

Seasonal activity and the body size–fecundity relationship in a population of *Physalaemus gracilis* (Boulenger, 1883) (Anura, Leptodactylidae) from Uruguay

Arley Camargo^{1,*}, Daniel E. Naya², Andrés Canavero¹, Inés da Rosa¹ & Raúl Maneyro^{1,3}

¹ Sección Zoología Vertebrados, Facultad de Ciencias, Universidad de la República, Montevideo 11400, Uruguay (*corresponding author's e-mail: arley@fcien.edu.uy)

² Center for Advanced Studies in Ecology and Biodiversity and Departamento de Ecología, Pontificia Universidad Católica de Chile, Santiago 6513677, Chile

³ Laboratório de Herpetologia, Museu de Ciências e Tecnologia & Faculdade de Biociências da Pontificia Universidade Católica de Rio Grande do Sul, 90619-900 Porto Alegre, RS, Brasil

Received 1 Dec. 2004, revised version received 15 Apr. 2005, accepted 18 Mar. 2005

Camargo, A., Naya, D. A., Canavero, A., da Rosa, I. & Maneyro, R. 2005: Seasonal activity and the body size–fecundity relationship in a population of *Physalaemus gracilis* (Boulenger, 1883) (Anura, Leptodactylidae) from Uruguay. — *Ann. Zool. Fennici* 42: 513–521.

Two key life history attributes are temporal reproductive patterns and inter- and intraspecific variation in clutch size. In this work, we collected individuals of *Physalaemus gracilis* in Espinas stream (Maldonado, Uruguay) to analyze the correlation of activity with environmental variables and to evaluate the influence of reproductive investment on the body size–fecundity (BSF) relationship. In contrast to previous reports, the reproductive activity peaked in spring and was not correlated with temperature or rainfall in either sex. Regression analysis showed that the BSF relationship varied with size, and that larger females had a steeper slope than smaller females. Reproductive investment data indicate that smaller females invested less energy in their offspring than larger females, which is probably due to the imposed cost of continued growth.

Introduction

The reproductive strategies of anurans are optimal combinations of morphological, physiological, behavioral, and life history traits that maximize reproductive success under particular environmental and evolutionary constraints (Duellman & Trueb 1994). Two key life history attributes related to reproductive strategies are seasonal reproductive patterns and inter- and intraspecific variation in clutch size (e.g., Salthe

& Duellman 1973, Crump 1974, Kuramoto 1978, Wake 1982). Whereas a bulk of data have accumulated on life history of frogs from temperate areas in the northern hemisphere, a similar knowledge for frogs in tropical and temperate regions of South America is far behind (see Donnelly *et al.* 2005).

The temporal reproductive pattern of anurans is continuous in tropical non-seasonal climates, and seasonally cyclic in tropical and temperate regions that have a marked dry or

cold season (Duellman 1978, Jørgensen 1992). In temperate regions, the seasonal increase in temperature plays a permissive role in the activation of gonads, and regulates the duration of the breeding season, whereas rainfall often triggers the onset of the breeding season (Stebbins & Cohen 1995). While these general patterns hold for the majority of anuran species in temperate regions, variation in other factors (e.g., internal rhythms) can cause some species to reproduce for longer or shorter periods than expected (Wells 1977, Brown & Shine 2002, Morrison & Hero 2003).

Regarding intraspecific variation in the body size–fecundity (BSF) relationship, most studies report a significant and strong correlation between body size and clutch size (Tejedo 1992, Gilbert *et al.* 1994, Kusano & Hayashi 2002, Wogel *et al.* 2002). However, other studies have not found such a consistent pattern, at least for some species (e.g., Duellman & Crump 1974, Elmberg 1991, Tarkhnishvili 1993, Buschmann 2002, Tsiora & Kyriakopoulou-Sklavounou 2002). One hypothesis for these contradictory results is that females vary in the amount of energy allocated for different activities (reproductive or otherwise). This may constrain clutch size and, consequently, affect the BSF relationship (Duellman & Trueb 1994). In this sense, Bonnet *et al.* (2003) found that fecundity correlates well with body size in high reproductive investment (RI) females. However, when females with increasingly lower RI are included in the analysis the strength of the BSF relationship weakens.

Herein, we investigated seasonal variation in the activity of male and female *Physalaemus gracilis* in a population from southern Uruguay. We chose *P. gracilis* as the focal species because it is one of the most abundant frogs in southern Uruguay (Nuñez *et al.* 2004). In addition, this leptodactylid frog inhabits both undisturbed as well as urbanized areas, where foam nests are placed among the aquatic vegetation in shallow swamps and flooded areas (Langone 1995, Maneyro *et al.* 1995, Achaval & Olmos 2003). Previous reports indicate that the seasonal breeding activity of *P. gracilis* occurs after heavy rains from September to March (Langone 1995, Achaval & Olmos 2003).

