

FILLING SOME KNOWLEDGE GAPS IN THE ECOLOGY OF THE SNOUTED TREEFROG, *OLOLYGON BERTHAE* (ANURA: HYLIDAE)

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Abstract.—We studied the ecology of the Snouted Treefrog (*Ololygon berthae*), providing new insights into sexual size dimorphism, fecundity, reproductive activity pattern, age, growth, and diet. We examined a set of 86 specimens from multiple localities from Corrientes Province, Argentina. *Ololygon berthae* exhibited sexual size dimorphism, with females averaging larger and heavier than males. The reproduction of *O. berthae* occurred during at least two periods of reproductive activity: in spring (September–October) and in summer (February–March). Gravid females contained an average of 331.1 mature ova. Based on skeletochronology, both sexes reached sexual maturity at 1 y old, while males exhibited longevity of 4 y compared to 3 y in females. Growth patterns for body size of males and females fit the von Bertalanffy’s growth model well, with a tendency of females to reach a larger asymptotic size and higher growth coefficients than males, although these differences were not significant. *Ololygon berthae* showed a generalist diet and a sit-and-wait predation strategy. The consumption of terrestrial prey by *O. berthae* revealed terrestrial behavior that was unexpected for a scansorial species. Filling such knowledge gaps in the ecology of *O. berthae* improves the understanding of this species and could help determine if conservation actions are needed.

Key Words.—age; conservation; fecundity; growth; reproductive activity pattern; sexual size dimorphism; trophic ecology.

INTRODUCTION

In conservation biology, scientists rank individual threats and classify the conservation status for each species to establish priorities and provide directions for conservation research (Primark and Sher 2016). Consequently, scientists prioritize the ecological studies of endangered or threatened species over those that are common or least concern species. This prioritization is justified by the urgent need for management actions to recover populations that are endangered or under threat. Similarly, governments and nonprofit institutions are more likely to allocate funds to support research and conservation initiatives focused on threatened species (Vaira et al. 2018).

The ecological knowledge of certain common species with extensive geographic ranges, however, such as those designated as Least Concern by the International Union for Conservation of Nature (IUCN 2024), can sometimes become unexpectedly scarce (e.g., Snout Treefrog, *Ololygon berthae*, Whistling Dwarf Frog, *Physalaemus fernandezae*, Common

Lesser Escuerzo, *Odontophrynus americanus*, Salta Treefrog, *Boana marianitae*). These species are often perceived and informally referred to as common anuran species (CAS; see Materials and Methods). Many CAS may have wide distributions and appear to be common and/or abundant, but, surprisingly, have poorly known life histories and ecologies. This knowledge shortage is reflected in some evaluation methodologies for anuran conservation status, where, due to data absence, conservation biologists are often compelled to make arbitrary decisions during conservation status evaluations to address uncertainties (Giraud et al. 2012). Thus, with gaps in information about the ecology of a species, the data of other, known related species are used to assess its conservation status (e.g., Giraud et al. 2012). Theories in ecology and evolution, however, predict differences in the use of resources and the evolution of adaptations among coexisting species (Schoener 1974). Therefore, directing research towards the ecology of CAS can yield distinct information compared to what is inferred through extrapolated



FIGURE 1. Calling male Snouted Treefrog (*Ololygon berthae*) from Santo Domingo Private Natural Reserve, Corrientes, Argentina. (Photographed by Rodrigo Cajade).

conservation analyses. This approach would also help prevent biased conservation policies and enhance evaluations when approached with accurate information.

The Snouted Treefrog (*Ololygon berthae*; Fig. 1) is widely distributed in Argentina, Brazil, Paraguay, and Uruguay. It is considered a Least Concern species by the IUCN (Aquino et al. 2023) and fits the description of a CAS. In Argentina, *O. berthae* was categorized as a Not Threatened species (Vaira et al. 2012). There is a need for updated information about the life history and ecology of this species for possible conservation action (Aquino et al. 2023). In the Argentinean conservation status assessment, *O. berthae* was considered to be a species with an intermediate degree of ecological specialization in terms of habitat use, diet, or substrate and was classified as Common and Frequently Registered (Vaira et al. 2012). Our knowledge acquired over many years through diverse, long-term, non-systematic surveys covering a significant part of its distribution in Argentina (e.g., provinces of Buenos Aires, Entre Ríos, Corrientes, and Misiones), however, suggests that despite its wide distribution, *O. berthae* is probably less abundant than other syntopic hylids within its range: the Striped Snouted Treefrog (*Scinax squalirostris*); Brown-bordered Snouted Treefrog (*Scinax fuscomarginatus*); or Lesser Snouted Treefrog (*Scinax nasicus*; see Lezcano 2021; Piñeiro et al. 2021). Despite the degree of ecological specialization assumed for *O. berthae* in its conservation assessment (Vaira et al. 2012), no ecological studies regarding this species have been carried out. These uncertainties in the

assessment of *O. berthae* revealed substantial gaps in basic ecological knowledge of the species and prompted us to study its ecology.

Our aim was to describe new relevant information about the ecology of *O. berthae* based on specimens from multiple populations in the province of Corrientes, Argentina. We investigated body size and sexual size dimorphism (SSD), fecundity and reproduction, age-related parameters, growth, and diet. Finally, we discussed the importance of this information to improve the conservation assessments that come from studying the ecology of a CAS species.

