COPEIA

Reproduction in the Lizard *Phyllodactylus lanei* (Squamata: Gekkonidae) from the Pacific Coast of Mexico

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Studies on reproductive biology of individual species provide data necessary for testing hypotheses that seek to explain the diversity of life histories observed in squamate reptiles. The reproductive cycle of *Phyllodactylus lanei* at Chamela Jalisco, Mexico was aseasonal and varied among months and between sexes. Males and females reached sexual maturity at 52.0 and 49.0 mm snout-vent length (SVL), respectively. Males and females were reproductively active throughout the year, but a distinct cycle was evident. Testes reached maximal size from August to March and began to decrease in size in April, reaching minimum size in July. Gonadal volume in females was greatest from January–April coincident with maximal egg production. However, some females were found with eggs in nine of the 12 months, indicating an extended egg-laying season. Some females (7.6%) contained eggs and vitellogenic follicles simultaneously. Females were capable of producing at least three clutches of two eggs during the reproductive season. The testicular cycle was correlated with photoperiod but not rainfall or temperature. The female gonadal cycle was correlated with mean monthly temperatures but not photoperiod or rainfall. Monthly production of oviductal eggs was correlated with monthly mean temperatures but not photoperiod or rainfall. Egg mass was significantly correlated with female mass but not with SVL. This study provides another example of a gecko species in which the reproductive season is extended, females reproduce repeatedly, but egg production is greatest during the dry season.

Estudios sobre la biología reproductiva de una especie proporcionan datos necesarios para probar hipótesis que traten de explicar la diversidad de historias de vida observadas en los reptiles squamata. El ciclo reproductivo de *Phyllodactylus lanei* de Chamela Jalisco, Mexico fue acíclico y varió entre meses y sexos. Los machos y las hembras alcanzares la madurez sexual a los 52.0 y 49.0 mm de longitud hocico-cloaca (LHC), respectivamente. Los machos y las hembras mostraron actividad reproductiva a lo largo del año, pero un ciclo distinto fue evidente. Los testículos alcanzaron el máximo tamaño de agosto a marzo, y comenzaron a decrecer en tamaño en abril, alcanzando el mínimo tamaño en julio. El volumen gonadal en las hembras fue más grande de enero a abril, coincidiendo con la máxima producción de huevos. Sin embargo, algunas hembras fueron encontradas con huevos en 9 meses de los 12, indicando una estación larga de puesta de huevos. Algunas hembras (7.6%) presentaron huevos oviductales y folículos vitelogénicos simultáneamente. Las hembras fueron capaces de producir al menos tres puestas de huevos durante la estación reproductiva. El ciclo testicular estuvo correlacionado con el fotoperiodo pero no con la precipitación o temperatura. El ciclo gonádico de las hembras estuvo correlacionado con la temperatura media mensual pero no con el fotoperiodo o precipitación. La producción mensual de huevos oviductales fue correlacionada con la temperatura media mensual, pero no con el fotoperiodo o lluvia. La masa del huevo fue significativamente correlacionada con la masa de la hembra pero no con la LHC. Este estudio proporciona otro ejemplo de una especie de gecko en la cual la estación reproductiva se extiende, las hembras se reproducen repetidas veces, pero la producción de huevos es más grande durante la estación de secas.

REPRODUCTION varies considerably among lizard species inhabiting seasonal tropical environments. In some, reproduction is cyclical, with courtship, mating, and copulation occurring at the beginning of the rainy season, incubation occurring during the rainy season, and hatching occurring at the end of the rainy season (Ramírez-Bautista and Vitt, 1997, 1998). In these species, rainfall appears to be the primary factor initiating reproduction (Ramírez-Bautista et al., 2000; Ramírez-Bautista and Pardo-De la Rosa, 2002), but temperature and photoperiod (Marion, 1982) may provide proximate cues. Some species living in tropical environments with distinct wet-dry seasonality have continuous reproduction, with egg production throughout the year (Vitt, 1986; Selcer, 1990). Factors that influence reproductive activity in these species are not well known (Selcer, 1990). However, it is becoming increasingly clear that the local environment alone does not determine reproductive seasonality in tropical lizards, because single tropical sites usually contain species with distinctly different reproductive patterns (James and Shine, 1985; Vitt, 1990, 1992), and some of this variation has a historical origin (see Dunham and Miles, 1985).

