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Spatio-temporal patterns of foraging and feeding behavior of *Elachistocleis bicolor* (Anura: Microhylidae)

Patrones espacio-temporales de forrajeo y comportamiento alimentario de *Elachistocleis bicolor* (Anura: Microhylidae)

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ABSTRACT

We analyzed spatio-temporal patterns and behavior of the foraging activity of the myrmecophagous frog *Elachistocleis bicolor*. We delimit ten 1m^2 plots and recorded the number of frogs, distance between individuals and foraging behavior at half-hour intervals, during nine days. Using a generalized linear mixed model, we evaluated the maximum, minimum, and average daily temperature, microhabitat temperature, relative humidity, atmospheric pressure, the number of days since the last rain and last 48 hours accumulated rainfall as explanatory variables of frogs' activity. The variables that best explained frogs' activity were: mean atmospheric pressure, number of days since last rain and accumulated rainfall. Frogs showed an aggregated distribution pattern when foraging (Morisita standardized index= 0.501). The average distance between frogs was 47.53±25.28 mm. Frogs displayed a combined (active-passive) foraging strategy, actively searching ant trails, digging with their heads on trails running under the mulch, and them passively preying on ants as they pass through. Results showed that the *E. bicolor* foraging activity followed a circadian cycle that is regulated by several climatic variables, and that these frogs aggregated when foraging for ants.

Key words. Mirmecophagy, phenology, feeding behavior, two-colored oval frog.

RESUMEN

Analizamos los patrones espacio-temporales y comportamiento de forrajeo de la rana mirmecófaga *Elachistocleis bicolor*. Delimitamos diez cuadrantes de 1 m^2 en los que registramos el número de ranas, distancia entre individuos y comportamiento a intervalos de media hora durante nueve días. Utilizando modelos lineales mixtos generalizados evaluamos el poder explicativo de las variables: temperaturas diarias máximas, mínimas y medias, temperatura de microhábitat, humedad relativa, presión atmosférica, días transcurridos desde la última lluvia y pluviosidad acumulada en las últimas 48 horas, sobre la actividad de las ranas. Las variables que mejor explicaron la actividad de las ranas fueron: presión atmosférica media, días desde la última lluvia y pluviosidad acumulada. Las ranas mostraron un patrón de distribución agregado durante el forrajeo (índice estandarizado de Morisita = 0,501). La distancia media entre ranas fue 47,53±25,28 mm. Las ranas exhibieron un comportamiento de forrajeo mixto (activo-pasivo), buscando activamente los caminos de hormigas y cavando con la cabeza en los sitios donde los caminos de hormigas discurrían bajo el mantillo, para luego depredar pasivamente sobre las hormigas que pasaban. Los resultados muestran que *E. bicolor* posee una actividad de forrajeo que sigue un ciclo circadiano regulado por varias variables climáticas y que estas ranas se agrupan durante la alimentación.

Palabras clave. Mirmecofagia, fenología, comportamiento de alimentación, sapito panza amarilla.

INTRODUCTION

Studies on amphibians' activity patterns classically refer to calling phenology, which is regulated by several abiotic and biotic environmental cues, such as climatic variables, intraspecific and interspecific social interactions, environmental physiology and reproductive behaviors (Feder and Burggren 1992, Oseen and Wassersug 2002, Saenz *et al*. 2006, Richter-Boix *et al*. 2006, Wells 2007, Canavero *et al*. 2008). Beyond reproduction, feeding is one of the activities that occupies most amphibians' time when they are not aestivating and, even though attention has been paid to some aspects of their feeding behavior, others remain poorly studied (Duellman and Trueb 1986).