Materials and methods

Study site and specimen collection

We collected *P. gracilis* along Espinas stream (34°47'S, 55°22'W, Departamento de Maldonado, Uruguay) between September 1998 and April 2000. The 2-km-long Espinas stream is dammed before flowing into the La Plata River and becoming a shallow, lentic area at sea level. Frogs were collected monthly in pitfall traps placed at about two meters from the stream border and remaining operative during the entire study period. Specimens were deposited in the Vertebrate Zoology Collection, Facultad de Ciencias, Universidad de la República (ZVCB). For all specimens we measured total snout-vent length (SVL) using a 0.005 cm precision digital caliper.

Patterns of activity

Activity patterns were described by considering monthly variation in the number of captures and body sizes. The period of reproductive activity of females was determined from the presence of gravid females with mature ovaries containing fully developed oocytes. The period of male reproductive activity was estimated during fieldtrips (*see below*), using the relative abundance of calling males based on the following ranking: (1) occasional: one male, (2) rare: two males, (3) common: three or more distinguishable males, and (4) chorus: many countless calling males (Moulton *et al.* 1996, Shiroye *et al.* 1997, Driscoll 1998). Fieldtrips were conducted each month (except for February 1999 and December 1999) for two consecutive nights, between sunset and 01:00. The relative abundance of calling males was recorded at seven sites. For each month, we summed ranks over all sites to obtain an estimate of male abundance across the study area. Correlation between the reproductive activity of males and females was estimated using non-parametric Spearman's rank test (Zar 1999). In addition, we obtained mean monthly records of temperature and accumulated rainfall from the Carrasco International Airport Weather Station, which is at sea level and near

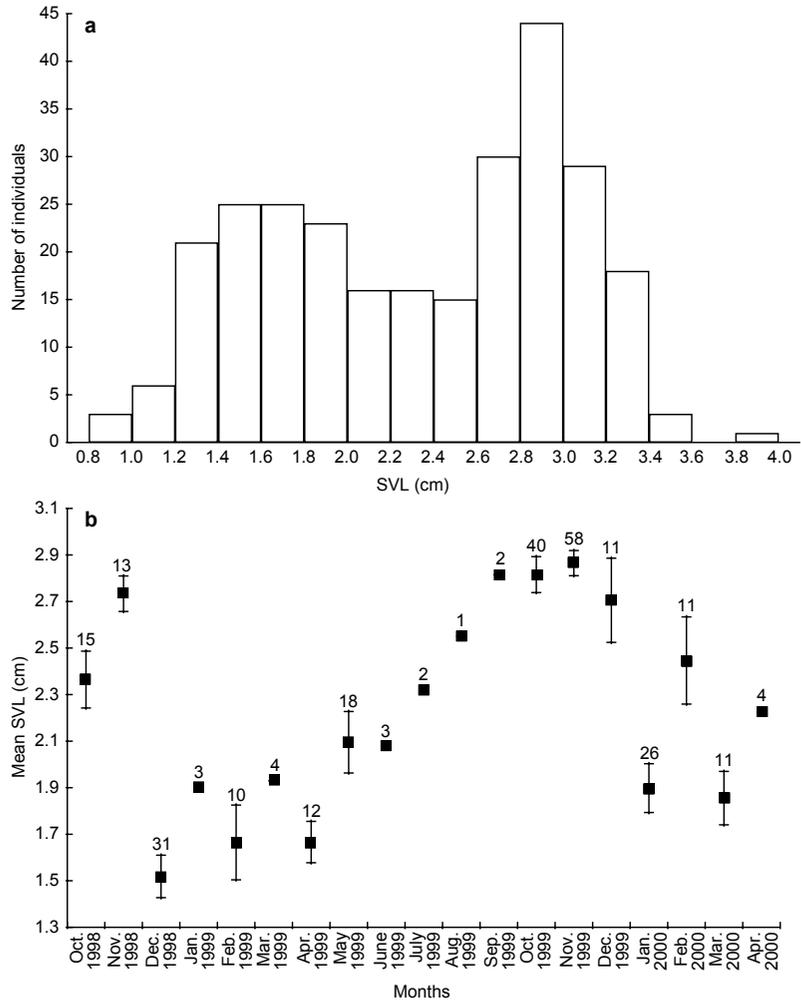


Fig. 1. (a) Snout-vent length (SVL) distribution of *P. gracilis* specimens collected in the study area between September 1998 and April 2000, and (b) monthly variation in snout-vent length (SVL). Dots represent mean values, vertical bars are standard errors, and numbers above bars indicate sample sizes.

to the coast (60 km west of the study site). We calculated non-parametric Spearman's rank correlations between each climatic variable and the reproductive activity of each sex.

