that a weak expression of seasonality in breeding might be a common state in Malagasy geckos.

In the present paper, we test this hypothesis in a further Malagasy species of *Lygodactylus*, *L. verticillatus* Mocquard 1895. This small species (with some males probably reaching maturity at 15 mm SVL) is widespread in the arid south–western part of Madagascar (Pasteur, 1965), a region characterized by a strong climatic seasonality. We examined the reproductive cycle in this species using a large number of preserved specimens available for examination and dissection.

2. Materials and methods

This study is based on specimens preserved in the Muséum national d'Histoire naturelle, Paris (MNHN) which were entirely collected by Charles Domergue in the years 1965–1982 in the surroundings of Lake Ihotry. The same series has already been studied in terms of changes in relative density of different species among years (Pasteur, 1977), and of rapid temporal changes in morphology (Pasteur and Lumaret, 1976). Lake Ihotry is located between 21°53′–22°00′S and 43°36′–43°45′E at an altitude of ca. 50 m above sea level and at approximate distances of 30 km from Morombe and 140 km from Toliara. Based on metereological data from Toliara, the climate in this region is markedly seasonal and characterized by a very long dry season between April and October, and a more wet and slightly warmer season between November and March (Fig. 1). Mean yearly temperature is 24°C, and the mean annual rainfall is 450 mm. Collections were made in all months except January and August, although numbers of specimens collected per month was variable. To obtain a maximum sample size, we pooled specimens from the different collection years.

A total of 1466 specimens were available for analysis. Males were recognized by the presence of preanofemoral pores (Greer, 1967; Röll, 2000, pp. 189–198). Based on the minimum size of females in the subsample sexed by gonad inspection (see below), we considered specimens with an SVL > 20 mm and without femoral pores as females. According to this definition, the total sample contained 595 males, 563 females, and 308 immatures. In all specimens we measured SVL to the nearest 0.1 mm using a caliper and counted number of preanofemoral pores (males only). Additionally, we recorded by external inspection whether females were ovigerous.

Depending on availability of specimens in the monthly subsamples, we examined gonads of up to 10 randomly selected males and 10 females of each month after dissection. Using a stereomicroscope with measuring device, the following character
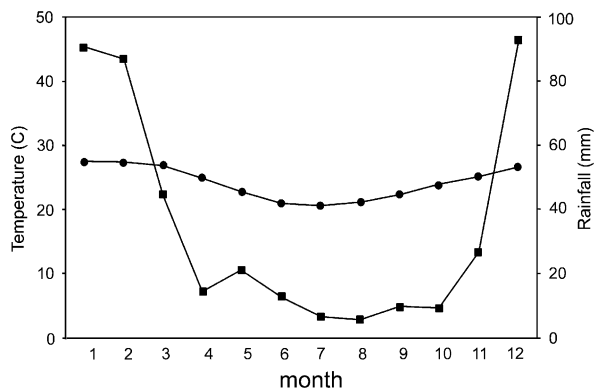

Fig. 1. Climate pattern in the Toliara region close to Ihotry. Mean data derived from the Global Historical Climatology Network corresponding to 468 months between 1951 and 1990. Squares represent rainfall (in mm), circles represent mean temperature (in °C).

states were assessed: (a) males: length and width of both testes and width of the epididymis. (b) Females: length and width of oviductal eggs and/or of the largest visible follicles, and number of visible follicles. Additionally, we recorded colour of male gonads and the presence of capillaries around them, and the presence of an eggshell in oviductal eggs. However, the latter could not be ascertained reliably in all cases because of partly poor states of preservation.

Statistical analysis was carried out with StatView on a Macintosh G4, and with SPSS for Windows, version 10, on a Pentium IV computer. Volumes of eggs and testes were calculated using the formula: $(4/3) \pi \, (\text{width}/2)^2 \, (\text{length}/2)$. Metric values are given as mean $\pm$ standard error (minimum and maximum in parentheses). To analyse monthly variation in testes and egg/follicle size we used indices of SVL-adjusted dimensions using residuals from the least-squares regression line between volume and SVL (both variables log-transformed).

3. Results

The smallest immature had a SVL of 8.1 mm, while the largest specimen (female MNHN 1990.2553) had a SVL of 27.4 mm. Sexual size dimorphism (Table 1) was significant (*t*-test; $p < 0.001$), but this result might be influenced by not considering specimens < 20 mm as females although some mature females at lower sizes might occur. Males had 6–10 preanofemoral pores (mean 8.93 ± 0.04). Number of preanofemoral pores was not correlated with SVL (Spearman rank correlation, $r = 0.03$, $p > 0.4$), indicating that the final number of pores becomes visible at once at sexual maturity.