There is a wide theoretical frame on feeding ecology of neotropical amphibians. Several topics have been studied such as diet composition of many anuran species, amphibians diet specializations, opportunism and ontogenetic changes, trophic plasticity, foraging modes, intraspecific trophic segregation (*e.g.* among sexes and age classes) and trophic resources partitioning among sympatric and syntopic species (Toft 1981, Maneyro and da Rosa 2004, Duré *et al.* 2009, López *et al.* 2007, 2015, Falico *et al.* 2012, Matsui 2016). But little is known about environmental variables such as microclimate, food availability, breeding season length, that regulate frogs spatio-temporal patterns of foraging (Feder and Burggren 1992, Solé and Pelz 2007, López *et al.* 2015).

Elachistocleis bicolor (Guérin-Méneville, 1838) is a small microhylid with nocturnal and fossorial habits (Zaracho *et al*. 2012). In The Middle Paraná River floodplain (Argentina), this species inhabits the vicinity of permanent and temporary lentic water bodies, with an intensive reproduction phase during the summer (Sánchez *et al*. 2009, 2013, López *et al*. 2011). Its' diet is based on termites or ants or both, depending on prey environment availability (Solé *et al.* 2002, Berazategui *et al*. 2007, Cossovich *et al*. 2011). In environments associated to The Middle Paraná River floodplain, ants comprises about 90% of their diet, being the genus *Solenopsis* (Formicidae) their most important prey item (López *et al*. 2007).

It has been suggested that some microhylids actively search for ant trails using olfaction (Duellman and Trueb 1986). Once trails are located, frogs consume these hymenopterans as they pass through the trail. In this study, we aimed to analyze spatio-temporal patterns of foraging and feeding behavior of *E. bicolor* in a temperate wetland from the floodplain valley of The Middle Paraná River, and to evaluate the influence of abiotic environmental cues on frogs' activity.

MATERIALS AND METHODS

The study was conducted on nine days between December 2010 and February 2011, in the protected area "Reserva Ecológica de la Ciudad Universitaria UNL" (RECU) located in the floodplain of The Middle

Paraná River (31°37' South, 60°41' West), near Santa Fe city, Argentina. The area (12 ha) includes a permanent lagoon, tall grass wetlands, and hydrophilous forests. Forest strip was between 10 and 40 meter wide, dominated by *Salix humboldtiana* (Willd) and *Tessaria integrifolia (*Ruiz et Pav.), accompanied with some specimens of *Albizia inundata* (Mart.), *Erythrina crista-galli* (L.) and *Acacia caven* (Mol.); shrub stratum was dominated by *Cortaderia selloana* (Schultes et Schultes Fil. Asch. et Graebner) and *Equisetum* and a rich sandy soil enriched with litter.

During December 2010 we conducted three exploratory searches to find the sites where frogs foraged and found shelter. Exploratory fieldwork was carried out between 19:00 hrs and 23:00 hrs. To analyze spatio-temporal patterns and foraging behavior, we delimited ten $1m^2$-plots on the perimeter of the lagoon, on an open space with grass (an area of ~$4,000m^2$). Plots were randomly allocated and the distances between them varied from 2−10 m. Frogs were observed foraging during 3 to 5 minutes per plot using a red light led flashlight. We recorded the number of individuals of *E. bicolor* observed per plot between 20:00 hrs and 00:30 hrs, at half an hour intervals. We estimated the distance between individuals (mm) when more than one frog was observed in one plot by carefully holding a carpentry meter a few centimeters (< 5 cm) above frogs. We analyzed the spatial distribution of frogs in the plots with standardized Morisita index (Ip) (Smith-Gill 1975). Observations were made by a single person (López J.A.) trying to keep the incidence of observer as low as possible.

