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Diet and sexual dimorphism of *Leptodactylus labyrinthicus* (Anura, Leptodactylidae) in a Cerrado area in Central Brazil

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Abstract. The genus *Leptodactylus* (Leptodactylidae) includes 74 species, distributed from southern North America to southern South America, and the West Indies. The species *Leptodactylus labyrinthicus* is popularly known as the pepper frog because it produces toxic substances, which causes irritation. The aims of this study were to (i) evaluate the composition and level of importance of the prey for this species; (ii) test the hypothesis that states organisms with wider jaws eat larger prey; (iii) investigate the effect of sex and ontogeny on diet; and, finally, (iv) test morphometric sexual dimorphism. We collected 43 individuals (13 males, 17 females, and 13 juveniles) from the Sóter Ecological Park, located in the city of Campo Grande, Mato Grosso do Sul. We identified 148 prey items distributed in 13 orders, with Coleoptera and Spirostreptida being the main food categories of this frog species. We also noticed variations between the diet of males and females and adults and juveniles of *L. labyrinthicus*. In addition, we report no relationship between the jaw widths of *L. labyrinthicus* with prey size. We registered sexual dimorphism in body size for the study population. In conclusion, our study reports natural history traits of the pepper frog; however, we point out the need to assess morphological and dietary singularities between sexes and along the ontogeny. Furthermore, it is also necessary to consider the inter-populational variations, especially in cases of widely distributed species.

Key words: Amphibia, autecology, natural history, urban park.

Natural history involves the study of ecological aspects of organisms, including spatial/temporal distribution, diet, and reproductive recruitment (Greene 1994). This research field is fundamental to several areas of biological sciences, such as ecology, evolutionary biology, and conservation (Greene & Losos 1988, Hillis 1995).

The genus *Leptodactylus* currently comprises 74 species and occurs from southern North America to southern South America and West Indies (Frost 2017). Within the genus, there are four species groups recognized: *L. fuscus, L. latrans, L. melanonotus* and *L. pentadactylus* (De Sá et al. 2014). The species *L. labyrinthicus* (Spix, 1824), also recognized as the pepper frog, belongs to the *L. pentadactylus* group which is distributed in the open formations of Argentina (in Misiones and Corrientes provinces), Brazil (including the Cerrado and Atlantic Forest) and Paraguay (De Sá et al. 2014). *Leptodactylus labyrinthicus* is territorial, large-sized, and breeds in foam nests deposited in basins excavated by males, usually in stream margins (Zina & Haddad 2005).

The reproductive mode, territoriality, and habitat use are aspects of *L. labyrinthicus*' natural history that were widely explored (França et al. 2004, Shepard & Caldwell 2005, Silva et al. 2005, Toledo et al. 2005, Tozetti & Toledo 2005, Zina & Haddad 2005, Silva & Giaretta 2008, 2009, Costa et al. 2015). Nevertheless, little is known about the diet of the species, especially about the partition of food resources between males and females, or between young and adults. This highlights the need of basic knowledge about this species natural history and the importance of this kind of information (Greene 1994, Shepard & Caldwell 2005, Silvano & Segalla 2005, Verdade et al. 2012, De Sá et al. 2014). The aims of the present study were to investigate the aspects of natural history of *L. labyrinthicus* in an urban park in the Campo Grande municipality, Mato Grosso do Sul State, Brazil. Specifically, we sought (i) to analyse the composition and level of importance of prey consumed by this species; (ii) to test the hypothesis that individuals with wider heads prefer larger prey; (iii) to investigate the effects of ontogeny (young versus adults) and sex on diet; and (iv) to test if there is morphometric sexual dimorphism in body size in the studied population.

Study area. We conducted the field work in the Sóter Ecological Park (20°25'45.52"S, 54°34'37.88"W) in the urban perimeter of Campo Grande, Mato Grosso do Sul State, Brazil. The climate is humid temperate, with higher temperature average in the summer (Cfa; Kottek et al. 2006). The Sóter stream crosses the park and the vegetation of its margins is formed by gallery forest, although grass and other introduced plants are present in some stretches of the watercourse (Fig. 1).