Body size–fecundity relationships and reproductive investment

The mature ovaries with post-vitellogenic oocytes were extracted from all gravid females, and the total mass of ovaries was measured with a digital balance with 0.01 g precision. Subsequently, ovisacs were removed to release mature oocytes and their total number (i.e. fecundity) was directly quantified for each ovary. The BSF relationship was evaluated through regression

analysis, testing both linear and exponential models. In addition, we fit a pair-wise regression to analyse the potential existence of a breakpoint in the BSF function. Reproductive investment of each individual was estimated as the ratio between ovary mass and SVL.

Results

Patterns of activity

A total of 275 specimens were collected during the study period. Peaks in capture number occurred during the warm months (October–February) of each year. The body size distribution had two peaks, with modal values of 1.60 and 2.90 cm (Fig.

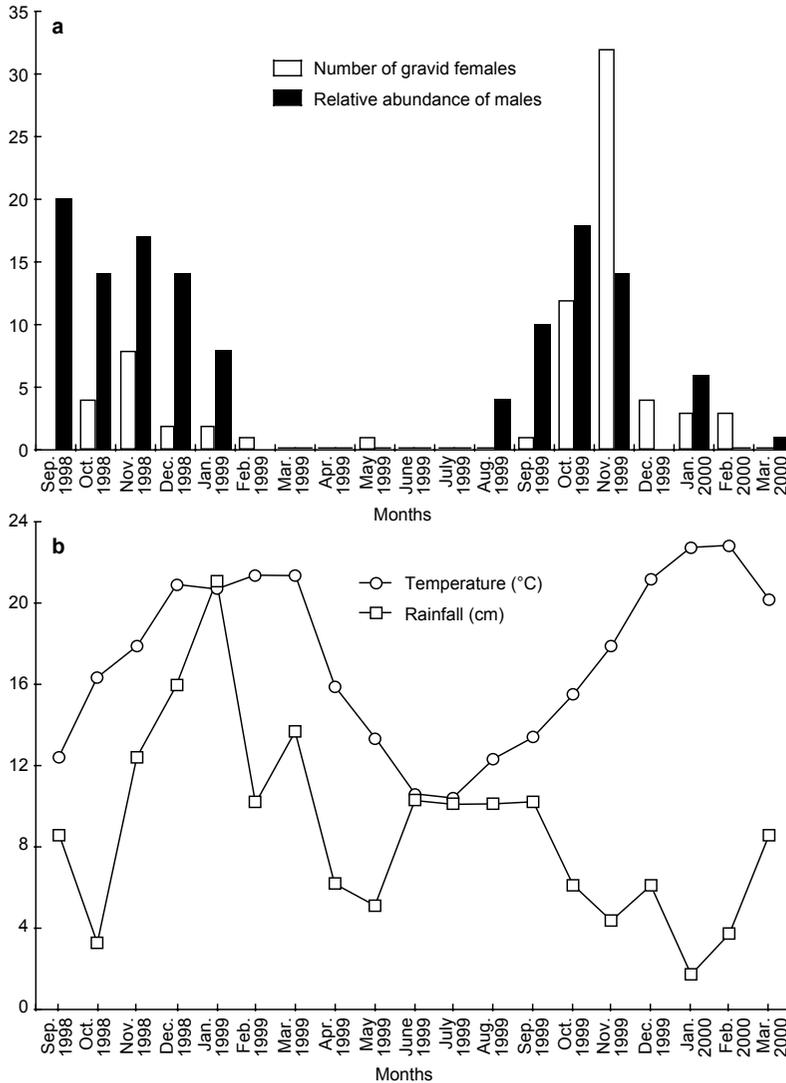


Fig. 2. Monthly variation in activity of *P. gracilis* and climatic variables in the study area. (a) Accumulated rank abundance of calling males and absolute number of gravid females and (b) monthly mean temperature and accumulated rainfall.

1a). Since the minimum SVL for a gravid female (2.46 cm) corresponds to the valley of this bimodal distribution, peaks probably represent adult and juvenile individuals. The monthly variation in mean SVL indicates that adults and juveniles did not necessarily occur in the study site at the same time. Adult individuals appeared first (October–December) and then the juveniles arrived abruptly (December–January), causing a marked drop in mean SVL during both years (Fig. 1b).

