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Ecology of *Lysapsus limellum* in the Brazilian Amazon river basin

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Lysapsus currently comprises three species distributed east of the Andes, from Guyana to northern Argentina. *Lysapsus limellum* occurs along the Amazon and Paraná river basins in ponds associated with river floodplains. We analyse geographic distribution, diet, reproduction, habitat use and diel activity of *L. limellum* from several populations in the Brazilian Amazon. Wide floodplains and open areas are common features of habitats of *L. limellum*, and populations are found either in savanna fragments or in floodplains along the Amazon river and its major tributaries. In savanna fragments of Humaitá, Amazonas, *L. limellum* is active during day and night and prefers areas with floating vegetation only. Frogs are active and prone to move during the day but remain motionless and call more at night. Most important diet items were dipterans, hemipterans/homopterans and odonates, underscoring the generalist behaviour of the species and its particular preference for dipterans. Females were significantly larger than males, but females and males were not different in shape. Neither number nor volume of eggs was related to female snout–urostyle length (SUL), while testis volume was significantly related to male SUL. In summary, *L. limellum* is a widely distributed small aquatic frog with a generalist diet that inhabits ponds in open floodplains.

Key words: Anura, diel activity, diet, geographic distribution, Hylidae, sexual dimorphism

INTRODUCTION

The genus *Lysapsus* currently comprises three species distributed east of the Andes, from Guyana and northern Brazil to northern Argentina. These small frogs, which attain snout–urostyle lengths (SUL) up to 24 mm, are commonly found in ponds in the Amazon, Paraná and Araguaia river floodplains (Garda & Cannatella, 2007). *Lysapsus laevis* is restricted to the Rupununi savanna in Guyana and Brazil (Roraima state), *L. caraya* is found along the river Araguaia in Brazil and *L. limellum* is found in the Paraná and Amazon basins in Argentina, Bolivia, Brazil and Paraguay (*L. limellum limellum* and *L. l. bolivianus sensu* Gallardo, 1961).

Lysapsus species distribution data are scattered in the literature and museum collections, and the most comprehensive listing of localities for these species was published 46 years ago (Gallardo, 1961). Garda & Cannatella (2007) outlined the distribution of Pseudae species in South America, but did not provide precise locations. Precise distributional data are necessary for conservation efforts and are currently being used to model species distributions and suggest priority areas for conservation (Tole, 2006). Niche modelling techniques can also help infer the distribution of species in remote and undersampled areas, such as the Brazilian Amazon. Records of *Lysapsus limellum* in the Brazilian Amazon suggest a wide east–west distribution associated with major rivers and savanna enclaves (Garda & Cannatella, 2007).

Despite this widespread distribution, little is known about the ecology of these species. *Lysapsus limellum* reproduces continuously throughout the year and is abundant where it occurs (Prado & Uetanabaro, 2000), preferring ponds to moving water in or near savanna enclaves in the Amazon region (Neckel-Oliveira et al., 2000). Tadpoles of *Lysapsus limellum* and *L. laevis* have been described (Caramaschi & Niemeyer, 2004; Kehr & Basso, 1990), and calls are known for *L. limellum* from the Amazon and Paraná regions (Bosch et al., 1996; Hödl, 1977). Diet data are available for two populations of *L. limellum*, the river Tapajós in Brazil (Vaz-Silva et al., 2005) and the river Paraná in Argentina (Duré & Kehr, 2001). Males of *Lysapsus* call from floating vegetation in permanent and temporary ponds, during both day and night (Hödl, 1977; Prado & Uetanabaro, 2000). Similarly, species of *Pseudis* (sister genus to *Lysapsus*) have been reported to call during the day (Brandão et al., 2003). Diel activity has not been quantitatively analysed for either genus. *Pseudis* prefers ponds with emergent vegetation (Brandão et al., 2003), while *Lysapsus* prefers areas with only floating vegetation (Hödl, 1977).