Seasonal and annual fluctuations of environmental variables (e.g., food availability, precipitation, and temperature) can induce proximate variation in life-history traits within populations (e.g., growth rates, clutch size, clutch frequency, and age and size at maturity; Ballinger, 1977; Dunham, 1982; Benabib, 1994). Variability in reproductive characteristics, such as timing of reproduction, clutch frequency, and egg size in gekkonid lizards, appears to be associated with variation in resource availability, temperature, and possibly rainfall in at least one tropical habitat. Geckos in Caatinga of northeastern Brazil produce eggs year round, but a reduction in egg production occurs during the dry season (Vitt, 1986). In other lizard species with continuous reproduction, particularly *Anolis*, reproductive activity can be influenced by temperature (Ramírez-Bautista and Vitt, 1997), precipitation (Wilhoft, 1963; Sexton and Turner, 1971; Ruibal et al., 1972), and food availability (Guyer, 1988a, 1988b).

We describe the reproductive cycle of male and female *Phyllodactylus lanei* studied at Chamela, Jalisco, Mexico. To date, only anecdotal descriptions of reproduction of *P. lanei* (Ramírez-Bautista, 1994) are available. We address the following questions: (1) Are sexually mature males and females the same size, and does sexual dimorphism in other morphological characteristics exist? (2) What is the reproductive cycle of males and females? (3) Is there a correlation between peak reproductive activity and environmental factors (temperature, photoperiod, and rainfall)? (4) Do egg size and reproductive potential vary with female size, and if such variation exists, what are potential proximate causes?

MATERIALS AND METHODS

Study area.—Reproductive data were obtained on individual females and males at Chamela, near the Estación de Biología ''Chamela'' (EBCH), along the Federal road between Chamela and Careyes town. The study area is located approximately three km E of the Pacific coast ($19°30'$N, $105°03'$W; elevation from 10 to 584 m) in Jalisco, Mexico. Dominant vegetation is tropical dry forest with rains occurring from June to October. Mean annual temperature is 24.9 C with an average annual rainfall of 748 ± 119 mm (585–961 mm; Bullock, 1986). Data on photoperiod were taken from the Astronomical Almanac of the World (1984). Annual mean temperature and precipitation over a ten-year period during the study were recorded at the Estación Metereológica of the Estación de Biología ''Chamela'' and have been reported elsewhere (Ramírez-Bautista and Vitt, 1997, 1998). To compare climatic variables with reproductive and organ cycles, we used a multiple regression with mean temperature, photoperiod, and precipitation as independent variables and $\log_{10}$-transformed organ masses or volumes as dependent variables.

Morphological analyses.—Morphological descriptions and comparisons were restricted to sexually mature males and females (see below). For all lizards collected, we measured SVL to 1.0 mm, mass to 0.01 g, head length (HL) and width (HW) to 0.1 mm. We measured forearm (FL) and tibia length (TL) to 0.1 mm from the elbow or knee, respectively, to the pad of the foot. The SVL of sexually mature males and females was compared with a Mann-Whitney U-test. To examine possible sexual dimorphism in bauplan, we performed a principal components analysis (PCA) using residuals of regressions of the $\log_{10}$-transformed morphological variables against $\log_{10}$ SVL. Variables included were mass, head length and width, forearm length, and tibia length. This procedure adjusts for the effects of body size on morphological characters allowing relatively size-independent comparisons (see Miles, 1994). Tail condition was scored as original (never broken), regenerated, and broken.
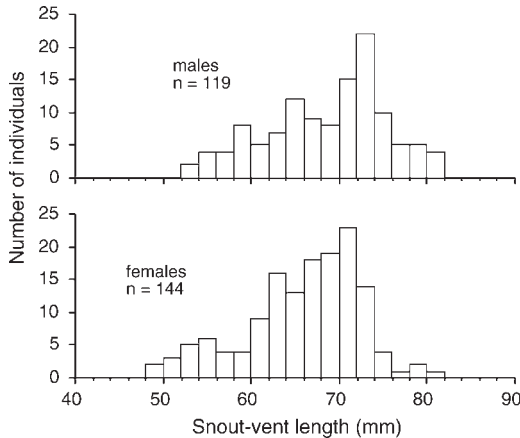
Fig. 1. Distribution of SVL for male and female *Phyllodactylus lanei*.