Table 1
SVL and gonad size in *L. verticillatus* specimens from Ihotry studied. In the complete sample, males were diagnosed by presence of femoral pores, while females were defined as specimens without femoral pores with a size > 20 mm. In the subsample of dissected specimens, sex was ascertained by gonad inspection

	Mean $\pm$ SE	CV	Min	Max	*N*
Complete sample					
SVL adult males	22.43 ± 0.08	8.70	14.6	26.0	595
SVL adult females (> 20 mm)	23.63 ± 0.06	6.13	20.0	27.4	563
Subsample (dissected)					
SVL males	23.33 ± 0.12	4.44	20.0	25.5	80
Testes length	1.97 ± 0.02	10.99	1.38	2.48	82
Testes width	1.43 ± 0.02	15.50	0.98	1.90	82
SVL females	24.22 ± 0.14	4.94	20.5	27.2	76
Egg/follicle length	2.73 ± 0.19	59.58	0.98	6.89	77
Egg/follicle width	1.92 ± 0.14	63.23	0.61	6.12	77

SE, standard error; CV, coefficient of variation; Min, Max, minimum and maximum values; *N*, number of specimens examined.

Juvenile specimens of 8–12 mm SVL were observed in April, May, June, September and December (Fig. 2). The smallest specimen of 8.1 mm SVL was found in May; the next largest specimens of 10.9–11.3 mm were found in April, June and September. Significant differences between months were found in male SVL (ANOVA; $F_{9,593} = 3.05$; $p < 0.005$) and female SVL (ANOVA; $F_{8,560} = 5.40$; $p < 0.001$). Scheffé's post hoc tests did not reveal significant differences between any comparison of values for 2 months in males, whereas female values were significantly different in three comparisons: March vs. September ($p < 0.05$), May vs. September ($p < 0.01$), June vs. September ($p < 0.05$). Mean female sizes in March (24.6 ± 0.2 mm; $n = 17$) and May (24.2 ± 0.2 mm; $n = 99$) were larger than in September (23.0 ± 0.2 mm; $n = 61$).

No significant differences among months in SVL-adjusted testis size were detected (residuals of the regression of testis volume on male SVL; ANOVA: $F_{9,79} = 1.89$; $p = 0.067$; Fig. 3). Although not significant, testis volumes decreased between April and August. The females examined had a maximum of two elements of largest size (yolking follicles or oviductal eggs; one per oviduct). These were of similar sizes in most specimens (volume ratios of left and right egg/follicle = 0.7–1.4 in 57 specimens), but in two females the larger egg had double the volume of the smaller egg (with the larger egg once in the left and once in the right oviduct), and two females had one large egg in their left oviduct but no recognizable element in their right oviduct. Summarizing, of 77 females, 57 (74%) had elements (eggs/follicles) of similar size in both oviducts (volume of the smaller element $\geqslant 80\%$ the larger element), four (5%) had a distinctly larger element in one of the two oviducts