In the present paper we describe geographic distribution, diet, reproduction, habitat use and activity of *L. limellum* from populations in the Brazilian Amazon. We gathered distribution data for this species based on museum records and inferred its geographic distribution using GARP. We also investigated the diet composition of three populations in the Amazon basin and analysed one population's diel activity. Morphometric measure-

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ments were used to examine sexual dimorphism in size and shape and to investigate the relationship between size and reproductive condition in males and females.

MATERIALS AND METHODS

Specimens

Frogs used in the present study were obtained from museum collections and field trips to Humaitá, Amazonas state, and Monte Alegre, Pará state, Brazil. Frogs were hand collected, taken to the field station, and killed in less than two hours by application of orthodontic xylocaine to the abdomen. Each specimen received an individual field number and was subsequently fixed in 10% formalin and permanently stored in 70% ethanol.

Geographic distribution

We compiled geographic distribution data for *L. limellum* from six museum and university collections (Table 1). Museum acronyms used are those given in Leviton et al. (1985). Several localities lacked associated coordinates, so we combined physical maps and electronic databases available from Google Earth to infer the best approximation of geographic coordinates from the information available in museum collections.

We used niche modelling techniques to generate a map of the predicted distribution of *L. limellum.* These methods identify unsampled locations with high probability of species occurrence based on the presence of environmental variables similar to localities where the species is known to occur. We used the software DesktopGARP®. This software uses the GARP algorithm (Genetic Algorithm for Rule-set Prediction), which includes several distinct algorithms in an iterative, artificial intelligence approach based on species presence data points (Stockwell & Peters, 1999). DesktopGARP® software generates a species' predicted distribution based upon characteristics of environmental–climatic variables for localities in which the species has been previously collected. We used a total of 22 variables: 1) annual mean temperature, 2) mean diurnal range, 3) isothermality, 4) temperature seasonality, 5) maximum temperature of warmest month, 6) minimum temperature of coldest month, 7) annual temperature range, 8) mean temperature of wettest quarter, 9) mean temperature of driest quarter, 10) mean temperature of warmest quarter, 11) mean temperature of coldest quar-

Table 1. Brazilian Amazon localities of *Lysapsus limellum*, museums where vouchers are deposited and corresponding geographical coordinates.

Collection	State	County/locality	Latitude	Longitude
CHUNB	Amapá	Amapá	2°03'20.2"N	50°47"33.4"W
CHUNB	Amapá	Tartarugalzinho	1°16'01.2"N	50°48'18.3"W
MNRJ	Amazonas	Borba	4°22'43.5"S	59°35'08.7"W
CHUNB, MNRJ	Amazonas	Humaitá	7°32'47.8"S	63°04'21.8"W
MNRJ	Amazonas	Manaus, Lago Jananacá	3°07'17.2"S	60°01'.02"W
MNRJ	Amazonas	Manaus, Reserva Ducke	2°58'49"S	59°50'33.7"W
MZUSP	Amazonas	Arquipélago de Anavilhanas	2°41'22.4"S	60°45"01.5"W
MZUSP	Amazonas	Beruri	3°54'02.2"S	61°21'11.5W
MZUSP	Amazonas	Boca do Manacapurú	3°17'23.9"S	60°36'51.6"w
MZUSP	Amazonas	Boca do Purús	3°41'16"S	61°26'45.8"W
MZUSP	Amazonas	Careiro	3°44'59.2"S	60°20'00.8"W
MZUSP	Amazonas	Coari	4°05'39.7"S	63°07'51.98"W
MZUSP	Amazonas	Igarapé Belém, Rio Solimões	4°14'39.2"S	69°45'39.3"W
MZUSP	Amazonas	Itacoatiara	3°08'31.0"S	58°26'14.3"W
MZUSP	Amazonas	Lago Amanã	2°46'S	64°39'W
MZUSP	Amazonas	Nhamundá	2°‘11'12.8”S	56°42'41.4”W
MCZ	Amazonas	Paraná de Itapiranga	2º 45' 31.0" S	58º 1' 37.9"W
MHN, ZUEC	Amazonas	Rio Preto da Eva	2°46'0.00"S	59°40'60.00"W
MZUSP	Pará	Taperinha	2°31'53"S	54°17'41.5"W
MCP	Pará	Itaituba	4°16'20.2"S	55°59'09.4"W
MZUSP	Pará	Óbidos	1°55'09.3"S	55°30'49.3"W
MCZ	Pará	Oriximiná	1°46'00.78"S	55°52'31"W
MNRJ	Pará	Alter do Chão	2°31'23.2"S	54°57'32.6"W
MNRJ	Pará	Rio Paru do Leste	1°24'11.7"N	54°46'20.4"W
MNRJ	Pará	Santarém	2°25'36.6"S	54°44'49.2"W
CHUNB	Pará	Monte Alegre	2° 0'18.86"S	54° 4'25.79"W
MCP	Pará	Alenquer	1°55'57.2"S	54°44'53.3"W
MZUSP	Rondônia	Machadinho D'Oeste	8°34'02.5"S	62°27'23.5"W
MNRJ	Rondônia	Porto Velho	8°45'34.5"S	63°54'38.7"W
MNRJ	Rondônia	Near Guajará-Mirim	10°51"23.8"S	65°16'53.7"W
CHUNB	Rondônia	Costa Marques	12°27'38.4"S	64°13'50.9"W