Samplings. We performed field excursions during May and June 2015 to carry out nocturnal visual encounter surveys (Heyer et al. 2014) between 19:00h and 22:00h, covering a 480-meter transect parallel to the stream. For each captured individual, we identified the sex through visualization of gonads, the developmental stage (e.g. adult, if reproductively active; or juvenile, if it was impossible to determine the sex) and the environment where the animal was registered (open vegetation, if tree canopies from opposite sides of the stream did not touch; semi-open vegetation, if only some tree canopies touched each other across the watercourse; and closed vegetation, if the stream was completely covered by the treetops). Besides that, we also registered the type of substrate occupied in the moment of capture (sandbanks, into the water, shrubs, and in cement structures of an existing bridge present in the area).

We put the collected frogs into cloth bags individually, which were later taken to the laboratory. We then euthanized the animals with 2% lidocaine overdose, fixed them in 10% formalin, and conserved them in 70% alcohol solution. The collected specimens were housed in the Zoological Collection of Reference of Federal University of Mato Grosso do Sul (ZUFMS). Collection license was provided by Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio 49080-1). For each individual, we took 11 morphometric measurements according to Heyer (1979) and Marcus (1990): snout-vent length (SVL), head width (HW), head length (HL), interorbital distance (IOD), eye-nose distance (END), thigh length (THL); tibia length (TIL), foot length (FOL), arm length (AL), forearm length

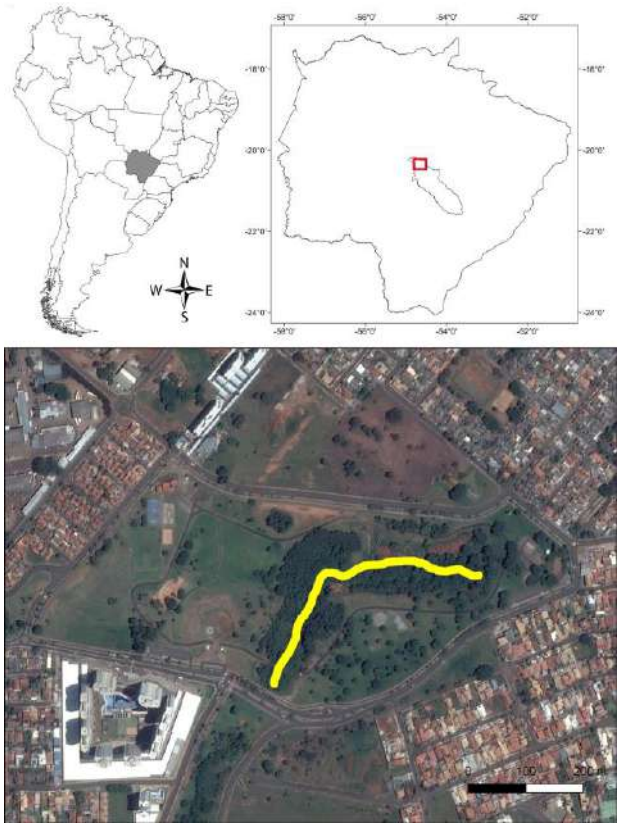

Figure 1. Map showing the sampled area (Sóter Ecological Park (20°25'45.52"S, 54°34'37.88"W) in the urban perimeter of Campo Grande / MS, Brazil. The yellow line represents the Sóter stream where we collected the individuals.

(FAL), and hand length (HL).

To evaluate the diet, in each specimen we removed the stomachs through a small abdominal incision and extracted its contents, which were preserved in individual flasks with 70% alcohol solution. Then we identified the prey with a stereoscope microscope to the order level and measured the length and width of the prey with a digital caliper (0.01mm precision). If the prey was at an advanced stage of decomposition, we considered it as unidentifiable.

Data analysis. For each stomach, we counted and measured the length (l) and width (w) of each prey to gauge the total volume of stomach content, using the ellipsoid formula proposed by Griffiths & Mylotte (1987):

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

To determine the importance of each prey category of *L. labyrinthicus*' diet, we calculated the relative importance index (Ix), by using the mean of the percentage of occurrence (F%), the numerical percentage (N%), and the volumetric percentage (V%), according to the Pinkas et al. equation (1971): Ix = F%(N%+V%). To test if individuals with wider heads ingested larger prey, we performed a simple linear regression, considering the prey with highest volume in each stomach. To test sexual dimorphism in size, we conducted a principal component analysis (PCA) and took the first two principal components of the ordination to create a MANOVA. We performed all analysis in R software (R Core Team 2014) using the package Vegan (Oksanen 2007).