The reproductive activity of both sexes was highly correlated ($r_s = 0.77$, $n = 17$, $P < 0.001$) due to the synchronous presence of calling males and gravid females in October and November of both years (Fig. 2a). However, male activ-

ity started earlier than female activity, which was characterized by a sudden occurrence and disappearance of gravid females in the study area. Although the number of gravid females in November 1998 ($n = 8$) was lower than in November 1999 ($n = 32$), the proportion was very similar (62% and 55%) in relation to the total number of captures during these months ($n = 13$ and 58, respectively).

Neither monthly variation in temperature nor rainfall was correlated with female activity (temperature: $r_s = 0.28$, $n = 19$, $P = 0.25$; rainfall: $r_s = -0.41$, $n = 19$, $P = 0.08$; Fig. 2b) or male activity (temperature: $r_s = -0.02$, $n = 18$, $P = 0.95$; rainfall: $r_s = -0.06$, $n = 18$, $P = 0.83$; Fig. 2b). Repro-

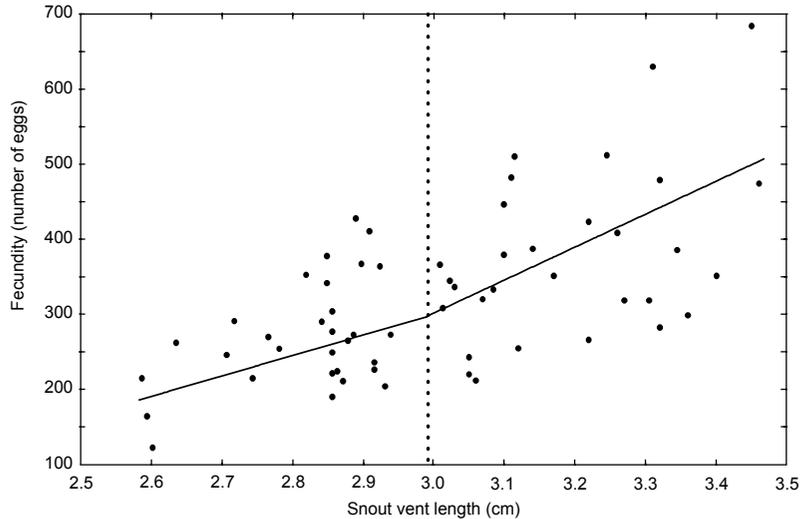


Fig. 3. Body size–fecundity relationship for *P. gracilis*. The line represents the pair-wise regression model.

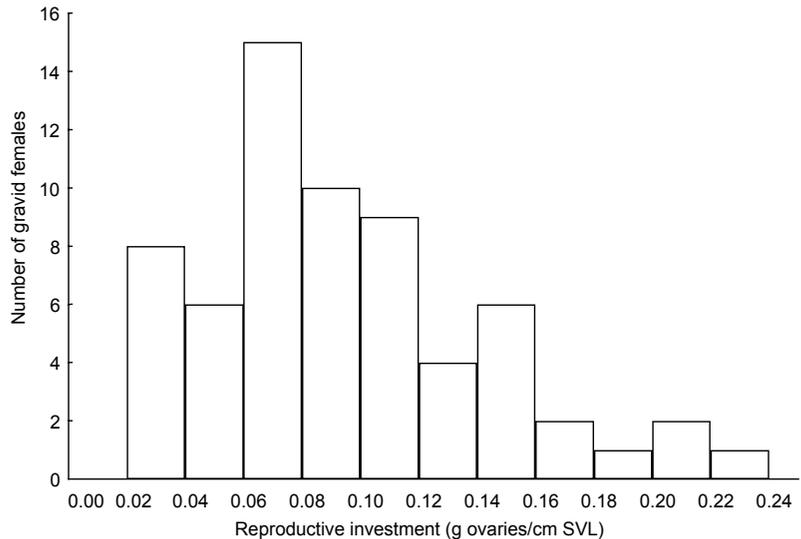


Fig. 4. Frequency distribution of reproductive investment for all gravid females collected during the study period.

ductive activity was not correlated with changes in temperature or rainfall that occurred in the previous month for either sex, but we did observe significant associations with the temperature one month in advance ($r_s = 0.62$, $n = 18$, $P < 0.01$ for females; $r_s = 0.52$, $n = 17$, $P < 0.05$ for males).