ter, 12) annual precipitation, 13) precipitation of wettest month, 14) precipitation of driest month, 15) precipitation seasonality, 16) precipitation of wettest quarter, 17) precipitation of driest quarter, 18) precipitation of warmest quarter, 19) precipitation of coldest quarter, 20) altitude, 21) aspect and 22) terrain declivity. Variables were downloaded from the Worldclim project (Hijmans et al., 2005); details, descriptions and files for download are available free on-line at www.worldclim.org.

Diel activity and habitat use

To evaluate habitat use and diel activity, we established four 10-m long parallel transects arranged 10 m apart from each other. These transects were within a 3-ha pond along the Transamazônica highway, inside a savanna fragment near the city of Humaitá, Amazonas state (07°32'47.8"S, 063°04'21.8"W). Transects ran from the pond margin, dominated by emergent vegetation, to the pond centre, where only floating vegetation was present. To evaluate diel activity, transects were checked 12 times a day for two consecutive days (30 June 2003 and 1 July 2003) in the morning (0800–1100), afternoon (1400–1700) and evening (1800–2100). Water temperatures were measured each time transects were checked. We allowed 30 min between transect checks to minimize disturbance effects. The number of calling males (vocalizing or with inflated vocal sacs) and immobile (resting or foraging) and jumping adults and juveniles were recorded. A chi-square test was used to evaluate if the frequency of jumping frogs was significantly different between day and night.

Reproduction and sexual dimorphism

Because reproductive data were obtained by specimen dissection, only specimens collected by the authors and those from the Coleção Herpetológica da Universidade de Brasília (CHUNB) were used. These included the following Brazilian populations: Humaitá (collected August 2003, n=67), Amazonas state; Amapá and Tartarugalzinho (collected April 1997, n=5, and March 2000, n=31, respectively), Amapá state; and Monte Alegre (collected December 2002, n=62), Pará state (n_{total}=165). We sexed individuals by directly examining gonads. Males with large, developed testes and secondary sexual characters (i.e. developed vocal sac) were considered reproductive. We measured length and width of the right testis in each reproductive male. Testis volume was estimated using the formula for an ellipsoid (see diet analyses below). Females with convoluted oviducts and developed eggs were considered reproductive. We counted the number of large, pigmented eggs (types II and III *sensu* Lima et al., 2002) and measured the diameter of two eggs with digital callipers (±0.01 mm). Number and volume of eggs were regressed against SUL to check for a possible relation between female size and fertility.