We used a generalized linear mixed model (GLMM), binomial error distribution and logit link, to assess the relationship between the presence and absence of *Elachistocleis bicolor* in the plots with climate variables. In the statistical analysis, plots were included as a random factor to account for repeated observations in each one (Zuur *et al.* 2009). Candidate explanatory variables were temperature of air in microhabitat (°C), obtained within the plots during each sampling time with a mercury glass thermometer placed five centimeters above ground level, and five climatic variables obtained from the weather station of the Centro de Informaciones Meteorológicas (CIM: FICH-UNL), located 200 m away from the study area: mean temperature (°C), relative humidity (HR%), atmospheric pressure recorded along the day (hPa), number of days since the last rain and accumulated rainfall (mm) in the past 48 hours. We used variance inflation factor (VIF) to assess multicollinearity among variables included in the models (Quinn and Keough 2002). VIF showed a high collinearity between temperature of microhabitat and mean temperature obtained in the weather station; thus, only the latter was maintained in the model. We used stepwise variable selection by backward elimination to build the model (Quinn and Keough 2002). We tested for individual effects by the likelihood ratio test for nested models; this statistic follows a X^2 distribution with one degree freedom (Zuur *et al.* 2009). GLMM analysis was performed through lme4 package (Bates *et al.* c2015) in R software (R Core Team c2015).

RESULTS

During exploratory searches, we observed frogs feeding after sunset in an area of low herbaceous vegetation alongside the fluvial forest that borders the south margin of a permanent lagoon of the RECU. This area was the selected one to place the $1m^2$-plots. A few specimens were found sheltered under fallen logs in the fluvial forest and no frog was found out of their refuge before sunset.

Between checking periods of the plots we observed frogs in the surroundings. Specimens of *E. bicolor* were found hunting for ants on their trails. Frogs were observed digging with their heads and introducing it under leaf litter right where the ant trails run as shallow tunnels under the mulch, remaining in this position for at least 5 min (Fig. 1).

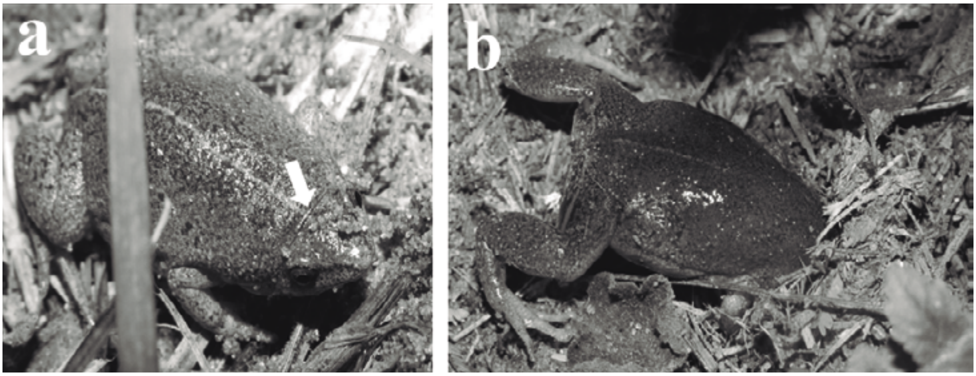

Figure 1. Frogs during foraging activity: **a.** frog digging with its head, arrow indicates nuchal fold, **b.** frog submerging its head under leaf litter right where ant trails run under the mulch.

In eight out of the nine sampled days frogs were recorded in plots. One of the days we recorded only one frog in plots. In the remaining seven days we recorded from five to 43 frogs foraging in the ten plots, showing a density of 0.4±0.8 frogs/m^2. In those seven days, between 21:00 hrs and 22:30 hrs, the time of the day with the highest activity, frogs' density reached 0.57±0.93 frogs/m^2. The maximum density recorded was 1.1 frogs/m^2, on 26th January at 21:30 hrs. The average distance between frogs within the plots was 47.53±25.28 mm; while the minimum distance was 15mm. An aggregated distribution pattern was observed (Ip = 0.501).

The daily activity of frogs showed a hump-shaped pattern (Fig. 2), finding higher frequencies between 21:00-22:00 hours. The activity of frogs varied among days (GLMM: x^2 = 53.38; p<0.001). Occurrence of *Elachistocleis bicolor* in the plots was higher in days with higher mean atmospheric pressure (GLMM: x^2 = 4.21; p = 0.04) and around two or three days after last rain (GLMM: x^2 = 15.62; p<0.001), while it was intermediate when there was accumulated rainfall in the last 48 hours (GLMM: x^2 = 13.24; p<0.001) (Fig. 3). Mean humidity and mean temperature did not account for *E. bicolor* occurrence on different days (GLMM: x^2 = 3.5; p>0.05, and x^2 = 2.01; p>0.05, respectively).