We captured 43 specimens of *L. labyrinthicus* (13 males, 17 females, and 13 juveniles). Both the PCA analysis (Fig. 2) and MANOVA (F = 3.54; p = 0.03) revealed size sexual dimorphism (males: SVL = 128.20 mm, SD: 15.64; females: SVL = 107.26 mm, SD: 16.28) in this population of *L. labyrinthicus*.

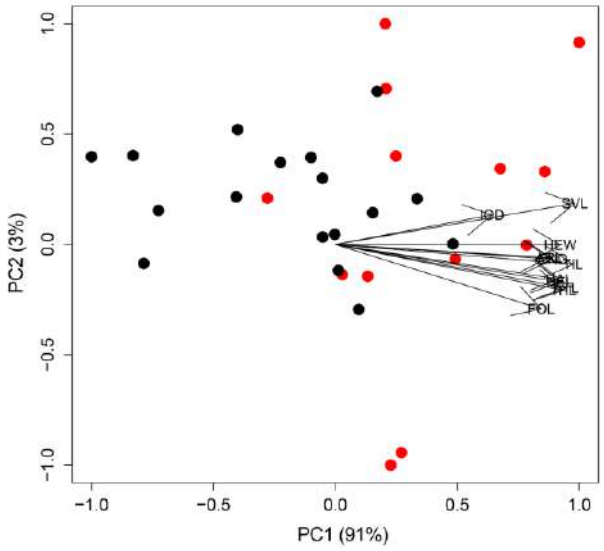

Figure 2. Principal components analysis to evaluate the morphometric sexual dimorphism in *Leptodactylus labyrinthicus* population sampled in Ecological Park Sóter, Campo Grande / MS, Brazil. Black dots indicate females and red dots indicate males. Arrows indicate the contribution in ordination of the each morphological variables: SVL – Snout-vent length; HEW – Head width; HEL – Head length; IOD – Inter-orbital distance; END – Eye-nostril distance; THL – Thigh length; TIL – Tibia length; FTL – Foot length; HAL – Hand length; ARL – Arm length; FOL – Forearm length.

Regarding diet, 11 stomachs (25.5%) were empty and 32 had some prey (74.5%). In total, we recorded 148 items, divided into 13 prey categories (Table 1). Coleoptera was the most frequent category occurring in 21% of stomachs and corresponding to 22.3% of the total volume of ingested prey, followed by Spirostreptida, with 19.7% of the records and 17.8% of the prey volume in the stomachs. We could not identify 3.38% of prey due to advanced stage of decomposition (Table 1). Among males, Coleoptera was the most frequent category (48.7%), with the highest importance index (Ix = 38.5) (Table 2). Regarding the females, Spirostreptida was the most recorded category (25.3%), and most important (Ix = 18.1) (Table 2). Prey items from the categories Ixodida, Odonata, and Scolendromorpha were registered exclusively in stomachs of females. We also observed that among adults, Spirostreptida was the most frequent category (24.53%) with the highest importance index (Ix = 21.57) (Table 2). However, in the juveniles the most frequent (31.82%) and more important category (Ix = 31.59) was Coleoptera (Table 3). Diptera and Scorpiones were observed only in juveniles. We did not find significant relation between head width and volume of larger prey consumed ($r^2 = 0.376$; p = 0.7).

Sexual dimorphism in amphibians is usually associated with males' territorial behavior (Shine 1979, Magalhães et al. 2016). According to Shine (1979), larger males would have the greatest advantage in an eventual corporal combat to defend their territories (e.g. breeding or feeding sites), thus being positively selected by females. Despite being territorial, which is a known behavior for *L. labyrinthicus*, previous studies did not report sexual dimorphism (Silva et al. 2005, Zina & Haddad 2005). However, our study reports a mor-

Table 1. Food items found as stomach contents of *Leptodactylus labyrinthicus* (n= 148) in Ecological Park Sóter, Campo Grande / MS, Brazil. Number (N), volume (V mm³), frequency (F) (percentage in parentheses) and the relative importance (Ix) of each item.