We recorded the following morphometric variables for each individual: snout–urostyle length (SUL); head width (at the middle of the tympanum) and length (from the tip of the snout to the corner of the mouth); tympanum and eye diameter; eye–nostril and eye–snout distances; arm length (from the elbow to the tip of finger III) and hand length (from the junction of finger I on the hand to the tip of finger III); tibia length and foot length (from heel to the tip of toe IV). We took all measurements with digital callipers to the nearest 0.01 mm. We log-transformed (base 10) all morphometric variables prior to analyses to meet the requirements of normality (Zar, 1999). Outliers and individuals with missing data were excluded from the analyses. We included 262 individuals from three collections (CHUNB=150, MCZ=42, MNRJ=69) in the final data set.

To partition the total morphometric variation between size and shape variation, we defined body size as an isometric size variable (Rohlf & Bookstein, 1987) following the procedure described by Somers (1986). We calculated an isometric eigenvector, defined *a priori* with values equal to $p^{-0.5}$, where p is the number of variables (Jolicoeur, 1963). Next, we obtained scores from this eigenvector, hereafter called body size, by post-multiplying the $n \times p$ matrix of log-transformed data (where n is the number of observations) by the $p \times 1$ isometric eigenvector. To remove the effects of body size from the log-transformed variables, we used residuals of a regression analysis between body size and each original variable. Hereafter we refer to the resulting size-adjusted variables as shape variables. To test the null hypothesis of no difference between sexes, we conducted separate analyses on body size (ANOVA) and the shape variables (MANOVA).

Diet

We analysed stomach contents of 172 individuals deposited at CHUNB. We identified prey items in broad taxonomic categories using a stereoscopic microscope. Intact prey length and width (±0.01 mm) were recorded with electronic callipers, and prey volume (V, mm^3) was estimated using the formula for an ellipsoid:

$$V = \frac{4}{3}\pi\left(\frac{w}{2}\right)^2\left(\frac{l}{2}\right)$$

where w is prey width and l is prey length (Caldwell & Vitt, 1999). We calculated the numeric and volumetric percentages of each prey category for individual frogs and for pooled stomachs. In addition, we calculated the percentage of occurrence of each prey category (number of stomachs containing prey category i, divided by the total number of stomachs). Prey items that were too fragmented to allow a reliable estimation of their volumes were excluded.

To determine the relative contribution of each prey category, we calculated a relative importance index for individuals and pooled stomachs using the following equation:

$$I = \frac{F\% + N\% + V\%}{3},$$

where $F\%$ is the percentage of occurrence, $N\%$ is the numeric percentage and $V\%$ is the volumetric percentage (George & Hadley, 1979).

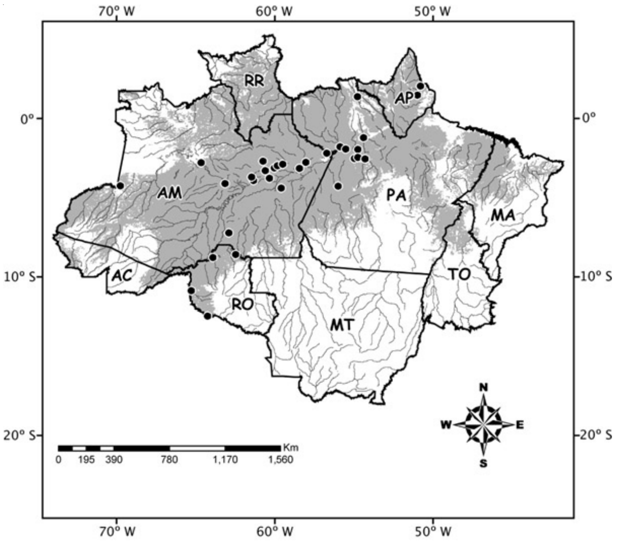

Fig. 1. Map showing the distribution of *Lysapsus limellum* in the Brazilian Amazon. Only Amazon states are depicted. Data points correspond to localities listed in Table 1. The shaded area is the predicted distribution of the species based on niche modelling. Political units of Brazil: AC – Acre, AP – Amapá, AM – Amazonas, MT – Mato Grosso, MA – Maranhão, PA – Pará, RO – Rondônia, RR – Roraima, TO – Tocantins.