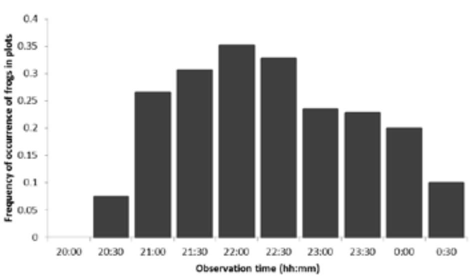

Figure 2. Foraging circadian cycle of *Elachistocleis bicolor*. Daily changes every half hour in frogs' frequency of occurrence in plots.

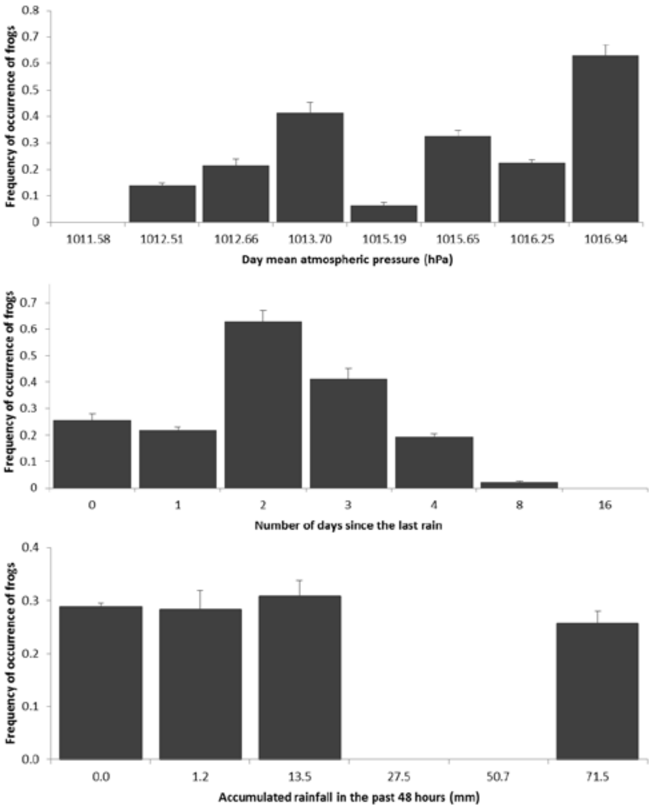

Figure 3. Frequency of occurrence of *Elachistocleis bicolor* frogs registered in relation to atmospheric pressure (hPa), days since the last rain and with accumulated rainfall in the past 48 hours (mm).

DISCUSSION

Until now, knowledge of *Elachistocleis bicolor* phenology was limited to its reproduction, which occurs explosively after heavy rains during spring and summer and that has also been related to variables such as temperature and humidity (Rodrigues *et al.* 2003, Martori *et al*. 2005, López *et al*. 2011, Sanchez *et al*. 2009, 2013). We found that foraging activity of *E. bicolor* was regulated by climatic variables such as atmospheric pressure, days since last rain and recently accumulated rainfall. Low barometric pressure has been associated with increase in calling activity in some amphibians (Henzi *et al*. 1995, Oseen and Wassersug 2002); however, in *E. bicolor* foraging activity increases with higher barometric pressure; thus, the rise of atmospheric pressure after rainfalls may be triggering foraging activity. Calling activity of some amphibians from temperate climates is positively correlated to one and two day's prior rainfall (Saenz *et al*. 2006), indicating a similar relation to the one found here for *E. bicolor*, which peaks occurred the second or third day after rains. Also, there is evidence that explosive breeders practically do not feed during reproduction (Solé and Pelz 2007). One possible explanation of the delay between precipitation and foraging peak is that frogs reproduce during the first days after rain, and then, they need to feed extensively to recover the energy spent (Feder and Burggren 1992).