Reproductive investment and body size–fecundity relationships

A total of 64 gravid females were collected and analysed. A significant correlation between fecundity and SVL was found, and both the

linear ($r = 0.60$, $F_{1,62} = 35.43$, $P < 0.001$) and the exponential ($r = 0.61$, $F_{1,62} = 5.93$, $P < 0.001$) model, had a similar fit to the data. Pair-wise regression explained 72.4% of the total variance (nearly twice the variance explained for the above mentioned models), and suggests the existence of a breakpoint in SVL at 2.98 cm (Fig. 3). Females with larger SVL had a steeper slope ($b = 360.3$, $SE = 137.0$, $n = 30$) than smaller females ($b = 206.6$, $SE = 78.1$, $n = 34$). RI reached a mean value of 0.10 ($SE = 0.006$), ranging from 0.02–0.23 g cm⁻¹. In addition, the RI frequency distribution showed that most females presented lower than average RI values,

with a long tail of few females showing very high RI (Fig. 4).

Discussion

Activity patterns

Annual and seasonal variation in species activity has profound implications on ecology, from the organism level (e.g., Jørgensen 1992) to the community level (e.g., Schoener 1974, Sandvik et al. 2002). Activity periods govern the length of the breeding season and also influence the timing of reproductive bouts and the number of clutches produced in a season (Bull & Shine 1979). In addition, the type of male competition for mates and female mating preferences greatly depend on the temporal pattern of reproduction and operational sex ratios (Eggert & Guyétant 2003).

Results obtained in the present work indicate that *P. gracilis* activity peaks were restricted to two or three months during the warm season (spring and summer). In both years, the presence of gravid females and male calling activities peaked from October to November (or December), and subsequently, a marked decline in mean body size occurred when juveniles dominated the captures. A similar pattern of body size variation was found in *P. cf. fuscocomaculatus* and is interpreted as the recruitment of new individuals emerging from the last breeding season (Giaretta & Menin 2004).

The phenology of *P. gracilis* in Uruguay corresponds to that of an early breeder, with a pattern that is characteristic of prolonged reproduction (*sensu* Wells 1977). The early arrival of males to form large aggregations and the emission of calls different from the specific advertisement call (A. Camargo pers. obs.) suggest that *P. gracilis* males spend considerable time in chorus formation. Prolonged breeders, in contrast to explosive breeders, reproduce in permanent sites, where males tend to form lek-like, spatially structured choruses and call antiphonally to minimize male-to-male interaction (Stebbins & Cohen 1995). In this sense, intensive social interactions, including male competition and female mate selection, have been reported for other *Physalaemus* species (e.g., *P. cuvieri* Barreto & Andrade 1995, *P. pustulosus*

Bosch et al. 2000, *P. signifer* Wogel et al. 2002, *P. enesevae* Tárano & Herrera 2003). Nevertheless, our results contrast with previous accounts of the phenology of *P. gracilis* in Uruguay, where a more extended breeding period was reported (Langone 1995, Achaval & Olmos 2003). These discrepancies may reflect the fact that the period of calling activities does not strictly coincide with breeding periods, at least in typical prolonged breeders. The fact that *P. gracilis* males start to call earlier than the actual beginning of reproductive activities (i.e., when mature females appear) could overestimate the duration of the breeding season. As mentioned above, prior to the onset of breeding activities, calling may play a role in chorus formation rather than in attracting mates (Wiest 1982, Bastos & Haddad 1996). In these cases, calls by males in full reproductive potential may promote the endocrinal activation of other males to incite them into calling activity (Chu & Wilczynski 2001), thus increasing the chorus size as well as its attractiveness for females (Lucas & Howard 1995).

Regarding climatic variables, although reproductive activity patterns and temperature showed cyclical variation throughout the year, there was no significant correlation because most activity occurred in spring months and decreased during the warmer summer months. We also did not observe a correlation between reproductive activity and rainfall, which is probably due to the fact that rainfall was marked lower in the second year. Taken together these results suggest that neither temperature nor rainfall exclusively control the breeding patterns of *P. gracilis* in Uruguay. Moreover, the correlation of activity in both sexes with future changes in temperature suggests that internal mechanisms may have been involved in shaping similar activity patterns during the two consecutive seasons. The contribution of internal rhythms may be relevant considering their demonstrated role in alternatively inducing and inhibiting the gonadal activity of bufonid, ranid, and leptodactylid frogs (Jørgensen 1988, Mosconi et al. 1996, Tsai et al. 2003). Alternatively, the restriction of activity mainly to spring months may reflect an adaptation to avoid reproduction during summer months, when presumably higher evaporation occurs. As a pond dries up, increased crowding between amphibian larvae may result

in increased competition, growth inhibition, and cannibalism (Griffiths 1997). The study of the reproductive cycles of *P. gracilis* at lower and higher latitudes may provide insight into this apparent preference to reproduce at mild temperatures.

