Reproductive Strategies of Leptodactylus chaquensis and L. podicipinus in the Pantanal, Brazil

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A great diversity of anurans occur in the American tropics (Duellman, 1988). Nevertheless, there are few detailed studies on the reproduction of these anurans and studies focusing on reproductive effort are even rarer (e.g., Lampo and Medialdea, 1996). For the Pantanal, a great flat plain with an area of approximately 140,000 km² in southwestern Brazil, there are only preliminary studies on the composition of the anuran fauna and few comments on their reproductive biology (Lutz, 1946, 1972).

Based on comparative morphology and behavior, Heyer (1969) divided the genus Leptodactylus into five species groups, where L. chaquensis Cei belongs to the 'ocellatus' group and L. podicipinus (Cope) to the 'melemanotus' group. According to the classification of Duellman and Trueb (1986), L. podicipinus and L. chaquensis have the same reproductive mode: eggs inside a foam nest on the surface of ponds with aquatic feeding larvae. Leptodactylus chaquensis occurs in Argentina, Paraguay, Uruguay, and Brazil (Frost, 1985) and L. podicipinus is found in open formations of Paraguay, Argentina, Bolivia, and central Brazil (Heyer, 1994). In spite of the wide geographical distribution of these species, information about their reproductive biology is scarce (Vizotto, 1967; Gallardo, 1987; Martins, 1996; Rossa-Feres and Jim, 1994, 1996).

Our aim was to study the reproductive strategies of L. chaquensis and L. podicipinus, which are very common in the study area. We investigated the reproductive period of each species, breeding sites, clutch and egg sizes, reproductive efforts, effects of female body size parameters on reproductive potential, and the occurrence of parental care and sexual size dimorphism.

Data were collected monthly from December 1996 to January 1998. Adults of L. chaquensis and L. podicipinus were hand-captured at night near ponds and flooded areas at Base de Estudos do Pantanal-Universidade Federal de Mato Grosso do Sul (57°00‘W; 19°34’S), in the municipal district of Corumbá, State of Mato Grosso do Sul, Brazil. The climate is hot and humid, with a dry period from May to September and a rainy season from October to April. Seasonal floodings are common in the area from January to April.

Reproductive period was determined based on calling activity of males, presence of amplexant pairs, and/or tadpoles. Breeding sites were characterized according to water depth, presence or absence of vegetation, and type of water body, which were classified as puddles, flooded areas, or permanent ponds. Occurrence of parental care was based on direct observations of the behavior of adults relative to nests and tadpoles. Snout-vent length (SVL) of adults was measured to the nearest 0.1 mm with a caliper. Individuals and their mature ovariates or testes were weighed to the nearest 0.001 g with an electronic balance (Marte-AL 500). Nests found in the field were collected and the eggs were immediately counted and individual egg diameters were measured to the nearest 0.1 mm with a micrometer, or preserved in 70% alcohol to be counted and measured later. As few spawnings were found, the number of mature ovarian eggs was used to estimate clutch size.

To analyze effects of female body size on reproductive potential, we calculated linear regressions between the following variables (Zar, 1984): female SVL and number of mature ovarian eggs, female SVL and ovary mass, female body mass and number of mature ovarian eggs, and female body mass and ovary mass. Net weight of female body was used (total body mass – ovary mass). Reproductive effort (RE) was measured as percentage of mature gonad mass relative to body mass.

Leptodactylus podicipinus reproduced throughout the year. Males called in every month, but mainly from November to March. Vocalizations and tadpoles of L. chaquensis were recorded from October to March, the rainy period in the study area. Leptodactylus podicipinus oviposited at the edges of permanent ponds and flooded areas, whether covered or cleared of vegetation, but generally in shaded areas with about 5 cm of depth, whereas L. chaquensis oviposited in puddles and flooded areas, covered or bare of vegetation, in water less than 15 cm deep.