Reproductive analysis.—A total of 267 (144 females, 119 males, and four juveniles) *P. lanei* were collected from 1981 to 1989. Because sample size for individual months was small, all data were pooled across years by month to describe the annual reproductive cycle. Thus, we ignore annual variation in reproduction for this study. All lizards were killed by cranial alcohol injection and fixed (10% formalin) in the laboratory where gonadal analyses were performed. Males were considered sexually mature if they contained enlarged testes and convoluted epididymides typically associated with sperm production (Goldberg and Lowe, 1966). Length and width of testes was measured to 0.1 mm, and mass of livers was measured to 0.001 g. Testis volume was calculated using the formula for the volume of an ellipsoid: $V = 4/3 \pi a^2 b$, where a is one-half the shortest diameter and b is one-half the longest diameter. Mean testis volumes and mean liver masses by month were used to describe the male cycle.

The smallest female containing enlarged vitellogenic follicles or oviductal eggs was used to estimate minimum SVL at maturity. Mass of livers was measured to 0.001 g. Follicular volume (hereafter, ''gonadal volume'') was calculated with the same formula used for testes volume. Mean gonadal volumes and mean liver masses by month were used to describe the female cycle. An oviductal egg for each gravid female was weighed to 0.0001 g and multiplied by the number of eggs (two, one each side) to estimate female clutch mass. Because organ mass or volume usually varies with body size, we $\log_{10}$ transformed all variables and conducted analyses of covariance (ANCOVA) with organ mass or volume as the dependent variable, SVL as the covariate, and

TABLE 1. FACTOR SCORES FROM A PRINCIPAL COMPONENT ANALYSIS ON SIZE (SVL) ADJUSTED MORPHOLOGICAL CHARACTERS.

Variable	Factor I	Factor II
Relative body mass	<0.001	0.886
Relative head length	0.510	0.422
Relative head width	0.602	0.544
Relative femur length	0.859	−0.010
Relative tibia length	0.827	0.136
Eigenvalue	2.311	46.2
Variance explained	46.2%	19.1%

month as the class variable to determine whether significant seasonal variation existed.

Annual reproductive potential was determined by counting eggs in the oviduct (one each oviduct) or vitellogenic follicles of adult females from the entire year. Incubation period was estimated as the interval between the date on which individual females had their first oviductal eggs during the reproductive season and the date on which first hatchlings appeared in the field. Means are presented ± SE unless otherwise indicated. All statistical analyses were performed with StatView IV (Abacus Concepts, Inc., Berkeley, CA, 1992).