Body size, fecundity and reproductive investments

How to partition a finite amount of energy into maintenance, growth and reproduction is one of the major concerns of life history theory, and, thus, a very important issue in evolutionary biology. Life history theory predicts that reproduction costs in a given year has profound effects on subsequent performance, via changing reproduction and survival in subsequent years (Roff 1992, Stearns 1992). In ectothermic animals, growth rates decrease greatly after individuals reach sexual maturity (Halliday & Verrell 1988, Hemelaar 1988). Thus, for these species growth may be considered an investment in future reproduction since large females frequently produce more young than small females (Lardner & Loman 2003, and references therein). In addition, a reduction in growth due to reproduction costs could increase the probability of death by keeping the organism within a size range that is preferred by predators (Roff 1992).

The BSF relationship of *P. gracilis*, shows that a two slopes function explains much more of the total variance than a linear or an exponential model. One possible explanation for this is that pair-wise regression allows the separation of females that reproduce for the first time (and yet have great energy investment in growth) from those females that entered into the reproductive pool at least one year earlier. Reproductive investment data support this idea: of the 34 females in the low SVL group, 27 showed RI values lower than the mean, whereas of the 30 females in the high SVL group only 12 showed RI values lower than the mean. Thus, in small females advantages related to continued growth may impose an important limitation on the amount of energy that can be allocated to reproduction. In contrast, for larger females other more variable factors, such as food supply,

competition or predation, may limit the amount of energy devoted to each reproductive event. In many amphibian species, fecundity is a plastic trait that can change with environmental conditions, among populations, among individuals within populations, and also among years within single individuals (Kaplan & King 1997, Morrison & Hero 2003, and references therein).

Finally, Bonnet *et al.* (2003) argued that studies based on hand-collected samples may overestimate the strength of the BSF relationship because low RI females are frequently discarded in the field as non-gravid females. It is possible that pitfall trapping outperforms the by-hand method in obtaining a representative sample of reproductively active *P. gracilis* females. However, pitfall traps may also undersample females with very high RI because they move less or stay hidden more often than other females (Bonnet *et al.* 2003, Shine 2003, and references therein). Thus, we suggest that a combination of manual collection and pitfall trapping may be more appropriate for assessing variation in the reproductive parameters of a given frog population.

Acknowledgements

We thank D. Nuñez and L. Ziegler for their help during the fieldwork, and P. Vaz and A. Jauri for valuable logistic support in the study area. We are also indebted to M. Arim for suggestions on data analyses and to M. Di Bernardo (Pontificia Universidade Católica de Rio Grande do Sul, Brasil), M. A. Lardies, M. L. McCallum, and an anonymous referee for comments on an earlier version of the manuscript. DEN and RM were supported by fellowships from Programa de Desarrollo de las Ciencias Básicas (PEDECIBA, Uruguay). DEN also acknowledges financial support from DIPUC (Chile), CONICYT (Chile), and CASEB (Program 1, Chile) and RM a doctoral fellowship from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES). Animal collection was conducted according to current Uruguayan law and under government permit #164/04 issued by Dirección General de Recursos Naturales Renovables, MGAP, Uruguay.

References

- Achaval, F. & Olmos, A. 2003: *Anfibios y Reptiles del Uruguay*, 2 ed. — Graphis Impresora, Montevideo.
- Barreto, L. & Andrade, G. V. 1995: Aspects of the reproductive biology of *Physalaemus cuvieri* (Anura: Leptodactylidae) in northeastern Brazil. — *Amphibia-Reptilia* 16: 67–76.