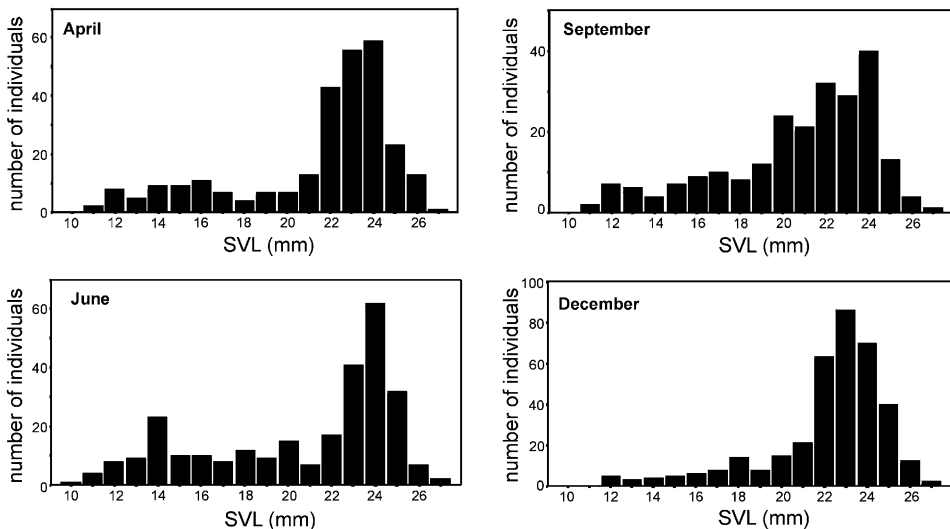
Fig. 2. Distribution of size clases of *L. verticillatus* in Ihotry in the 4 months for which sufficiently large sample sizes were available. Juveniles (8–12 mm) were found in all seasons of the year, indicating year-round hatching.
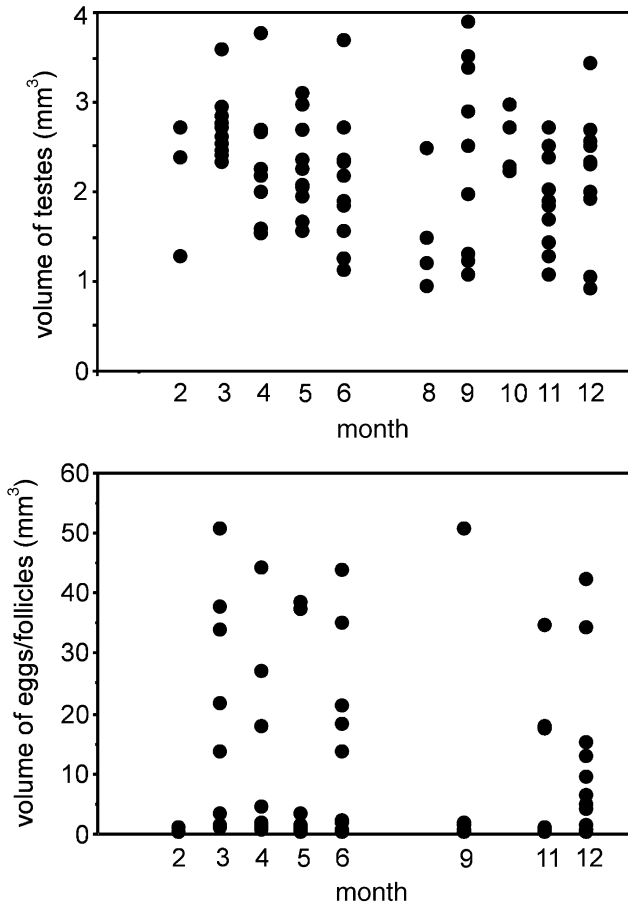
Fig. 3. Gonad size (volume) in male and female *L. verticillatus* in different months. No obvious seasonal variation of testes volume (mean of left and right testis) in males is observed. In females data show size of the largest follicles or eggs (mean from the two oviducts); in all seasons, specimens with large oviductal eggs (volume $>30\,\mathrm{mm^3}$) are observed. Data were only available for the months indicated on the axis.

(smaller element $\leqslant 50\%$ of the larger element), and 16 (21%) had intermediate states. No correlation was found between female SVL and the volume ratio between the smaller and the larger element (Spearman rank correlation, $r = 0.125$, $p = 0.294$).

We did not detect significant differences in the mean volume of the largest follicle/ oviductal egg of females among months (ANOVA; $F_{7,75} = 0.72$; $p = 0.656$). The largest mean values of follicle/egg size were detected in the months between March and June. Eggshells were present in all oviductal eggs of lengths $>4.5\,\mathrm{mm}$; using this as minimum size, mature oviductal eggs ranged from 4.5 to 6.7 mm in length and 3–5.25 mm in width ($N = 13$). Mean egg volume was not significantly correlated with SVL among the 13 females with mature oviductal eggs, but a trend of larger eggs with increasing body size was clearly visible and became significant (regression
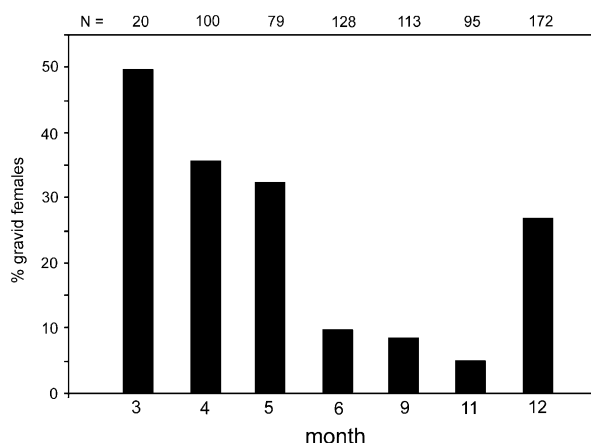
Fig. 4. Percentage of ovigerous *L. verticillatus* females from Ihotry as recognizable by external inspection. Data are only given for months for which representative sample sizes were available (>10 specimens). Values above columns are total number of female specimens examined.

analysis; $p<0.05$; $N = 12$) after elimination of one outlier in which one egg was much larger than the other one.