Item	N (%)	F (%)	V mm³ (%)	Ix
Aranae	5 (3.38)	3 (3.95)	13708.72 (32.08)	13.13
Coleoptera	38 (25.68)	16 (21.05)	9532.80 (22.30)	23.01
Diptera	1 (0.68)	1 (1.32)	0.60 (<0.01)	0.66
Hemiptera	6 (4.05)	4 (5.26)	1174.40 (2.75)	4.02
Hymenoptera	19 (12.84)	12 (15.79)	462.70 (1.08)	9.90
Ixodida	2 (1.35)	2 (2.63)	223.20 (0.52)	1.50
Lepdoptera	9 (6.08)	2 (2.63)	1618.50 (3.79)	4.17
Odonata	2 (1.35)	1 (1.32)	1190.50 (2.79)	1.82
Opiliones	4 (2.70)	4 (5.26)	3026.00 (7.08)	5.02
Orthoptera	9 (6.08)	6 (7.89)	5029.50 (11.77)	8.58
Scolopendromorpha	12 (8.11)	5 (6.58)	534.70 (1.25)	5.31
Scorpiones	1 (0.68)	1 (1.32)	161.40 (0.38)	0.79
Spirostreptida	35 (23.65)	15 (19.74)	5716.70 (13.38)	18.92
Not identified	5 (3.38)	4 (5.26)	359.20 (0.84)	3.16
Total	148 (100%)	76 (100%)	42738.92 (100%)	100%

Table 2. Food items of male and female *Leptodactylus labyrinthicus* in Ecological Park Sóter, Campo Grande / MS, Brazil. Number (N), volume (V mm³), frequency (F) (percentage in parentheses) and the relative importance (Ix) of each item.

Item	N	F	V mm³ (%)	Ix
Males (n = 13)	-	-	-	-
Aranae	2 (4.88)	1 (5.26)	13535.8 (57.24)	22.46
Coleoptera	20 (48.78)	4(21.05)	5915.9 (25.02)	31.62
Hemiptera	2 (4.88)	2 (10.53)	319.5 (1.35)	5.59
Hymenoptera	2 (4.88)	2 (10.53)	41.7 (0.18)	5.19
Lepidoptera	1 (2.44)	1 (5.26)	53 (0.22)	2.64
Opiliones	1 (2.44)	1 (5.26)	1784.8 (7.55)	5.08
Orthoptera	2 (4.88)	2 (10.53)	123.3 (0.52)	5.31
Spirostreptida	11 (26.83)	6 (31.58)	1873.8 (7.92)	22.11
Total	41 (100%)	19 (100%)	23647.8 (100%)	100%
Females (n = 17)	-	-	-	-
Coleoptera	9 (12.00)	5 (14.71)	1374.30 (9.31)	12.00
Hemiptera	4 (5.33)	2 (5.88)	854.80 (5.79)	5.67
Hymenoptera	12 (16.00)	6 (17.65)	300.80 (2.04)	11.89
Ixodida	1 (1.33)	1 (2.94)	7.00 (0.05)	1.44
Lepidoptera	8 (10.67)	1 (2.94)	1565.50 (10.60)	8.07
Odonata	2 (2.67)	1 (2.94)	1190.50 (8.06)	4.56
Opiliones	3 (4.00)	3 (8.82)	1241.20 (8.41)	7.08
Orthoptera	7 (9.33)	4 (11.76)	4906.20 (33.23)	18.11
Scolendromorpha	10 (13.33)	4 (11.76)	503.30 (3.41)	9.50
Spirostreptida	19 (25.33)	7 (20.59)	2821.30 (19.11)	21.68
Total	75 (100%)	34 (100%)	14764.90 (100%)	100%

Table 3. Food items of adults and juveniles of the *Leptodactylus labyrinthicus* in Ecological Park Sóter, Campo Grande / MS. Number (N), volume (V mm³), frequency (F) (percentage in parentheses) and the relative importance (Ix) of each item.