RESULTS

Body size, maturity, and dimorphism.—Sexually mature males ranged in size from 52.0–81.0 mm SVL ($x = 68.1 \pm 0.63$, $n = 119$), whereas sexually mature females ranged in size from 49.0–80.0 mm SVL ($x = 65.5 \pm 0.54$, $n = 144$:Fig. 1). Males and females reached their first reproductive season in the second year after hatching (based on unpubl. capture-recapture data). Mean SVL of sexually mature males was significantly larger than that for females (Mann-Whitney U-test, $z = -3.14$, $P < 0.05$). The PCA on morphological characters produced two factors that together explained 65.3% of the morphological variation. Factor I described a gradient in forearm and tibia length accounting for 46.2% of the variance (Table 1). Factor II described a gradient in body mass accounting for 19.1% of the variance (Fig. 2). Factor I scores differed significantly between sexes ($F_{1,204} = 12.2$, $P = 0.0006$), but factor II scores did not differ between sexes ($F_{1,204} = 1.5$, $P = 0.2154$). Thus, males tend to have longer lower limbs than females. Analyses of covariance on morphological characters comparing sexes produced similar results except that head size of males is larger than that of females (Factor II was not significant in the PCA). Significant differences in slopes
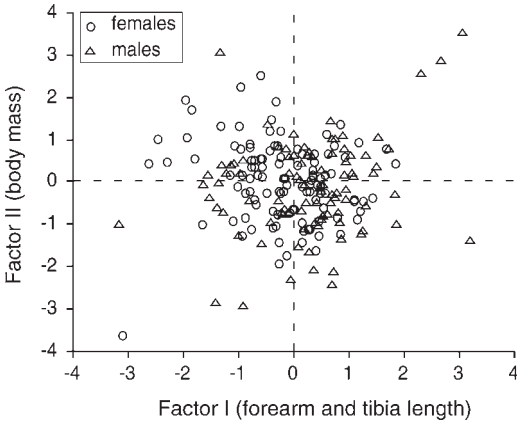
Fig. 2. Plot of the first two factors from PCA on size-adjusted morphological variables of *Phyllodactylus lanei*.

Fig. 3. Monthly means of male testis volumes and liver masses of *Phyllodactylus lanei* from Chamela, Jalisco. Standard error bars are shown.

$(F_{1,202} = 8.4, P = 0.0042)$ and intercepts $(F_{1,202} = 8.7, P = 0.0036)$ were detected in the comparison of head length between sexes. Slopes did not differ in the relationship of head width to SVL between sexes $(F_{1,202} = 0.49, P = 0.4849)$. With the interaction term (SVL*sex) removed, head width of males was slightly larger than that of females $(F_{1,203} = 5.9, P = 0.0161)$. Thus, sexual dimorphism in SVL, mass, and other morphological characters exists.

Among mature males, 64 (53.3%) had original tails, 38 (31.7%) had regenerated tails, and 18 (15.0%) had recently lost their tails. Among mature females, 96 (66.7%) had original tails, 32 (22.2%) had regenerated tails, and 16 (11.1%) had recently lost their tails.

Reproduction.—A significant relationship existed between $\log_{10}$-SVL and $\log_{10}$-testes volume ($r^2 = 0.126, F_{1,117} = 17.98, P < 0.0001$) and $\log_{10}$-liver mass ($r^2 = 0.486, F_{1,118} = 113.7, P < 0.0001$). Testes increased in size from August ($x = 51.5 \pm 8.9$ mm^3) through January ($x = 40.2 \pm 7.4$ mm^3), reaching maximum size in February ($x = 78.9 \pm 12.9$ mm^3), followed by a decrease in testicular size from April to July (Fig. 3). An ANCOVA on $\log_{10}$ testes volume with $\log_{10}$ SVL as the covariate revealed a significant interaction between month and SVL ($F_{11,95} = 1.94, P = 0.046$) with intercepts differing as well ($F_{11,95} = 2.2, P = 0.0204$). Nevertheless, testes volumes were much lower during April–July than during the remainder of the year. An ANCOVA on liver mass revealed no interaction between month and SVL ($F_{11,96} = 0.96, P = 0.4902$). Removing the interaction term revealed no significant seasonal effect of season on liver mass ($F_{11,107} = 1.6, P =$
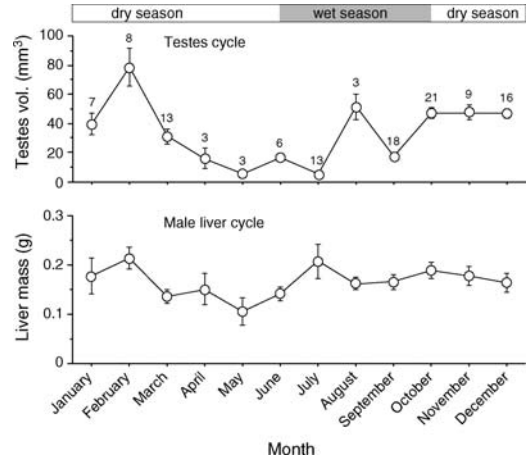
0.1008). Thus, testes mass cycles seasonally but liver mass does not vary seasonally.