- Bastos, R. P. & Hadad, C. F. B. 1996: Breeding activity of the neotropical treefrog *Hyla elegans* (Anura, Hylidae). — *J. Herpetol.* 30: 355–360.
- Bonnet, X., Shine, R., Lourdaux, O. & Naulleau, G. 2003: Measures of reproductive allometry are sensitive to sampling bias. — *Funct. Ecol.* 17: 39–49.
- Bosch, J., Rand, A. S. & Ryan, M. J. 2000: Acoustic competition in *Physalaemus pustulosus*, a differential response to calls of relative frequency. — *Ethology* 106: 865–871.
- Brown, G. P. & Shine, R. 2002: Influence of weather conditions on activity of tropical snakes. — *Austral Ecol.* 27: 596–605.
- Bull, J. B. & Shine, R. 1979: Iteroparous animals that skip opportunities for reproduction. — *Am. Nat.* 114: 296–303.
- Buschmann, H. 2002: Fecundity of yellow-bellied toads *Bombina variegata* under free-range conditions: an indication of risk-spreading strategy. — *Amphibia-Reptilia* 23: 362–369.
- Chu, J. & Wilczynski, W. 2001: Social influences on androgen levels in the southern leopard frog, *Rana sphenoccephala*. — *Gen. Comp. Endocr.* 121: 66–73.
- Crump, M. L. 1974: Reproductive strategies in a tropical anuran community. — *Misc. Publ. Mus. Nat. Hist. Univ. Kansas* 61: 1–68.
- Donnelly, M. A., Crother, B. I., Guyer, C., Wake, M. H. & White, M. E. (eds.) 2005: *Ecology and evolution in the tropics: a herpetological perspective*. — The University of Chicago Press, Chicago.
- Driscoll, D. A. 1998: Counts of calling males as estimates of population size in the endangered frogs *Geocrinia alba* and *G. vittellina*. — *J. Herpetol.* 32: 475–481.
- Duellman, W. E. 1978: The biology of an equatorial herpetofauna in amazonian Ecuador. — *Misc. Publ. Mus. Nat. Hist. Univ. Kansas* 65: 1–352.
- Duellman, W. E. & Crump, M. L. 1974: Speciation in frogs of the *Hyla parviceps* group in the upper Amazon basin. — *Occas. Pap. Mus. Nat. Hist. Univ. Kansas* 23: 1–40.
- Duellman, W. E. & Trueb, L. 1994: *Biology of amphibians*. 2nd ed. — The Johns Hopkins University Press, Baltimore.
- Eggert, C. & Guyétant, R. 2003: Reproductive behaviour of spadefoot toads *Pelobates fuscus*: daily sex ratios and males' tactics, ages and physical condition. — *Can. J. Zool.* 81: 46–51.
- Elmberg, J. 1991: Ovarian cyclicity and fecundity in boreal common frogs *Rana temporaria* L. along a climatic gradient. — *Funct. Ecol.* 5: 340–350.
- Giaretta, A. A. & Menin, M. 2004: Reproduction, phenology and mortality sources of a species of *Physalaemus* (Anura: Leptodactylidae). — *J. Nat. Hist.* 38: 1711–1722.
- Gilbert, M., Leclair, R. Jr. & Fortin, R. 1994: Reproduction of the northern leopard frog *Rana pipiens* in floodplain habitat in the Richelieu River, P. Quebec, Canada. — *J. Herpetol.* 28: 465–470.
- Griffiths, R. A. 1997: Temporary ponds as amphibian habitats. — *Aquat. Conserv.* 7: 119–126.
- Halliday, T. R. & Verrell, P. A. 1988: Body size and age in amphibians and reptiles. — *J. Herpetol.* 22: 253–265.
- Hemelaar, A. 1988: Age, growth and other population characteristics of *Bufo bufo* from different latitudes and altitudes. — *J. Herpetol.* 22: 230–235.
- Jørgensen, C. B. 1988: The role of endogenous factors in seasonal maturation in temperate zone female toads, *Bufo bufo*. — *J. Herpetol.* 22: 295–300.
- Jørgensen, C. B. 1992: Growth and reproduction. — In: Feder, M. E. & Burggren, W. W. (eds.), *Environmental physiology of amphibians*: 437–466. The University of Chicago Press, Chicago.
- Kaplan, R. H. & King, E. G. 1997: Egg size is a developmentally plastic trait: evidence from long term studies in the frog *Bombina orientalis*. — *Herpetologica* 53: 149–165.
- Kuramoto, M. 1978: Correlations of quantitative parameters of fecundity in amphibians. — *Evolution* 32: 287–296.
- Kusano, T. & Hayashi, T. 2002: Female size-specific clutch parameters of two closely related stream-breeding frogs, *Rana sakuraii* and *R. tagoi tagoi*: female size-independent and size-dependent egg sizes. — *Current Herpetol.* 21: 75–86.
- Langone, J. A. 1995: *Ranas y sapos del Uruguay (Reconocimiento y aspectos biológicos)*. — Intendencia Municipal de Montevideo, Museo Dámaso Antonio Larrañaga, Montevideo.
- Lardner, B. & Loman, J. 2003: Growth of reproduction? Resource allocation by female frogs *Rana temporaria*. — *Oecologia* 44: 541–546.
- Lucas, J. R. & Howard, R. D. 1995: On alternative reproductive tactics in anurans: dynamic games with density and frequency dependence. — *Am. Nat.* 146: 365–397.
- Maneyro, R., Forni, F. & Santos, M. 1995: *Anfibios del Departamento de Rocha*. — Probidés, Editorial Hemisferio Sur, Montevideo.
- Morrison, C. & Hero, J. M. 2003: Geographic variation in life-history characteristics of amphibians: a review. — *J. Anim. Ecol.* 72: 270–279.
- Mosconi, G., Ceí, J. M., Ibañez, N., Alvarez, B. B., Carnevali, O., Battisti, A. & Polzonetti-Magni, A. M. 1996: Changes in sex plasma steroids in females of two sympatric *Lepidodactylus* from subtropical South America. — *J. Herpetol.* 30: 68–70.
- Moulton, C. A., Fleming, W. J. & Nerney, B. R. 1996: The use of PVC pipes to capture hylid frogs. — *Herpetol. Rev.* 27: 186–187.
- Núñez, D., Maneyro, R., Langone, J. & de Sá, R. O. 2004: Distribución geográfica de la fauna de anfibios del Uruguay. — *Smithsonian Herpetol. Inform. Serv.* 134: 1–36.
- Roff, D. A. 1992: *The evolution of life histories. Theory and analysis*. — Chapman and Hall, New York.
- Saltre, S. N. & Duellman, W. E. 1973: Quantitative constraints associated with reproductive mode in anurans. — In: Vial, J. L. (ed.), *Evolutionary biology of the anurans*: 229–249. University of Missouri Press, Columbia.
- Sandvik, G., Seip, K. L. & Pleym, H. 2002: An anatomy of interactions among species in a seasonal world. — *Oikos* 99: 260–271.
- Schoener, T. W. 1974: Resource partitioning in ecological communities. — *Science* 185: 27–39.
- Shine, R. 2003: Locomotor speeds of gravid lizards: placing 'costs of reproduction' within an ecological context.