For L. podicipinus the average (+SD) number of eggs per clutch was 2034 ± 493 (range = 1708–2960, N = 17) and in L. chaquensis, 4936 ± 1720 (range = 3007–8375, N = 32). Egg diameter was significantly larger (t = 18.8, P < 0.0001) for L. chaquensis (1.5 mm ± 0.09; range = 1.4–1.7, N = 35) than for L. podicipinus (1.1 mm ± 0.05; range = 1.0–1.2, N = 21). There were no significant differences in SVL and body mass between males and females of L. chaquensis but females of L. podicipinus were larger and heavier than males (Table 1). Reproductive effort was similar for females of both species but males of L. podicipinus invested less in tests than those of L. chaquensis (Table 2).

For L. chaquensis there was a positive relationship between female SVL and number of mature ovarian eggs (r² = 0.29, P < 0.01; N = 26) (Fig. 1a), SVL and ovary mass (r² = 0.39, P < 0.01; N = 26), body mass and number of mature ovarian eggs (r² = 0.41, P <
0.01; N = 26), and body mass and ovary mass (r² = 0.43, P < 0.01; N = 26) (Fig. 1b). For *L. podicipinus* only female body mass was positively correlated with ovary mass (r² = 0.57, P < 0.01; N = 10) (Fig. 2).

In 1996, 1997, and 1998, from October to April, single adults of *L. podicipinus* (N = 9) were observed next to tadpole schools at different times of the day. All adults were captured and dissected: ovaries of females were empty, and may have spawned recently. It is probable that females attend tadpoles up to metamorphosis because we observed schools of tadpoles with attending adults in different developmental stages. During this period we found two nests but it was not possible to detect the presence of any adult, possibly due to our disturbance.

Four females attending tadpoles behaved aggressively toward observers, raising their back and rapidly moving up and down in the water several times ("pumping" sensu Wells and Bard, 1988), jumping toward a stick held near to the tadpoles, and knocking it with their heads. After constant disturbances, females moved away or hid in vegetation. Tadpoles followed females, increased school cohesion, and decreased locomotory activity, suggesting the occurrence of parental care in *L. podicipinus*.

Single adults of *L. chaquensis* were observed in a hole in the middle of the foam nest on two occasions. In a nest observed in November 1995, the individual was a male and in the other, in January 1996, it was a female. A female attending a tadpole school was observed in January 1998 and her ovaries were also empty. This female was not aggressive and did not exhibit pumping movements. With our disturbance she moved away from the tadpoles which gradually followed her.

**Breeding Activity.**—In the seasonably dry tropics, anuran reproductive activity is closely associated with the rainy season (Duellman and Trueb, 1986; Aichinger, 1987). However, Hoogmoed and Gorzula (1979) reported that in the Venezuelan llanos, although most species reproduce in the rainy season, some did so during the dry season when there were unexpected rains. This fact and the reproduction of *L. podicipinus* throughout the year suggest that this species is opportunistic and capable of continuous reproduction when environmental conditions are favorable.

This is the first record of continuous reproduction for *L. podicipinus*. In southeastern Brazil, the species reproduces from November to March, during the rainy season (Vizotto, 1967; Rossa-Feres and Jim, 1994) and during the period of transition between dry and rainy seasons (Martins, 1996). *Leptodactylus podicipinus* was observed reproducing at the edges of permanent ponds and flooded areas in the present study. In southeastern Brazil, the species used only permanent ponds (Rossa-Feres and Jim, 1996; Martins, 1996). In Argentina, Gallardo (1987) observed *L. podicipinus* reproducing in riparian vegetation. Continuous reproduction of this species at the study site seems possible, in part, because availability of favorable habitats throughout the year, contrasting with the seasonal breeding pattern reported elsewhere (Vizotto, 1967; Rossa-Feres and Jim, 1994; Martins, 1996; Rossa-Feres and Jim, 1996).

There is little information concerning period and site of reproduction for *L. chaquensis*. Gallardo (1987) reported that peak reproductive activity in Argentina occurs in late January. As observed in the present study, the species also reproduces in the rainy season in Argentina.