For males, $\log_{10}$ of mean monthly testes volumes were significantly correlated with climatic variables ($R^2 = 0.656, F_{3,11} = 5.086, P = 0.0293$). Only photoperiod contributed significantly (t = $-3.343, P = 0.0102$) to the multiple regression. $\log_{10}$ of mean monthly liver mass of males was not correlated significantly with climatic variables ($F_{3,11} = 1.2, P = 0.3716$). Nevertheless, when considering mass of livers and testes among individual males, a significant correlation exists ($R^2 = 0.111, F_{1,117} = 15.7, P < 0.0001$) indicating that as testes enlarge, so do livers.

In females, a significant relationship existed between $\log_{10}$-transformed SVL and $\log_{10}$-transformed liver mass ($R^2 = 0.37, F_{1,142} = 84.5, P < 0.0001$) but not with gonadal volume ($R^2 = 0.009, F_{1,142} = 1.29, P > 0.05$). An ANCOVA on $\log_{10}$ liver mass with $\log_{10}$ SVL revealed significant differences in slopes ($F_{11,120} = 4.88, P < 0.0001$) and intercepts ($F_{11,120} = 4.81, P = < 0.0001$) among months. A liver mass cycle in which livers were smallest during May and June was apparent (Fig. 4). Significant monthly variation was detected in female gonadal volume ($F_{11,132} = 18.58, P < 0.0001$) with gonadal volume reaching largest size during September–March (Fig. 4). Finally, gonadal mass of individual females was correlated with female liver mass ($R^2 = 0.034, F_{1,142} = 6.06, P = 0.0150$) indicating that liver mass was greatest during production of vitellogenic follicles.

Females with either vitellogenic follicles or eggs were observed throughout the year (Fig. 5). Vitellogenic follicles were present in females during all months except January and July, with
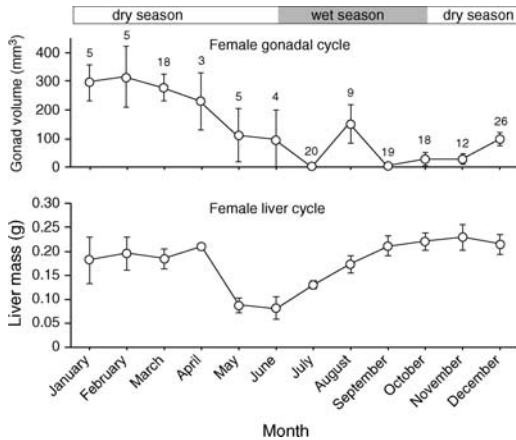
Fig. 4. Monthly means of female gonadal volumes and liver masses of *Phyllodactylus lanei*. Standard error bars are shown.

Fig. 5. Seasonal changes in the frequencies of various reproductive states for females *Phyllodactylus lanei*.

a maximum peak in December (54%, $n = 14$). Maximum egg production (oviductal eggs and/or vitellogenic follicles) occurred during December (30.0%, $n = 7$), January (100%, $n = 5$), February (60%, $n = 3$), and March (67.0%, $n = 12$).