We also considered humidity and air temperature as candidate explanatory variables, but both failed to explain foraging activity of *E. bicolor*. Humidity mediates reproductive activity in several amphibian species (Oseen and Wassersug 2002, Richter-Boix *et al.* 2006), and air temperature has been associated to activity of other species of genus *Elachistocleis* and is classically related to amphibian activity in temperate environments (Oseen and Wassersug 2002, Saenz *et al.* 2006, Richter-Boix *et al.* 2006, Canavero *et al.* 2008). Therefore, reproduction and foraging activities are regulated by different climatic variables. Indeed, we observed the presence of moisture at ground level on the days associated with frogs' foraging activity, and this variable should be tested on future studies (Dodd 2009).

Most anurans have adopted a sit-and-wait strategy for preys' location, leading to a generalist diet (Duellman and Trueb 1986). However, *Elachistocleis bicolor* is a specialist forager (Berazategui *et al.* 2007, López *et al.* 2007, Cossovich *et al.* 2011), displaying a combined active-passive foraging strategy (Donnelly 1991, Maneyro and da Rosa 2004). The combined foraging strategy of *E. bicolor* consists of an 'active' searching of ant trails, which sometimes includes digging right where ant trails ran as shallow tunnels under the mulch (active foraging strategy), and then, the 'passive' predation of ants as they pass through following a sit-and-wait foraging strategy. It has been mentioned that the nuchal fold of *E. bicolor* serves as protection against ant bites, since it can be extended forward to cover the eyes when frogs are hunting, while the skin secretes a viscous substance (Langone 1994) (Fig. 1). We did not observe this behavior.

Elachistocleis bicolor preference for small, hard prey like ants or mites (Solé *et al.* 2002, Berazategui *et al.* 2007, López *et al.* 2007, Cossovich *et al.* 2011), coincides with the feeding preference of other specialist anurans (Toft 1981, Lajmanovich 1995, Duré *et al.* 2009). Along its distribution area, *E. bicolor* is sympatric with diurnal and nocturnal mirmecophagous anurans (*e.g.* Bonansea and Vaira 2007, Duré *et al.* 2009, Da Rosa *et al.* 2002, Bortolini *et al.* 2013). An spatio-temporal segregation in foraging activity may reduce food competition with other ant predators. Day time activity could contribute to trophic segregation with sympatric diurnal toads of genus *Melanophryniscus* (Bonansea and Vaira 2007, Bortolini *et al.* 2013). While microhabitat segregation could diminish trophic niche overlap with sympatric nocturnal toads of genus *Rhinella* (Duré and Kher 2004, Duré *et al.* 2009, Matsui 2016). In this study area, *E. bicolor* is syntopic with *Rhinella fernanadezae* (Gallardo, 1957), which also specializes in ant predation in open terrestrial habitats (Duré *et al.* 2009); but we did not observe *E. bicolor* overlapping foraging microhabitats with *R. fernanadezae* in the RECU. Indeed, seasonal activity of *R. fernanadezae* concentrates in spring, while *E. bicolor* activity concentrates in summer (López *et al.* 2011); thus, temporal, or seasonal segregation should be favoring coexistence of these species.

Species of the genus *Elachistocleis* are usually associated with open environments (Lavilla *et al.* 2003, Rodrigues *et al.* 2003). And, although *E. bicolor* foraging habitat was an open area of low herbaceous vegetation, the few frogs that found shelter were found in the adjacent fluvial forest besides the RECU lagoon (*E. bicolor* refugees in fossae or under fallen logs: Maneyro and Carreira 2012). Therefore, studied frogs should have move after sunset from their day shelters in the fluvial forest (forest strip of 10 to 40 m wide) to contiguous foraging sites. In the foraging area, where observation plots were delimited, *E. bicolor* displayed an aggregate distribution. This pattern probably reflected the patchy distribution of ants (Theunis *et al*. 2005, Andersen 2008), their principal food resource (Berazategui *et al.* 2007, López *et al*. 2007).