Item	N	F	V mm³ (%)	Ix
Adults (n = 30)	-	-	-	-
Aranae	2 (1.69)	1 (1.89)	13535.8 (35.25)	12.95
Coleoptera	28 (23.73)	9 (16.98)	7290.2 (18.99)	19.90
Hemiptera	6 (5.08)	4 (7.55)	1174.4 (3.06)	5.23
Hymenoptera	14 (11.86)	8 (15.09)	324.4 (0.84)	9.27
Ixodida	1 (0.85)	1 (1.89)	7 (0.02)	0.92
Lepidoptera	9 (7.63)	2 (3.77)	1618.5 (4.22)	5.21
Odonata	2 (1.69)	1 (1.89)	1190.5 (3.10)	2.23
Opiliones	4 (3.39)	4 (7.55)	3026 (7.88)	6.27
Orthoptera	9 (7.63)	6 (11.32)	5029.5 (13.10)	10.68
Scolendromorpha	10 (8.47)	4 (7.55)	503.3 (1.31)	5.78
Spirostreptida	33 (27.97)	13 (24.53)	4695.1 (12.23)	21.57
Total	118	53	38394.7	100
Juveniles (n = 13)	-	-	-	-
Aranae	3 (9.09)	2 (9.09)	172.9 (2.75)	6.98
Coleoptera	9 (27.27)	7 (31.82)	2242.5 (35.69)	31.59
Diptera	1 (3.03)	1 (4.55)	0.6 (0.01)	2.53
Hymenoptera	8 (24.24)	5 (22.73)	262.4 (4.18)	17.05
Ixodida	1 (3.03)	1 (4.55)	216.1 (3.44)	3.67
Orthoptera	2 (6.06)	1 (4.55)	2119 (33.73)	14.78
Scolendromorpha	2 (6.06)	1 (4.55)	31.4 (0.50)	3.70
Scorpiones	1 (3.03)	1 (4.55)	161.4 (2.57)	3.38
Spirostreptida	6 (18.18)	3 (13.64)	1076.5 (17.13)	16.32
Total	33 (100%)	22 (100%)	6282.8 (100%)	100

phometric sexual dimorphism for this population, with males larger than females recovered mainly in the first PCA axis. Alternatively, to associate dimorphism with territoriality and sexual selection, we propose that our results are related to the wide distribution of *L. labyrinthicus* (Valdujo et al. 2012). Within the distribution gradient of a species, the demographic history (e.g. dispersal followed by isolation) and contemporary ecological factors (e.g. climate and vegetation) can form populations with different phenotypes (e.g. Juncá et al. 2008, Marcelino et al. 2009, Hoogmoed & Avila-Pires 2012, Gehara et al. 2013, 2014). Thus, statements about morphological traits of this species should always consider several factors (e.g. geographic distribution, phylogenetic determination, ecological factors, and sexual selection). Despite the first record of sexual dimorphism of size in *L. labyrinthicus* in the present study, we highlight the sexual dimorphism by the presence of secondary sexual characteristics, such as forelimb hypertrophy and nuptial spines in males at reproductive maturity, demonstrating aggressive characteristics and territorially behavior among them (Shine 1979; Toledo et al. 2005). Lastly, the number of specimens analyzed in the present study was greater than in previous works (França et al. 2004, Shepard & Caldwell 2005, Silva et al. 2005, Toledo et al. 2005, Tozetti & Toledo 2005, Zina & Haddad 2005, Silva & Giaretta 2008, 2009, Costa et al. 2015). Thus, the difference between our results and the previous ones can be due to sampling artifacts.

We recorded high diversity in the diet, which reflects the opportunistic/generalist behavior of this species. The great amplitude of prey also shows that *L. labyrinthicus* is a sit-and-wait forager, similar to other species of the genus (Maneyro et al. 2004, Sugai et al. 2012, Camurugi et al. 2017). Considering the study population, the most abundant food category and that presented most relative importance for the species was Coleoptera, previously recorded in other species of the genus (Maneyro et al. 2004, Araujo et al. 2007, De-Carvalho et al. 2008). This is the most diverse order of insects and is known to be quite abundant in hot climates (Teixeira et al. 2009, Rafael et al. 2012), which partly explains its high importance in their diet. We also found an indication of differences in the prey diversity consumed between males, females, and juveniles. This result may possibly be due to distinct foraging strategies within each of these groups (Simon &Toft 1991, Duré & Keher 2004, Solé & Rodder 2010). However, since we have not evaluated prey availability, we cannot associated these differences directly with diet preferences. For instance, adult males tend to move less than females, due to their territorial behavior (Silva et al. 2005,