For females, $\log_{10}$ of mean monthly gonad volumes were significantly correlated with climatic variables ($R^2 = 0.751$, $F_{3,11} = 12.074$, $P = 0.0024$). Only temperature contributed significantly ($t = -4.622$, $P = 0.0017$) to the multiple regression. $\log_{10}$ of mean monthly liver mass of females was not correlated significantly with climatic variables ($F_{3,11} = 2.818$, $P = 0.1073$).

We observed significant variation in SVL among females in different reproductive categories (ANOVA, $F_{3,140} = 3.61$, $P < 0.015$). The reproductive categories and mean SVL for each were: 1) females with non-vitellogenic follicles only (65.1 ± 0.8 mm, $n = 69$), 2) females with vitellogenic follicles but not oviductal eggs (65.9 ± 1.0, $n = 38$), 3) females with oviductal eggs only (63.6 ± 1.5, $n = 26$), and 4) females with oviductal eggs plus vitellogenic follicles (71.0 ± 1.1, $n = 11$). A Games-Howell *post hoc* test indicated that females simultaneously containing vitellogenic follicles and oviductal eggs were larger than those in the other three categories (all P values < 0.05). We used multiple regression analyses to determine effects of temperature, photoperiod, and precipitation on number of females in each of the four reproductive states described above. The relationship between oviductal eggs and climatic variables was significant ($R^2 = 0.508$, $F_{3,11} = 4.79$, $P = 0.0339$) with only monthly mean temperature contributing significantly to the relationship ($t = -2.48$, $P = 0.0381$). The relationship between vitellogenic
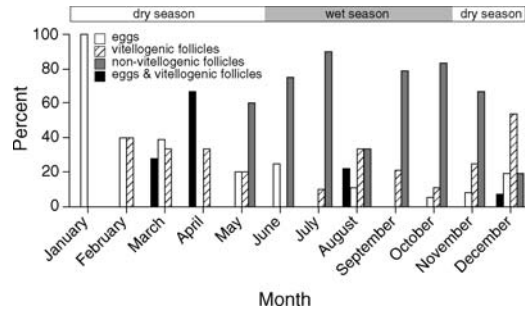
follicles and climatic variables was not significant ($R^2 = 0.231$, $F_{3,11} = 0.80$, $P = 0.5278$). The relationship between non-vitellogenic follicles and climatic variables was significant ($R^2 = 0.562$, $F_{3,11} = 5.70$, $P = 0.0219$) with monthly mean temperature contributing significantly to the relationship ($t = 2.74$, $P = 0.0253$) and photoperiod having a marginally significant effect ($t = -2.297$, $P = 0.0507$). The relationship between oviductal eggs + vitellogenic follicles and climatic variables was not significant ($R^2 = 0.165$, $F_{3,11} = 1.73$, $P = 0.2388$).

In *P. lanei* clutch size was always two. Clutches of *P. lanei* were frequently observed in rock crevices in the field, under bark or dead branches of trees, and in narrow crevices in human dwellings. We found groups of eggs of several clutches produced by 2–3 females (4–6 eggs) along drains in the road (where we had marked lizards; unpubl. data). Mass of the oviductal eggs was significantly correlated with female mass ($R^2 = 0.14$, $F_{1,26} = 4.13$, $P < 0.05$) but not with SVL ($R^2 = 0.09$, $F_{1,26} = 2.84$, $P > 0.05$). Egg volume varied monthly; January ($x = 296.5 ± 61.8$ mm^3), February ($x = 314.4 ± 107.2$ mm^3), March ($x = 279.8 ± 45.4$ mm^3), April ($x = 231.4 ± 99.8$ mm^3), May ($x = 114.2 ± 92.7$ mm^3), June ($x = 100.3 ± 98.6$ mm^3), August ($x = 151.7 ± 66.5$ mm^3), and December ($x = 99.4 ± 23.2$ mm^3). Neonates were observed in the field from October to August. A gravid female (marked lizard) deposited her eggs on 12 March and they hatched on 18 April. Based on these data, the incubation period was about 37 days. Mean SVL of neonates at hatching was 26.6 ± 2.1 mm (22.0–31.0, $n = 5$) and mean mass was 0.48 ± 0.07 g (0.30–0.60).