- *Funct. Ecol.* 17: 526–533.
- Shirose, L. J., Bishop, C. A., Green, D. M., MacDonald, C. J., Brooks, R. J. & Helferty, N. J. 1997: Validation tests of an amphibian call count survey technique in Ontario, Canada. — *Herpetologica* 53: 312–320.
- Stearns, S. C. 1992: *The evolution of life histories*. — Oxford University Press, Oxford.
- Stebbins, R. C. & Cohen, N. W. 1995: *A natural history of amphibians*. — Princeton University Press, Princeton.
- Tárano, Z. & Herrera, E. A. 2003: Female preferences for call traits and male mating success in the neotropical frog *Physalaemus enesefae*. — *Ethology* 109: 121–134.
- Tarkhnishvili, D. N. 1993: Anurans of Borjomi Canyon: clutch parameters and guild structure. — *Alytes* 11: 140–154.
- Tejedo, M. 1992: Effects of body size and timing of reproduction on reproductive success in female natterjack toads *Bufo calamita*. — *J. Zool.* 228: 545–555.
- Tsai, P. S., Lunden, J. B. & Jones, J. T. 2003: Effects of steroid hormones on spermatogenesis and GnRH release in male leopard frogs, *Rana pipiens*. — *Gen. Comp. Endocr.* 134: 330–338.
- Tsiora, A. & Kyriakopoulou-Sklavounou, P. 2002: Female reproductive cycle of the water frog *Rana epeirotica* in northwestern Greece. — *Amphibia-Reptilia* 23: 269–280.
- Wake, M. H. 1982: Diversity within a framework of constraints: amphibian reproductive modes. — In: Mossakowski, D. & Roth, G. (eds.), *Environmental adaptation and evolution*: 87–106. Gustav Fischer, Stuttgart.
- Wells, K. D. 1977: The social behavior of anuran amphibians. — *Anim. Behav.* 25: 666–693.
- Wiest, J. A. Jr. 1982: Anuran succession at temporary ponds in a post oak-savanna region of Texas. — In: Scott, N. J. Jr. (ed.), *Herpetological communities*: 39–47. United States Department of the Interior, Fish and Wildlife Service, Washington, D.C.
- Wogel, H., Abruñhosa, P. A. & Pombal, J. P. Jr. 2002: Breeding activity of *Physalaemus signifer* (Anura, Leptodactylidae) in a temporary pond. — *Iheringia, Sér. Zool.* 92: 57–70.
- Zar, J. H. 1999: *Biostatistical analysis*, 4th ed. — Prentice Hall, Englewood Cliffs.