Tozetti & Toledo 2005). Besides that, the food item variation between adults and juveniles can be explained by the considerable size difference between the two groups (adults SVL: ~116 mm; juveniles SVL: ~58 mm), making a wider prey range available for adults (Solé & Rodder 2010). However, we emphasize that we did not observe a significant relationship between head size and prey volume. In fact, for some species this relationship is significant (Maneyro et al. 2004, Solé & Rodder 2010, Pacheco et al. 2017), but it is not in others (Biavati et al. 2004, Sanabria et al. 2005, Almeida-Gomes et al. 2007), which is apparently the result of environmental factors interacting with phylogenetically defined traits.

In conclusion, we point out that to satisfactorily report the natural history of a species, or the morphological singularities between sexes, it is necessary to consider the inter-populational variation, especially in cases of widely distributed species.

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References

Almeida-Gomes, M., Hatano, F.H., Van Sluys, M., Rocha, C.F.D. (2007): Diet and microhabitat use by two Hylodinae species (Anura, Cycloramphidae) living in sympatry and syntopy in a Brazilian Atlantic Rainforest area. Iheringia 97(1): 27-30.

Araujo, F.R.R.C., Bocchiglieri, A., Holmes, R.M. (2007): Ecological aspects of the *Hypsiboas albopunctatus* (Anura, Hylidae) in Central Brazil. Neotropical Biology and Conservation 2(3): 165-168.

Biavati, G.M., Wiederhecker, H.C., Colli, G.R. (2004): Diet of *Epipedobates flavopictus* (Anura: Dendrobatidae) in a Neotropical Savanna. Journal of Herpetology 38(4): 510-518.

Camurugi, F., Magalhães, F.M., Campos de Queiroz, M.H., Sena de Oliveira Pereira, T.C., Tavares-Bastos, L., Lopes-Marinho, E.S., Neves, J.M.M., Garda, A.A. (2017): Reproduction, sexual dimorphism, and diet of *Leptodactylus chaquensis* (Anura, Leptodactylidae) in Northeastern Brazil. Herpetological Conservation and Biology 12(2): 498-508.

Costa, R.N., Bauer, A.G., Magalhães, R.F., Nomura, F. (2015): *Leptodactylus labyrinthicus* (Pepper Frog) Diet. Herpetological Review 46: 233.

De Sá, R.O., Grant, T., Camargo, A., Heyer, W.R., Ponssa, M.L., Stanley, E. (2014): Systematics of the Neotropical Genus *Leptodactylus* Fitzinger, 1826 (Anura: Leptodactylidae): Phylogeny, the Relevance of Non-molecular Evidence, and Species Accounts. South American Journal of Herpetology 9(S1): S1-S100.

De-Carvalho, C.B., Freitas, E.B.D., Faria, R.G., Batista, R.D.C., Batista, C.D.C., Coelho, W.A., Bocchiglieri, A. (2008): História natural de *Leptodactylus mystacinus* e *Leptodactylus fuscus* (Anura: Leptodactylidae) no Cerrado do Brasil Central. Biota Neotropica 8(3): 105-115.

Duré, M.I., Kehr, A. (2004): Influence of microhabitat on the trophic ecology of two leptodactylids from northeastern Argentina. Herpetologica 60(3): 295-303.

França, L., Facure, K., Giaretta, A.A. (2004): Trophic and spatial niches of two large-sized species of *Leptodactylus* (Anura) in southeastern Brazil. Studies on Neotropical Fauna and Environment 39(3): 243-248.

Frost, D.R. (2017): Amphibian Species of the World: an Online Reference [Internet]. Version 6.0. New York: American Museum of Natural History. <www.research.amnh.org/herpetology/amphibia/index.html>, accessed at: 2018.02.15.