Within a given reproductive mode, larger species produce more eggs (Salthe and Duellman, 1973) and in species that deposit eggs directly in the water, there is a trend of larger egg size with larger clutch size, probably related to body size (Crump, 1974). Although only two species were compared in the present study, the results demonstrate that in this reproductive mode there is a similar trend, with *L. chaquensis*, the larger species, exhibiting larger clutches and larger eggs than *L. podicipinus*.

Females of *L. podicipinus* were larger than males, but sexual size dimorphism was not found for *L. chaquensis*. According to Shine (1979), females are larger than males in 90% of anurans. A variety of factors can contribute to inter- and intraspecific variation in sexual size dimorphism (Stamps, 1995) and many studies fo-

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**TABLE 1.** Comparisons of mean snout–vent length and mean mass of males and females of *Leptodactylus chaquensis* and *L. podicipinus.*

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<th>Males</th>
<th>Females</th>
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<td></td>
<td>N Mean ± SD</td>
<td>Range</td>
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<tr>
<td><em>L. chaquensis</em></td>
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<tr>
<td>SVL (mm)</td>
<td>34 71.34 ± 5.11</td>
<td>58.2–82.8</td>
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<tr>
<td>Mass (g)</td>
<td>34 35.87 ± 8.36</td>
<td>18.43–63.05</td>
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<td><em>L. podicipinus</em></td>
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<tr>
<td>SVL (mm)</td>
<td>21 35.19 ± 1.34</td>
<td>31.6–37.0</td>
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<tr>
<td>Mass (g)</td>
<td>20 4.33 ± 0.55</td>
<td>3.20–5.32</td>
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**TABLE 2.** Mean (±SD) gonad mass and reproductive effort (RE), measured as percentage of gonad mass relative to body mass, for *Leptodactylus chaquensis* and *L. podicipinus.*

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<th><em>L. chaquensis</em></th>
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<td>N Gonad mass (g) RE</td>
<td>N Gonad mass (g) RE</td>
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<tr>
<td>Males</td>
<td>24 1.34 ± 0.48 3.89 ± 1.17</td>
<td>20 0.033 ± 0.01 0.77 ± 0.25</td>
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<tr>
<td>Females</td>
<td>26 5.87 ± 1.72 15.93 ± 2.92</td>
<td>10 1.08 ± 0.28 15.07 ± 2.6</td>
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cuss on female fecundity, in which larger females produce larger clutches or eggs (Crump, 1974; Woolbright, 1989). However, Howard (1981), studying *Rana catesbeiana*, offered other explanations for the larger size of females, such as precocious maturity of males and stronger predation pressure on larger males. More studies on ecological and reproductive aspects are necessary to explain why there is sexual size dimorphism in *L. podicipinus* but not in *L. chaquensis*.

Males of *L. podicipinus* invested less in gonads than males of *L. chaquensis*. Behavioral differences could explain this observation; *L. podicipinus* called every night during the reproductive period, whereas *L. chaquensis* called only on rainy days. Therefore *L. podicipinus* appears to expend more energy in calling activities. Females of both species invested similar proportions of energy in ovaries; gonad mass ranged from 15 to 16% of body mass. Our results are consistent with those of Crump and Kaplan (1979) who also observed that females tend to expend the same proportion of energy per clutch regardless of body size and reproductive mode.

For *L. chaquensis*, female body mass accounted for most of the variation in number of mature ovarian eggs and in ovary mass. In *L. podicipinus* there was a significant relationship only between body mass and ovary mass. For 41 anuran species in Ecuador, belonging to different families, only 26.8% showed a positive correlation between SVL and number of mature ovarian eggs. Among 23 species examined, all showed significant positive correlations between body volume and ovary volume (Crump, 1974). Mass and volume are probably more accurate measures of size in the determination of the effects of body size on reproductive potential than body length.