Table 3. Summary statistics of morphometric measurements of *Lysapsus limellum* from the Brazilian Amazon. Values indicate mean ± SD; ranges are given in parentheses. All values are in millimetres.

Character	Males (*n*=113)	Females (*n*=148)
Body size (log transformed)	1.39±0.03 (1.31–1.44)	1.42±0.04 (1.31–1.52)
Snout–urostyle length	17.79±1.31 (14.04–20.97)	19.34±2.07 (14.54–24.10)
Head width	6.51±0.43 (5.30–7.66)	7.07±0.69 (5.19–9.34)
Head length	6.29±0.42 (5.21–7.49)	6.76±0.60 (5.27–8.92)
Tympanum diameter	1.74±0.20 (1.34–2.22)	1.77±0.22 (1.04–2.43)
Eye diameter	2.60±0.20 (2.13–3.12)	2.72±0.25 (2.05–3.38)
Eye–nostril distance	1.50±0.13 (1.11–1.83)	1.63±0.18 (1.20–2.08)
Eye–snout distance	2.53±0.2 (1.73–3.24)	2.74±0.29 (1.85–3.40)
Arm length	9.79±0.70 (7.64–11.14)	10.70±1.11 (8.07–13.28)
Hand length	6.19±0.54 (4.72– .26)	6.78±0.77 (5.08–8.88)
Tibia length	11.50±0.75 (9.81–13.04)	12.58±1.16 (9.67–15.88)
Foot length	14.98±1.18 (12.46–18.52)	16.44±1.67 (12.08–20.81)

Table 2. Diel activity patterns of *Lysapsus limellum* in Humaitá, Amazonas state, Brazil. Cells show pooled number of individuals for the two consecutive days of observations.

	Morning	Afternoon	Night	Total
Calling males	10	12	58	80
Immobile adults	43	53	68	164
Jumping adults	33	40	0	73
Immobile juveniles	38	41	68	147
Jumping juveniles	46	42	2	90
Total	170	188	196	554

RESULTS

Geographic distribution

Most of the 31 localities we obtained for *L. limellum* are along the Amazon and its major tributaries, the rivers Tapajós, Negro and Madeira (Fig. 1). Some localities are in the upper regions of smaller tributaries, such as Rio Paru do Leste. Specific locations, geographic coordinates and museum or herpetology collections where vouchers are deposited are listed in Table 1. The predicted distribution of *L. limellum* in the Brazilian Amazon is also shown in Figure 1.

Diel activity and habitat use

Of 554 individuals observed in two days, only 15 were seen in areas of the pond with emergent vegetation (Table 2). Water temperatures were stable in the morning (range 26–27.2 °C), increased during the afternoon (range 28.6–32 °C), and dropped slowly at night (26.4–28 °C). The number of jumping frogs was significantly larger during daytime ($\Pi^2_{0.05,1}=93.62$, $P<0.001$). The total number of calling males was greater at night, and individuals were less prone to move at night. The absolute number of individuals observed in each period was similar, and most animals seen in all periods were immobile (311 out of 554). Immobile and calling individuals sit on floating vegetation and only rarely submerge or dive into the water. This behaviour was usually observed when animals jumped away from the observer during daytime. One common fleeing tactic observed was to jump three or four times consecutively and then dive into the water, which usually triggered a similar behaviour in several other nearby frogs. No adults were observed to jump at night. Frogs were so prone to remain immobile at night that several times individuals would not move even if touched by the observer.

Reproduction and sexual dimorphism

Reproductive females ranged from 17.15 to 23.37 mm (20.17±1.36, *n*=50) in SUL and males from 14.68 to 20.97 mm (17.93±1.30, *n*=77). Snout–urostyle length was not significantly related to either number (*r*=0.13, *P*=0.37) or volume (*r*=0.21, *P*=0.14) of eggs found in females. Average egg diameter was 0.85±0.16 mm (*n*=50, range 0.48–1.28 mm) and average egg number was 35.78±34.67 (*n*=50, range 10–182). Average testis volume was 2.10±1.19 mm^3. Testis volume was positively correlated with SUL (*r*=0.47, *P*<0.01).