Gehara, M., Crawford, A.J., Orrico, V.G.D., Rodríguez, A., Lotters, S., Fouquet, A., Barrientos, L.S., Brusquetti, F., De la Riva, I., Ernst, R., Urrutia, G.G., Glaw, F., Guayasamin, J.M., Holting, M., Jansen, M., Kok, P.J.R., Kwet, A., Lingnau, R., Lyra, M., Moravec, J., Pombal, J.P., Rojas-Runjaic, F.J.M., Schulze, A., Señaris, J., Solé, M., Rodriguesm, M.T., Twomey, E., Haddad, C.F.B., Vences, M., Kohler, J. (2014): High Levels of Diversity Uncovered in a Widespread Nominal Taxon: Continental Phylogeography of the Neotropical Tree Frog *Dendropsophus minutus*. Plos One 9(9): e103958.

Gehara, M., Summers, K., Brown, J.L. (2013): Population expansion, isolation and selection: novel insights on the evolution of color diversity in the strawberry poison frog. Evolutionary Ecology 27: 797-824.

Greene, H.W., Losos, J.B. (1988): Systematics, natural history and conservation: field biologists must fight a public-image problem. BioScience 38(7): 458-452.

Greene, H.W. (1994): Systematics and natural history, foundations for understanding and conservation biodiversity. American Zoologist 34(1): 48-56.

Griffiths, R.A., Mylotte, V.J. (1987): Microhabitat selection and feeding relations of smooth and warty newts, *Triturus vulgaris* and *T. cristatus*, at an upland pond in mid-Wales. Ecography 10(1): 1-7.

Heyer, R., Donnelly, M.A., Foster, M., McDiarmid, R. (2014): Measuring and monitoring biological diversity: standard methods for amphibians. Smithsonian Institution Press, Washington DC.

Heyer, W.R. (1979): Systematics of pentadactylus species group of the frog genus *Leptodactylus* (Amphibia: Leptodactylidae). Smithsonian Institution Press, Washington, DC.

Hillis, D.M. (1995): American molecular naturalist (review of Avise, J. C. 1994. Molecular Markers, Natural History and Evolution, Chapman; Hall, New York). Ecology 76(3): 1017-1018.

Hoogmoed, M.S., Avila-Pires, T.C.S. (2012): Inventory of color polymorphism in populations of *Dendrobates galactonotus* (Anura: Dendrobatidae), a poison frog endemic to Brazil. Phyllomedusa 11(2): 95-115.

Juncá, F.A., Carneiro, M.C.L., Rodrigues, N.N. (2008): Is a dwarf population of *Corythomantis greening* Boulenger, 1896 (Anura, Hylidae) a new species? Zootaxa 1686: 48-56.

Kottek, M., Grieser, J., Beck, C., Rudolf, B., Rubel, F. (2006): World map of the Köppen-Geiger climate classification updated. Meteorologische Zeitschrift 15(3): 259-263.

Magalhães, R.F., Garda, A.A., Marques, N.C.S., Brandão, R.A. (2016): Sexual dimorphism and resource utilisation by the Veadeiros waterfall frog *Bokermannohyla pseudopseudis* (Anura: Hylidae). Salamandra 52(2): 171-177.

Maneyro, R., Naya, D.E., Rosa, I., Canavero, A., Camargo, A. (2004): Diet of the South American frog *Leptodactylus ocellatus* (Anura: Leptodactylidae) in Uruguay. Iheringia 94(1): 57-61.

Marcelino, V.R., Haddad, C.F.B., Alexandrino, J. (2009): Geographic Distribution and Morphological Variation of Striped and Nonstriped Populations of the Brazilian Atlantic Forest Treefrog *Hypsiboas bischoffi* (Anura: Hylidae). Journal of Herpetology 43(2): 351-361.

Marcus, L.F. (1990): Proceedings of the Michigan morphometrics workshop. pp. 77-122. In: Bookstein, F.L., Rohlf, F.J. (eds.), Traditional morphometrics. University of Michigan Museum of Zoology.

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, M.H.H. (2007): Vegan: community ecology package, Department of Statistics and Mathematics, Vienna University of Economics and Business Administration. Vienna. <https://cran.r-project.org/>, accessed at: 2016.11.20.

Pacheco, E.O., Ferreira, V.G., De Carvalho, R.M.H. (2017): Diet of *Boana albopunctata* (Anura: Hylidae) in an Atlantic Forest fragment of southeastern Brazil. Phyllomedusa 16(1): 57-62.

Pinkas, L., Oliphant, M.S., Iverson, Z.L. (1971): Food habits of albacore bluefin, tuna and bonito in California waters. Fish Bulletin 152: 1-105.