DISCUSSION

Body size and sexual dimorphism.—Sexual dimorphism with larger SVL and relative HL, HW, FL,

and TL in males of *P. lanei* was observed. This pattern has been reported in some other gekkonids (Vitt, 1986; Okada et al., 2002) and many other lizard species (Butler and Losos, 2002; Molina-Borja, 2003; Schwarzkopf, 2005). At least a portion of sexual dimorphism can be attributed to sexual selection (e.g., Trivers, 1972; Molina-Borja, 2003). Contributing factors include differential growth rates (Trivers, 1976), male combat (Ruby, 1981; Kratochvíl and Frynta, 2002; Olsson et al., 2002), and territoriality (Greer, 1967; Stamps, 1977).

Reproductive cycle.—Our results indicate that males of *P. lanei* had an extended reproductive season (August–March) with two peaks. One peak occurred during mid to late wet season (August–October; Fig. 3), and the other peak occurred during the first five months of the dry season (November–March). Reproductive behavior, such as courtship and mating, began in August coincident with the beginning of the wet season. Testes volume increased when temperature and photoperiod increased. Consequently temperature and photoperiod, or a combination of the two factors, appear to stimulate gonadal activity in males (Licht and Gorman, 1970; Marion, 1982). This pattern differs from some other gekkonid species, in which reproductive activity of males was greatest during the wet season (Vitt, 1986). To date, several studies on lizards inhabiting tropical dry forest have shown that precipitation, temperature, and photoperiod or a combination of these factors play an important role in reproductive activity (Ramírez-Bautista et al., 1995; Ramírez-Bautista and Vitt, 1997, 1998). However, at Chamela, reproductive activity of each species may be influenced by different proximal factors. For example, in *Anolis nebulosus* (Ramírez-Bautista and Vitt, 1997) and *Urosaurus bicarinatus* (Ramírez-Bautista and Vitt, 1998), gonadal activity was correlated with temperature and photoperiod. In contrast, temperature and precipitation appear to be most important in *Aspidoscelis lineatissima* (Ramírez-Bautista et al., 2000) and *Sceloporus utiformis* (Ramírez-Bautista and Gutiérrez-Mayén, 2003), while in *A. communis* (Ramírez-Bautista and Pardo-De la Rosa, 2002) the three factors are important in reproductive activity of males.

Male reproductive activity was also extended, such as occurs in other gekkonid (Vitt, 1986; Shanbhag et al., 2000; Vences et al., 2004) as well as many other tropical and subtropical lizards (James and Shine, 1988; Ramírez-Bautista et al., 2000; Ramírez-Bautista and Pardo-De la Rosa, 2002). Liver mass of males was highly variable during the dry season, but not in the wet season

when the reproductive season began. This pattern is similar to those of *A. nebulosus* and *U. bicarinatus* (Ramírez-Bautista and Vitt, 1997, 1998) and different from those of *A. communis* and *A. lineatissima* (Ramírez-Bautista et al., 2000; Ramírez-Bautista and Pardo-De la Rosa, 2002) that occur in the same habitat. Because *P. lanei* are sit-and-wait foragers (Cooper, 1995) and presumably do not expend much energy in searching for the food, energy stored in the liver may contribute to the extended reproductive season.