Table 4. Diet composition of *Lysapsus limellum* from the Brazilian Amazon river basin (n=91). F is the number of stomachs containing each prey item, and N is the number and V the volume of prey in each category. IIS = importance index based on individual stomachs; IPS = importance index based on pooled stomachs.

	Occurrence		Stomach means				Pooled stomachs				Importance	
Prey item	F	F%	N	N%	V(mm^3)	V%	N	N%	V	V%	IIS	IPS
Araneae	7	7.70	1.00±0.00	3.43±14.13	1.72±11.60	4.07±17.02	7	3.54	156.91	9.73	5.07	6.99
Arthropoda	7	7.70	1.00±0.00	5.68±21.69	–	–	7	3.54	–	–	–	–
Blattaria	7	7.70	1.57±0.98	4.67±18.10	0.15±0.99	2.74±14.15	11	5.56	13.68	0.85	5.04	4.70
Coleoptera	10	10.99	1.00±0.00	7.05±22.56	0.42±1.85	5.72±21.56	10	5.05	38.14	2.37	7.92	6.14
Decapoda	1	1.10	1.00±0.00	0.37±3.49	0.02±0.18	0.14±1.30	1	0.51	1.72	0.11	0.54	0.57
Diptera	42	46.14	1.64±0.96	30.93±39.02	1.24±6.56	31.14±43.08	69	34.85	112.88	7.00	36.07	29.33
Hemiptera/ Homoptera	22	24.49	2.04±1.17	16.88±33.01	1.18±5.91	12.47±29.86	45	22.73	106.91	6.63	17.95	17.95
Hymenoptera	13	14.29	1.08±0.28	6.55±19.00	0.36±1.37	6.44±19.63	14	7.07	32.84	2.04	9.09	7.80
Insect pupae	3	3.30	1.33±0.58	2.02±12.13	0.60± 3.50	2.57±14.34	4	2.02	55.02	3.41	2.63	2.91
Odonata	18	19.78	1.00±0.00	16.30±34.87	10.93±28.66	18.03±38.09	18	9.09	994.81	61.69	18.04	30.19
Orthoptera	4	4.40	1.00±0.00	3.66±18.22	1.09±6.80	3.26±17.74	4	2.02	99.33	6.16	3.77	4.19
Plant material	1	1.10	5.00±0.00	1.10±10.48	0.003±0.003	1.24±11.11	5	2.53	0.28	0.02	1.15	1.22
Syphonoptera	2	2.20	1.50±0.71	1.37±10.78	0.001±0.006	1.34±10.70	3	1.52	0.08	0.00	1.64	1.24

Morphometric measurements for males and females are given in Table 3. Females were significantly larger than males (ANOVA, $F_{1,225}$=116.59, P<0.01), but analysis of shape variables (i.e. corrected residuals) failed to identify a significant difference between sexes (Wilk's lambda=0.97, P=0.99).

Diet

Ninety-one stomachs contained prey items; 81 individuals had empty stomachs. We identified 13 prey categories taken by *Lysapsus*, of which dipterans, odonates and hemipterans/homopterans were most common (Table 4). Numerically, dipterans were most common in the diet, while odonates were more important volumetrically. The importance indices of prey categories calculated from individual and pooled stomachs were similar, with dipterans and odonates being the most important items, followed by hemipterans/homopterans.