R Core Team (2014): A language and environment for statistical computing. Vienna. <www.R-project.org>, accessed at: 2016.11.20.

Rafael, J.A., Melo, G.A.R., De Carvalho, C.J.B., Casari, A.S., Constantino, R. (2012): Insetos do Brasil: Diversidade e Taxonomia. Holos Editora, Ribeirão Preto.

Sanabria, E.A., Quiroga, L.B., Acosta, J.C. (2005): Diet of *Leptodactylus ocellatus* (Linnaeus, 1758) (Anura: Leptodactylidae) in a western swamp of Argentina. Revista Peruana de Biologia 12(3): 473-477.

Shepard, D.B., Caldwell, J.P. (2005): From foam to free-living: ecology of larval *Leptodactylus labyrinthicus*. Copeia 2005(4): 803-811.

Shine, R. (1979): Sexual selection and sexual dimorphism in the Amphibia. Copeia 2: 297-306.

Silva, W.R., Giaretta, A.A. (2008): Further notes on the natural history of the South American pepper frog, *Leptodactylus labyrinthicus* (Spix, 1824) (Anura, Leptodactylidae). Brazilian Journal of Biology 68(2): 403-407.

Silva, W.R., Giaretta, A.A. (2009): On the natural history of *Leptodactylus syphax* with comments on the evolution of reproductive features in the *L. pentadactylus* species group (Anura, Leptodactylidae). Journal of Natural History 43(3-4): 191-203.

Silva, W.R., Giaretta, A.A., Facure, K.G. (2005): On the natural history of the South American pepper frog, *Leptodactylus labyrinthicus* (Spix, 1824) (Anura, Leptodactylidae). Journal of Natural History 39(7): 555-566.

Silvano, D., Segalla, M.V. (2005): Conservation of the Brazilian amphibians.

Conservation Biology 19(3): 653-658.
Simon, M.P., Toft, C.A. (1991): Diet specialization in small vertebrates: mite-eating in frogs. Oikos 61: 263-278.
Solé, M., Rödder, D. (2010): Dietary assessments of adult amphibians. pp. 167-184. In: Dodd Junior, C.K. (ed.), Amphibian ecology and conservation: a handbook of techniques. Oxford University Press.
Sugai, J.L.M.M., Terra, J.S., Ferreira, V.L. (2012): Diet of *Leptodactylus fuscus* (Amphibia: Anura: Leptodactylidae) in the Pantanal of Miranda river, Brazil. Biota Neotropica 12(1): 99-104.
Teixeira, C.C.L., Hoffmann, M., Silva-Filho, G. (2009): Community of soil fauna Coleoptera in the remnants of lowland Atlantic Forest in state of Rio de Janeiro, Brazil. Biota Neotropica 9(4): 91-95.
Toledo, L.F., Tozetti, A.M., Zina, J. (2005): *Leptodactylus labyrinthicus* (pepper frog): Repertoire of defensive behavior. Herpetological Bulletin 91: 29-31.
Tozetti, A.M., Toledo, L.F. (2005): Short-Term Movement and Retreat Sites of *Leptodactylus labyrinthicus* (Anura: Leptodactylidae) during the Breeding Season: A Spool-and-Line Tracking Study. Journal of Herpetology 39(4): 640-644.
Valdujo, P.H., Silvano, D.L., Colli, G., Martins, M. (2012): Anuran species composition and distribution patterns in Brazilian Cerrado, a Neotropical hotspot. South American Journal of Herpetology 7(2): 63-78.
Verdade, V.K., Valdujo, P.H., Carnaval, A.C., Schiesari, L., Toledo, L.F., Mott, T., Andrade, G.V., Eterovick, P.C., Menin, M., Pimenta, B.V.S., Nogueira, C., Lisboa, C.S., Paulam, C.D., Silvano, D.L. (2012): A leap further: the Brazilian Amphibian Conservation Action Plan. Alytes 29: 27-42.
Zina, J., Haddad, C.F.B. (2005): Reproductive activity and vocalizations of *Leptodactylus labyrinthicus* (Anura: Leptodactylidae) in southeastern Brazil. Biota Neotropica 5(2): 119-129.