Foraging activity of *Elachistocleis bicolor* is nocturnal, with a peak activity around 22:00 hours. The highest foraging activity of the frogs coincided with the times of the day where ant workers of the genus *Solenopsis* explore the environment searching for food (Claborn and Phillips 1986, Norasmah *et al*. 2006), suggesting synchronization with the activity of their prey. Studies on diet of *E. bicolor* showed an average of about thirty ants per digestive tract (Berazategui *et al*. 2007, López *et al*. 2007). With the high densities that *E. bicolor* can reach while foraging (more than one frog/m^2), this species should be considered an important ant predator. Taking into account that is a frequent species in agroecosystems (Sánchez *et al*. 2013), its role as biological control organism should be investigated.

Finally, when analyzing the role of abiotic environmental cues in amphibian activity, we should consider not only interspecific differences, but also differences among activity types within each species (*e.g.* reproduction or feeding). Since the same variable could relate in opposite directions to calling or foraging activity such is the case of atmospheric pressure. Also, variables classically related to reproductive activity not necessary explain foraging activity (*e.g.* temperature or humidity). Additionally, biological variables such as prey availability certainly are likewise influencing *E. bicolor* foraging activity (Falico *et al*. 2012, López *et al*. 2015). Moreover, environmental conditions could directly influence prey activity and then be indirectly correlated to frogs foraging activity (Donnelly 1991). Fully understanding of foraging activity implies the knowledge of a diversity of factors such as spatio-temporal patterns of activity, predator diet, prey-predator relationships and trophic niche segregation among predators, feeding strategy and related behaviors. And many of these issues are still unknown for most of amphibian species.

AUTHORS PARTICIPATION

JAL, RG and CEA conception and design; JAL, RG, CEA and RL exploratory field work; JAL field data collection; JAL, CEA and RL data analysis; JAL, RG, CEA and RL manuscript writing.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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LITERATURE CITED

Andersen AN. 2008. Not enough niches: non-equilibrial processes promoting species coexistence in diverse ant communities. Austral. Ecol. 33(2):211–220. doi: 10.1111/j.1442-9993.2007.01810.x.

Bates D, Maechler M, Bolker B, Walker S. c2015. lme4: Linear Mixed-Effects Models

Using Eigen and S4. R package version 1.1-8. [last accessed: 12 Jun 2017]. http://CRAN.R-project.org/package=lme4.

Berazategui M, Camargo A, Maneyro R. 2007. Environmental and seasonal variation in the diet of *Elachistocleis bicolor* (Guérin-Méneville**,** 1838) (Anura: Microhylidae) from Northern Uruguay. Zool. Sci. 24(3):225–231. doi:10.2108/zsj.24.225.

Bonansea MI, Vaira M. 2007. Geographic Variation of the Diet of *Melanophryniscus rubriventris* (Anura: Bufonidae) in Northwestern Argentina. J. Hepatol. 41(2):231–236. doi: 10.1670/0022-1511(2007)41[231:GVOTDO]2.0.CO;2

Bortolini SV, Maneyro R, Coppes FA, Zanella N. 2013. Diet of *Melanophryniscus devincenzii* (Anura: Bufonidae) from parque Municipal de Sertão, Rio Grande do Sul, Brazil. Herpetol. J. 23:115–119.

Canavero A, Arim M, Naya DE, Camargo A, Da Rosa I, Maneyro R. 2008. Calling activity patterns in an anuran assemblage: the role of seasonal trends and weather determinants. North-West J. Zool. 4:29–41.

Claborn DM, Phillips SA Jr. 1986. Temporal Foraging Activities of *Solenopsis invicta* (Hymenoptera: Formicidae) and Other Predominant Ants of Central Texas. Southwest. Nat. 31(4):555–557. doi: 10.2307/3671722.

Cossovich S, Aun L, Martori R. 2011. Análisis trófico de la herpetofauna de la localidad de Alto Alegre (Depto. Unión, Córdoba, Argentina). Cuad. Herpetol. 25(1):11–19.