DISCUSSION

Taxonomic considerations

Populations of *Lysapsus limellum* in the Amazon basin have been incorrectly referred to as *L. laevis* (see Garda et al. (2004) and Vaz-Silva et al. (2005) for examples). Klappenbach (1985) elevated *L. limellum caraya* and *L. l. laevis* to species and suggested that *L. l. bolivianus* should be considered a subspecies of *L. laevis*. This suggestion was based solely on geographic distribution, because both these species occur in northern South America (Amazon basin and Guiana Shield, respectively). By examining specimens included in the present work and samples of *L. laevis* from two collections (MNRJ and CHUNB, n>200), we conclude that populations from the Amazon and Paraná basins are closely related and characterized by individuals with granulated skin. In contrast, *L. laevis* has smooth skin and larger size (Gallardo, 1961). Furthermore, tadpoles of *L. laevis* are morphologically distinct (Caramaschi & Niemeyer, 2004) from tadpoles of *L. limellum* in the Paraná basin (Kehr & Basso, 1990), which are similar to Humaitá and Tartarugalzinho larvae (AAG, pers. obs.). This arrangement is concordant with a recent cytogenetic assessment of the genus *Lysapsus* (Busin et al., 2006). Based on these characters the authors concluded that *L. l. bolivianus* is closer to Paraná river basin populations than to *L. laevis*. De la Riva et al. (2000) commented on two *Lysapsus* morphs with distinct calls from the river Beni (a tributary of the Madeira) in Bolivia. Nevertheless, Brazilian populations analysed herein constitute a single morph and have similar advertisement calls (AAG, pers. obs.). Until the identity of Beni morphs is clarified, we believe all Amazon basin populations should be regarded as *L. limellum*.

Geographic distribution

Lysapsus limellum occurs in areas with two common characteristics in the Brazilian Amazon basin. Populations from Amapá, Tartarugalzinho, Humaitá, Paru do Leste, Monte Alegre, Alenquer and Alter do Chão are found near or in savanna enclaves (da Silva & Bates, 2002). Several others, such as Oriximiná, Itaituba, Borba, Boca do Manacapuru and Carareiro are found along large rivers and therefore subjected to large-scale changes in water flow that generate wide floodplains with associated ponds, ranging from perennial to extremely ephemeral. Scarce or absent canopy cover and availability of substantial water seem to be prerequisites for the occurrence of *L. limellum*.

The same habitat characteristics are used by populations of *L. limellum* in the Paraná river basin. They are distributed in regions with large floodplains, such as in northern Argentina, where the Paraguay and the

Paraná merge, the Chaco along the river Pilcomayo, and the Pantanal (Cei, 1980; Gallardo, 1961). *Lysapsus caraya* and *L. laevis* occur in regions with similar characteristics. *Lysapsus laevis* is restricted to the Rupununi savanna in Guyana and Brazil and is associated with large rivers, such as the Rio Branco in Roraima (Gallardo, 1961). The wide Araguaia river floodplain, extending along the Amazon–cerrado ecotone, is the second largest floodplain in Brazil and the habitat of *L. caraya* (Gallardo, 1964).

The predicted distribution of *L. limellum* inferred by niche modelling is consistent with the widespread range of this species in the Brazilian Amazon (see Fig. 1). The model predicts the occurrence of *L. limellum* in places where it is currently known not to occur, such as in rivers draining to the São Marcos bay region in Maranhão state (the Mearin and Pericumã rivers, for example) and savanna fragments in Roraima state. Results of such models cannot be considered unequivocally true because niche-based models cannot account for factors that may have limited species distributions historically, such as geographical barriers resulting in speciation events. In addition, some species may have specific habitat requirements, which seems to be the case for *L. limellum*. The distribution of *Lysapsus limellum* in the Amazon basin is most likely due to a recent dispersal (Garda & Cannatella, 2007), and therefore not all suitable habitats may be occupied by the species. Ecological factors such as competition may underlie the absence of this species from Roraima and regions along the river Araguaia, the current habitats of *L. laevis* and *L. caraya*, respectively. Inclusion of more localities of known occurrence will improve the inferred distribution and possibly clarify whether history and/or ecological interactions are limiting the species distribution.

Habitat use and diel activity

As previously reported, *L. limellum* prefers areas in ponds with floating vegetation that lack vertical structure (Hödl, 1977). Jumping on the water surface is the primary method of locomotion used for escaping predators, which may explain the need for open areas.