**Parental Care.**—Although females of *L. podicipinus* were not found attending nests at our study site, in southeastern Brazil females remain with their nests and tadpoles (Martins, 1996). Martins (1996) also observed pumping movements, and after each movement the female moved away, followed by the tadpoles. He did not observe aggressive behavior. Females of *Leptodactylus validus*, another species within the ‘melanonotus’ group, were observed attending nests and tadpoles (Downie, 1996). Females also exhibited pumping movements similar to those described for *L. podicipinus* but were not aggressive (Downie, 1996).

Among the species of the ‘ocellatus’ group, parental care on nests and tadpoles has been reported for *L. ocellatus* (Vaz-Ferreira and Gehrau, 1975) and *L. bolivianus* (Wells and Bard, 1988; Vaira, 1997). In the present study a female of *L. chaquensis* was observed attending a school of tadpoles and on two different occasions single adult frogs, a male and a female, were observed in their nests. These observations suggest parental care also in this species; it may be a common feature of the ‘ocellatus’ group.

Vaz-Ferreira and Gehrau (1975) did not observe pumping display in *L. ocellatus*, but such a behavior was observed for *L. bolivianus* and it is possible that it is a form of communication between adults and aquatic larvae (Wells and Bard, 1988). Females of *L. ocellatus* have been observed to actively protect the tadpoles by attacking a potential predator (Vaz-Ferreira and Gehrau, 1975), and Vaira (1997), simulating predator attacks, observed females of *L. bolivianus* jumping toward an object.
In our study and in a study with *L. validus* (Downie, 1996), the most important manner in which the parental care functions was not determined. Even so, Downie (1996) suggested that in *L. ocellatus* and *L. bolitarius*, both large species (SVL = 9 and 11 cm respectively), a direct protection against predators seems feasible. This could also apply to *L. chaquensis* (SVL = 7 cm). In smaller species, as *L. validus* and *L. podicipinus* (SVL = 4.5 and 3.5 cm respectively), it is more probable that females attempt to lead tadpoles to safety and, as observed by Martins (1996), also attempt to frighten small predators.

Adults attendance of tadpoles is rare in frogs, probably because most adults are terrestrial whereas tadpoles are aquatic (Wells, 1981). In leptodactylid frogs this form of parental care has been reported only in the 'melanonotus' and 'ocellatus' groups. These observations on parental care are consistent with Heyer's (1969) view that these groups are the most closely related of the five Leptodactylus groups he identified (Downie, 1996), and it is possible that attendance on nests and tadpoles also occurs in other species of the 'melanonotus' and 'ocellatus' groups.

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LITERATURE CITED


Exploitation of Avian Nestlings and Lizards by Insular Milksnakes, Lampropeltis triangulum

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Populations of animals on oceanic islands usually exhibit dietary and life-history traits that differ from those on the mainland, due to long-term isolation and differential selection pressures. Snakes on islands are often larger, show more pronounced sexual dimorphism, and have higher growth rates, enabling juveniles to reach adult size quickly (Case, 1978, 1982; Parker and Plummer, 1987; Shine, 1987; Schwaner and Sarre, 1988; King, 1989; Mori, 1994; King and Lawson, 1997). These differences in life-history attributes seem to be associated with higher food availability and absence of predators on islands (Carpenter, 1952; Campbell, 1969; Shine, 1977; Plummer, 1987).

Some species of snakes consume large numbers of birds, particularly nestlings, on islands and few or none of these on the mainland (Carpenter, 1952; Shine, 1987; Schwaner and Sarre, 1990; Kohno and Ota, 1991; Mori, 1994). For example, on Nakanokamishima Island Dinodon rufozonatua ate sooty terns (Sterna fuscata) whereas on the Japanese mainland it mostly consumed fish, lizards and toads (Kohno and Ota, 1991). On Mitlenatch Island in British Columbia, western terrestrial garter snakes (Thamnophis elegans) preyed upon nestlings of glaucous-winged gulls (Larus glaucescens) when these were available (Campbell, 1969), while on the mainland they ate fish, leeches frogs, lizards, earthworms, slugs, and salamanders (Fitch, 1941; Arnold, 1980). Similarly, avian nestlings were opportunistically consumed by tigersnakes on islands off Australia (Notechis spp; Shine, 1977, 1987; Schwaner and Sarre, 1988, 1990) and cottonmouths on an island off Florida (Agkistrodon piscivorus, Wharton, 1969), in contrast with those snakes’ usual amphibious and aquatic prey on the mainland.