Da Rosa I, Canavero A, Maneyro R, Naya DE, Camargo A. 2002. Diet of four sympatric anuran species in a temperate environment. Bol. Soc. Zool. Uruguay 13:12–20.

Dodd CK Jr, editor. 2009. Amphibian Ecology and Conservation. A Handbook of Techniques. Oxford: Oxford University Press.

Donnelly MA. 1991. Feeding patterns of the strawberry poison frog, *Dendrobates pumilio* (Anura: Dendrobatidae). Copeia 1991(3):723–730. doi: 10.2307/1446399.

Duellman WE, Trueb L. 1986. Biology of Amphibians. New York: McGraw-Hill.

Duré MI, Kehr AI. 2004. Influence of microhabitat on the trophic ecology of two leptodactylids from northeastern Argentina. Herpetologica 60(3):295–303. doi:10.1655/03-51.

Duré MI, Kehr AI, Schaefer EF. 2009. Niche overlap and resource partitioning among five sympatric bufonids (Anura, Bufonidae) from northeastern Argentina. Phyllomedusa 8(1):27–39. doi: 10.11606/issn.2316-9079.v8i1p27-39.

Falico DA, López JA, Antoniazzi CE, Beltzer AH. 2012. Variación interpoblacional y ontogenética de la dieta de rana llorona *Physalaemus albonotatus* (Anura: Leiuperidae). Rev. Mex. Biodiv. 83(4):1187–1193. doi: 10.7550/rmb.28122.

Feder ME, Burggren WW. 1992. Environmental physiology of the amphibians. Chicago, Illinois: The University of Chicago Press.

Henzi SP, Dyson ML, Piper SE, Passmore NE, Bishop P.1995. Chorus attendance by male and female painted reed frogs (*Hyperolius marmoratus*): environmental factors and selection pressures. Funct. Ecol. 9(3):485–491. doi: 10.2307/2390013

Lajmanovich R. 1995. Relaciones tróficas de bufónidos (Anura, Bufonidae) en ambientes del Río Paraná, Argentina. Alytes 13(3): 87–103.

Langone JA.1994. Ranas y sapos del Uruguay: Reconocimiento y aspectos biológicos. Museo Dámaso Antonio Larrañaga. Serie de Divulgación 5:1–123.

Lavilla EO, Vaira M, Ferrari L. 2003. A new species of *Elachistocleis* (Anura: Microhylidae) from the Andean Yungas of Argentina, with comments on the *Elachistocleis ovalis*-*E. bicolor* controversy. Amphibia-Reptilia 24(3):269–284. doi: 10.1163/156853803322440754.

López JA, Ghirardi R, Scarabotti PA, Medrano MC. 2007. Feeding ecology of *Elachistocleis bicolor* (Anura, Microhylidae) in a riparian locality of Middle Paraná River. Herpetol. J. 17:48–53.

López JA, Scarabotti PA, Ghirardi R. 2011. Seasonal patterns of abundance and recruitment in an amphibian assemblage from the Middle Paraná River floodplain. Interciencia 36(7):538–544. doi: 0378-1844/11/07/538-07.

López JA, Scarabotti PA, Ghirardi R. 2015. Amphibian trophic ecology in increasingly human-altered wetlands. Herpetol. Conserv. Biol. 10(3):819–832.

Maneyro R, Da Rosa I. 2004. Temporal and spatial changes in the diet of *Hyla pulchella* (Anura, Hylidae) in southern Uruguay. Phyllomedusa 3:101–113. doi: 10.11606/issn.2316-9079.v3i2p101-103.

Maneyro R, Carreira S. 2012. Guía de anfibios del Uruguay. Montevideo: Ediciones de la Fuga.

Martori R, Aún L, Birri A, Rozzi Giménez C, Heredia E. 2005. Reproducción comparada de tres especies de anuros sintópicos de una localidad del sudeste de Córdoba. Cuad. Herpetol. 18(2):43–59.