During this study, several predators were observed in or on the water, such as fishes (*Cichlas* and *Hoplias*), spiders (large Lycosidae) and insects (Belostomatidae). During our observations, one frog was preyed upon by a large water spider and another by a water bug (Belostomatidae). The difference in activity patterns between day and night may be related to the different set of predators in each period, which are known to influence species' behaviour both on a small and large time scale (Lima & Dill, 1990). Visually oriented predators (like birds) are more likely to be confused by a jumping frog; in contrast, jumping on water at night can give away the frog's position to movement-sensitive predators. Behavioural and life-history switches in response to the presence of predators have been widely studied in anuran larvae (Caldwell, 1982; Skelly, 1994; Werner, 1986). Few anurans are active during both day and night and can have their behaviour as easily quantified as *Lysapsus*, which may explain the lack of studies on diel behaviour shifts in frogs.

Diet

The diets of *L. limellum* in Itaituba, Pará state, Brazil (Vaz-Silva et al., 2005), and Corrientes, Argentina (Duré & Kehr, 2001) were dominated numerically by dipterans, as is the case in the present study. Mites were only found in Argentina, and odonates were particularly common in the present study, although they were absent in Itaituba and only found in one stomach in Argentina. Our data support previous suggestions of a generalist foraging pattern for the species (Duré & Kehr, 2001; Vaz-Silva et al., 2005).

Vaz-Silva et al. (2005) suggested a passive foraging strategy for the species in contrast to Duré and Kehr (2001), who classified it as an active forager. Dipterans, with an importance index of 29.3 for pooled stomachs in the present study and also the most important ones in the two previous assessments, are mobile and therefore typically preyed upon by sit-and-wait foragers (Huey & Pianka, 1981). Intermediate foraging modes are also possible and cannot be excluded (Toft, 1981). One unanswered question is during which period or periods individuals are foraging. Our activity data suggest that the species could be foraging during day and night. Still, most amphibians are active only in a relatively narrow range of light levels during the day and feed within an even smaller range (Jaeger & Hailman, 1981). Species with bimodal diel activity periods (such as *Dendrobates auratus*) tend be active during periods with similar light intensities (early morning and late evening) (Jaeger & Hailman, 1981). Specific experiments designed to evaluate during which period of the day *Lysapsus* forages are therefore warranted.

Sexual dimorphism and reproduction

Lysapsus lacks sexual dimorphism in shape, at least considering morphological variables measured herein. Populations of *Lysapsus* in the Brazilian Pantanal (Prado & Uetanabaro, 2000), Corrientes province in Argentina (Marangoni & Kehr, 2000) and the river Tapajós (Vaz-Silva et al., 2005) are sexually dimorphic in size, as observed in the present study. Females are larger than males, but female size is not significantly related to either number or volume of eggs. Such a relationship is expected because higher fertility is the most common explanation for females being larger than males (Woolbright, 1983). The values we obtained for number of eggs are within the ranges described for the Paraná river basin population of Corrientes (Marangoni & Kehr, 2000). Egg volume average, however, is larger than those reported for Argentine populations (Marangoni & Kehr, 2000).

The lack of a significant relationship between female size and number or volume of eggs contrasts with findings for this species in the Pantanal region (Prado & Uetanabaro, 2000). This discrepancy might be due to the fact that we analysed number of eggs in female ovaries and ovisacs, not number of eggs deposited by the female, like Prado & Uetanabaro (2000). Counting ovarian eggs as an approximation of clutch size can be misleading. Individuals from different years and months were included in our analysis. This could add the confounding effect of comparing spawns from the beginning (usually larger) and end of the reproductive season. Given the strong relationship found by Prado and Uetanabaro (2000) between female size and clutch size in *L. limellum* in the Pantanal, our results might be biased for these reasons.

CONCLUSIONS

Lysapsus limellum is widespread in the Brazilian Amazon from east to west, with most records associated with large rivers and savanna enclaves. The inferred distribution obtained through niche modelling included areas occupied by other *Lysapsus* species, regions where it is known not to occur, and in undersampled regions in the Brazilian Amazon. Because of their conspicuousness, continuous activity and high local abundance, we believe the species is ideal for future ecological and behavioural studies, especially on predation risks and flock behaviour. Other interesting questions include the function of calls emitted during daytime, and time of the day devoted to foraging.

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