Here, we describe the diet of the milksnake Lampropeltis triangulum sinaloae on a tropical Pacific island where several species of marine birds breed (Isla Isabel, Mexico), and analyze dietary variation associated with season and habitat. The feeding habits of this subspecies have not been described, but mainland populations of the species apparently prey mainly on lizards as well as small mammals and insects (Fitch and Fleet, 1970; reviewed in Williams, 1988). Surface (1906, in Williams, 1988) also reported that L. t. triangulum fed on ground-nesting birds. On Isla Isabel, milksnakes have been observed at dusk and nighttime ingesting recently hatched blue-footed booby nestlings (Sula nebouxii), either beside nest scrapes or inside them, under brooding parents (Drummond, unpublished data; Castillo and Chavez-Peón, 1983; Drummond et al., 1991). Cohen (1988) observed milksnakes visiting nests of the island’s brown boobies (S. leucogaster) containing nestlings up to 6 d old; when these boobies detected the snakes and pecked at them, the snakes sometimes withdrew. Particular nests were visited by the (same?) snake up to three times in a single night, its approaches and retreats spanning several minutes or up to two hours. One milksnake found on Isla Isabel by J. L. Osorno (pers. comm.) had black iguana eggs (Ctenosaura pectinata) in its stomach.

Isla Isabel is a small (98 ha) volcanic island, 28 km off the coast of Nayarit (map in Osorio-Beristain and Drummond, 1993). Rain falls in summer, from June to September. Seventy percent of the island is covered by tropical deciduous forest mainly composed of two tree species (Crataeva tapia and Euphorbia schlechtendalii). The remaining 30% is covered by grasses (Trichachne insularis, Cyperus ligularis, and Cenchrus viridis), or comprises disturbed zones with plants introduced by fishermen nearly 80 yr ago. Nine species of seabirds nest on the island, including five residents and four migrants, and six species of reptiles are present. The only mammals are non-native black rats (Rattus rattus) and feral cats (Felis catus), introduced by fishermen approximately 80 yr ago.

We captured snakes at six sites on five plains and one hillside, in the island’s three main habitats: forest, grassland, and disturbed zones. Forest sites included the area in the northwest of the island facing Las Mosnas sea stacks, where blue-footed boobies nest densely on the forest floor and brown boobies nest sparsely in the grass around the forest edge, and on the north end of the island near Cerro Pelón, where black iguanas are abundant. At both forest sites, numerous magnificent frigatebirds (Fregata magnificens) perch and nest in the canopy; whiptail lizards (Cnemidophorus insularis, Cyperus ligularis, and Cenchrus viridis), and cats are also common, and rats are present at low density (Torres and Osorio-Beristain, unpublished data). Grassland sites included the Central Trail and the Northwest slope of Cerro de los Pelicanos, where rats and cats are common (Torres and Osorio-Beristain, unpublished data). In the grassland, sooty terns nest in grass bunches from February to May, whiptail lizards are common in bare areas, and black iguanas seek refuge and bask around scattered rock outcrops. Disturbed zones included a banana plantation (Musa paradisiaca) in the North-central part of the island, where snakes sometimes drink from a brackish spring (pers. obs.), and a low-lying sugarcane plantation (Saccharum officinarum) near the southern end of the island, where whiptail lizards and rats are abundant.

We captured snakes during three periods in 1992: 1 March to 23 April, 15 May to 15 June, and 15 July to 15 August; only the last period fell in the rainy season.