Matsui M. 2016. Food partitioning in three syntopic frogs in a bornean plantation. Current Herpetology 35(2):83–92. doi: 10.5358/hsj.35.83.

Norasmah B, Abu Hassan A, Che Salmah MR, Nurita AT, Nur Aida H. 2006. Daily foraging pattern and proteinaceous food preferences of *Solenopsis geminata* (Fabricius) (Hymenoptera: Formicidae). Trop. Biomed. 23:134–139.

Oseen KL, Wassersug RJ. 2002. Environmental factors influencing calling in sympatric anurans. Oecologia 133:616–625. doi: 10.1007/s00442-002-1067-5.

Quinn GP, Keough MJ. 2002. Experimental design and data analysis for biologists. New York: Cambridge University Press.

R Core Team. c2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. [last accessed: 12 Jun 2017]. URL http://www.R-project.org/

Richter-Boix A, Llorente GA, Montori A. 2006. Breeding phenology of an amphibian community in a Mediterranean area. Amphibia-Reptilia 27(4):549–559. doi: 10.1163/156853806778877149.

Rodrigues DJ, Lopes FS, Uetanabaro M. 2003. Padrão reprodutivo de *Elachistocleis bicolor* (Anura, Microhylidae) na Serra da Bodoquena, Mato Grosso do Sul, Brasil. Iheringia Sér. Zool. 93(4):365–371.

Saenz D, Fitzgerald LA, Baum KA, Conner RN. 2006. Abiotic correlates of anuran calling phenology: the importance of rain, temperature, and season. Herpetol. Monogr. 20(1):64–82. doi: 10.1655/0733-1347(2007)20[64:ACOACP]2.0.CO;2.

Sanchez LC, Peltzer PM, Lajmanovich RC. 2009. Structure of wetland-breeding anuran assemblages from the southern section of the Paraná River, Argentina. Herpetol. J. 19:173–184.

Sanchez LC, Peltzer PM, Lajmanovich RC, Manzano AS, Junges CM, Attademo AM. 2013. Reproductive activity of anurans in a dominant agricultural landscape from central-eastern Argentina. Rev. Mex. Biodivers. 84(3):912–926. doi: 10.7550/rmb.32842.

Smith-Gill SJ. 1975. Cytophysiological basis of disruptive pigmentary patterns in leopard frog *Rana pipens*. II. Wild type and mutant cell specific patterns. J. Morphol. 146(1):35–54. doi: 10.1002/jmor.1051460103.

Solé M, Pelz B. 2007. Do male tree frogs feed during the breeding season? Stomach flushing of five syntopichylid species in Rio Grande do Sul, Brazil. J. Nat. Hist. 41(41–44):2757–2763. doi: 10.1080/00222930701661282.

Solé M, Ketterl J, Di-Bernardo M, Kwet A. 2002. Ants and termites are the diet of the microhylid frog *Elachistocleis ovalis* (Schneider, 1799) at an Araucaria forest in Rio Grande do Sul, Brazil. Herpetol. Bull.79:14–17.

Theunis L, Gilbert M, Roisin Y, Leponce M. 2005. Spatial structure of litter-dwelling ant distribution in a subtropical dry forest. Insect. Soc. 52(4):366–377. doi: 10.1007/s00040-005-0822-0.

Toft CA. 1981. Feeding ecology of Panamanian litter anurans: patterns in diet and foraging mode. J. Herpetol. 15(2):139–144. doi: 10.2307/1563372.

Wells KD. 2007. The ecology and behavior of amphibians. United States of America: University of Chicago Press.

Zaracho VH, Céspedez JA, Álvarez BB, Lavilla EO. 2012. Guía de campo para la identificación de los anfibios de la Provincia de Corrientes, Argentina. Primera Edición, Tucumán: Fundación Miguel Lillo.

Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM. 2009. Mixed Effects Models and Extensions in Ecology with R. Statistics for Biology and Health. New York: Springer Science+Business Media, LLC.

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