Female reproduction was continuous throughout the year and vitellogenic follicles began to increase in size from July to May. Egg production occurred throughout the year, but most egg production occurred from December to March, coinciding with the dry season when levels of liver mass were higher. This pattern suggests that the liver may be involved in synthesis or storage of lipids for egg production during dry season, when resources are scarce as in other lizard species (Selcer, 1987, 1990; Ramírez-Bautista and Vitt, 1997). In *Hemidactylus turcicus*, liver mass increased during maximum egg production, suggesting that fat body lipids were mobilized to the liver during reproduction (Selcer, 1986, 1987, 1990). A similar pattern may exist in *P. lanei*. Although females of *P. lanei* showed continuous reproduction, vitellogenesis coincided with increases in rainfall and temperature and, although the correlation with photoperiod was not significant, a combination of the three factors likely plays an important role in the reproduction (Marion, 1982; Licht, 1984). Female reproduction is typically extended in other tropical gekkonids, including *Hemidactylus frenatus*, *Cosymbotus platyurus*, *Peropus mutilatus* (Church, 1962) and *Lygodactylus klugei* and *Gymnodactylus geckoides* (Vitt, 1986), but in other species is highly seasonal such as *Gekko hokouensis* (Okada et al., 2002). Although many gekkonid species produce eggs continuously throughout the year, the proportion of monthly female samples containing oviductal eggs or vitellogenic follicles varies considerably. In geckos from northeastern Brazil (Vitt, 1986), most egg production occurred from May to November, whereas in other geckos from southern Okinawajima (Okada et al., 2002) and Cerrados of central Brazil (Colli et al., 2003), the period of egg production was shorter, from April to July and May to September, respectively. *Phyllodactylus lanei* showed a different pattern in egg production compared with the above species.

Clutch size and egg size.—Females of *P. lanei* produce clutches of two eggs per episode and

appear to be able to produce eggs in rapid succession similar to many other geckos based on simultaneous presence of oviductal eggs and vitellogenic follicles (Vitt, 1986; Selcer, 1990). Our data also suggest that maternal body mass influences offspring size to some extent. A significant relationship exists between egg mass and female mass as in some other species (Doughty, 1996, 1997). In many other geckos, egg size does not appear to vary with body size (e.g., How et al., 1986; Vitt, 1986; Selcer, 1990). Some larger females of *P. lanei* (7.6% of those collected) produced at least two clutches. Compared with smaller females, these females appear to gain in offspring size/quality and frequency. Presumably, larger hatchlings or hatchlings with greater lipid reserves have higher survivorship than smaller ones (Selcer, 1990).

Even though egg mass was correlated with female mass, such a small portion of the variation in egg mass was explained by lizard mass that it may have little biological significance. Egg mass is related to female size across species of gekkonids (Vitt, 1986; Doughty, 1996, 1997) and in some other lizard genera species with genetically fixed clutch size (Andrews and Rand, 1974). Seasonal variation in egg size was also apparent, but could reflect seasonal size differences among females containing eggs. Because of limited sample size, we cannot sort out differential effects of body size, season (and thus resource availability), or reproductive category. Nevertheless, the ability to vary egg size should balance potential gains of producing the largest offspring possible under current resource conditions and body size constraints against potential survivorship associated with investing heavily in a reproductive episode during periods of low resource availability. The lack of relationship of reproductive potential to body size is not surprising. In species that cannot vary clutch size with body size, the number of ovarian follicles that a female contains at the beginning of its first reproduction should be optimized such that under the best of conditions, a female could deposit all of her eggs during that breeding season. Although several hypotheses exist that explain invariant clutch size in gekkonid species (Vitt, 1986; Doughty, 1996, 1997), it remains unclear what proportion of females or how frequently females actually produce their full complement of eggs during a single year.

Several points emerge from the study within the context of what we currently know about gekkonid species reproduction. First, like many other non-sphaerodactyl gekkonids studied, clutch size is fixed at two eggs (e.g., Vitt, 1986;

Doughty, 1997; but see Vitt and Zani, 1997 for an exception) and eggs are produced in rapid succession. Consequently, a strong phylogenetic component prevails among gekkonid lizard species. In addition, plasticity in reproductive traits exists (''reaction norms'' of Stearns, 1993) as suggested by the high variation among individuals reported here. Finally, related species show different reproductive characteristics, particularly in the relationship between egg size or egg mass and female SVL.

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