Monthly differences in the percentage of ovigerous females in the complete sample of specimens were highly significant (Chi square test, df $= 9$, $p<0.001$). Considering only months for which sample sizes >10 specimens were available (Fig. 4), the highest percentages were observed in March (50%) and April (36%).

4. Discussion

Fitch (1982), in his extensive survey of reproductive cycles in tropical reptiles, concluded that "a relatively small group of species has been found to breed continuously with no seasonal change. All of these occur in aseasonal climates having high precipitation throughout the year; most are inhabitants of rainforest or cloud forest". A larger number of species has been found to be more or less continuous breeders, in which the level of reproduction is triggered by climatic conditions, such as the onset of rainfall in the dry season. But also these examples mostly came from wet tropical climates.

The uninterrupted breeding of *L. verticillatus* in the highly seasonal climate of Ihotry is thus outstanding among lizards, although it agrees with the observations of two montane geckos in Madagascar, *L. mirabilis* and *Phelsuma barbouri* (Vences et al., 2002). The lower limit of body size has several physiological limitations, and is accompanied by high surface to volume ratios, thus potentially increasing the rate of water loss (Hedges and Thomas, 2001). Nevertheless, the miniaturized *L. verticillatus* maintains activity and reproduction during the dry season at Ihotry, indicating that such effects are not decisive for gekkonine lizards. It also is remarkable that most of the dissected ovigerous females of *L. verticillatus* were found to contain two eggs or

two large follicles of similar size, indicating a clutch size of two eggs in at least 74% of the population, and a probable clutch size of one egg in only 5% of the population. In *Tarentola* geckos from the Canary islands, it is known that clutch sizes of one and two eggs can occur, with young females having a larger proportion of one-egg clutches (Báez et al., 1998, pp.161–175; Hielen et al., 1998, pp.109–130; Joger, 1998, pp. 177–184; Rykena et al., 1998, pp. 137–160). However, no such trend seems to exist in *L. verticillatus*: we found no correlation between egg volume ratio and SVL, and the two females with a single large egg in one oviduct only were not particularly small (22.4 and 25.5 mm SVL).

Among continuously breeding reptiles, examples of gecko species are relatively common (e.g. Church, 1962; Vitt, 1986, 1990; Meshaka, 1994; Ota, 1994; Werner and Chou, 2002). Also the only weakly marked changes of size and condition of the testes in *L. verticillatus* over the whole year agree with the state in three tropical house geckos studied by Church (1962). This stands in contrast to most other tropical lizards. For instance, *Anolis* species usually have distinct seasonal testis cycles (Ruibal et al., 1972; Licht and Gorman, 1975; Stamps and Crews, 1976), although some species of this Neotropical genus are also characterized by small clutch sizes and reproduce more or less continuously (Ruibal et al., 1972). The weak seasonal changes in *L. verticillatus* reproduction are especially outstanding, because other geckos from seasonal environments seem to exhibit strict seasonal reproduction patterns (e.g. Vitt, 1986; Báez et al., 1998; Hielen et al., 1998).

James and Shine (1985, 1988) found indications that phylogenetic relationships and biogeographic history of taxa have major influences on their life-history strategies and timing of reproduction (see also Dunham and Miles, 1985). Vitt (1990) correlated seasonality of reproduction with foraging mode in a Brazilian lizard fauna, and found that widely foraging lizards reproduced more or less continuously, while seasonality was found among sit-and-wait foragers with the exception of gekkonids. Similar to other geckos, *Lygodactylus* can be considered as sit-and-wait ''ambush'' predators (Greer, 1967), but seem to show a trend towards continuous reproduction.

Fitch (1982) interpreted the limitation to small clutch sizes as an adaptation of scansorial and crevice-living habits, because larger clutches would constitute an important handicap of ovigerous females under such conditions. Frequent oviposition might be a strategy to compensate such small clutch sizes. Anolines and gekkonids were the lizards with the lowest relative clutch mass in the analysis of Shine (1992). If it is true that reproductive cycles of species in the Gekkoninae are less marked by seasonality than those of many other lizard groups, then this fact might be related to their obligate small clutch size (1–2 eggs) and triggered by the possibly higher dessication tolerance of their calcareous egg shells as compared to the non-calcified shells of other squamates.

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