MATERIALS AND METHODS

Definitions and specimens studied.—We define common anuran species (CAS) as those species within the framework of anuran conservation assessment in Argentina that yielded uncertainty category values not matching any conservation category. This occurred when the SUMIN index (from the Spanish *Suma de indices*, meaning sum of index) yielded values between 13 and 17, where values below 13 determine categories of Not-Threatened conservation status and values above 17 determine Threatened categories (Giraudó et al. 2012). Subsequently, specialist evaluators arbitrarily classified these species into the Not Threatened category (Giraudó et al. 2012). The value for *O. berthae* was 13.

Due to the low densities of *O. berthae* found during our regular field work in Corrientes Province, Argentina, and to obtain the most representative samples possible for the ecological study of this species, we used 82 specimens from three sources collected from multiple localities within this province. The area encompassed by these localities was approximately 16 km² and all occurred in the ecoregion of Campos y Malezales (Burkart et al. 1999). The habitat of wetlands with abundant emerging aquatic vegetation used by *O. berthae* is widely distributed in this ecoregion. The climate is characterized by a mean annual temperature of 21.5° C and mean annual precipitation of 1,500 mm, which occurs mainly during spring and summer (Carnevali 1994).

We obtained specimens from three sources. **Source 1 (S1):** 52 specimens (seven males, nine females, and 36 postmetamorphic juveniles) that we collected between July 2012 and July 2013 using pitfall traps filled with 10% formalin, activated throughout the entire year, and sampled monthly.

We located the traps in a hydrophilic forest close to a semipermanent wetland with abundant emergent vegetation at Santo Domingo Private Natural Reserve, Tapebicuá, Corrientes, Argentina (29°35'59.9"S; 56°59'19.5"W; 52 m elevation). **Source 2 (S2):** 14 specimens (12 males and two females) from multiple localities in Corrientes Province housed at the Colección Herpetológica de la Universidad Nacional del Nordeste (UNNEC; for detail of collection dates and localities see Appendix). **Source 3 (S3):** 16 calling males and four females that we collected by hand during a reproductive event on 3 September 2018 at Reserva Natural Rincón de Santa María, Corrientes Province, Argentina (27°31'44.68"S; 56°36'0.69"W; 88 m elevation). After collection we euthanized the specimens with 2% lidocaine and fixed them in 10% formalin. All specimens collected were housed at (UNNEC; see Appendix).

Body size and sexual size dimorphism.—We assessed sexual size dimorphism (SSD) analyzing 35 male specimens (seven from S1, 12 from S2, 16 from S3) and 15 female specimens (nine from S1, two from S2, four from S3). We used a multivariate analysis to assess differences in adult body size between sexes. We considered adult specimens as those > 14 mm snout-vent length (SVL) and also by recognizable sexual maturity features, such nuptial vocal sacs in males and mature gonads in females. We determined net body mass (total body mass excluding gonad mass) to the nearest 0.01 g using a digital balance (Ohaus traveler scale TA320, Ohaus, Parsippany, New Jersey, USA) and SVL of all adult preserved specimens to the nearest 0.001 mm using a digital caliper. We generated a biological data matrix using the samples for each variable and a Euclidean dissimilarity matrix, and we constructed and subsequently used a one-factor (sex) Permutational Multivariate Analyses of Variance (PERMANOVA) to test the null hypotheses of no differences in body size (net body mass and SVL) between sexes (Anderson 2001). When this analysis yielded significant differences, we used one-factor Permutational Univariate Analyses of Variance (ANOVA) from a Euclidean dissimilarity matrix to test the null hypotheses of no differences between body mass and SVL. We conducted data analyses using non-transformed data, and we constructed null hypotheses using unrestricted permutations of raw data. We ran each test using 4,999 permutations (Anderson 2001). We conducted all analyses using PRIMER 6.1.13 and PERMANOVA + 1.0.3. (PRIMER-E Ltd 6, Plymouth, Devon, UK). We also

measured SVL and total body mass of juveniles, defined as those individuals lacking external sex characteristics, small size (SVL \leq 14 mm), and absence of LAGs (lines of arrested growth; described below). We assumed juveniles to be in their first growth period.

Fecundity and reproductive field observations.—We used a sample of 10 females (six from S1, two from S2, and two from S3) to assess the following reproductive variables: (1) ovary mass (OM) using a digital balance; (2) ovarian complement (OC), representing the number of mature ova; and (3) mature ovum diameter (OD), determined from 100 randomly selected mature ova per female and measured using a Leica Stereomicroscope EZ4E (Leica Microsystems, Wetzlar, Hesse, Germany). We determined maturity of the ova by degree of pigmentation (Crump 1974). Additionally, we used the net body mass for correlation and comparative analysis. We quantified reproductive effort (RE) as a percentage of mature gonad mass relative to body mass (Kuramoto 1978) and we calculated an ovarian size factor (OSF, which relates the ovarian complement and ovum diameter with body length; Crump and Duellman 1974) to compare the fecundity and egg size relative to adult body size. We recorded observations on reproductive activity of *O. berthae* during the monthly trips made between July 2012 and July 2013 to Santo Domingo (S1) to check the pitfall traps for samples on three consecutive nights. We made acoustic and visual observations after dark (2000 to 2200) in a semipermanent pond near the pitfall traps (29°36'1.31"S; 56°59'21.56"W) located in a patch of pine forest. We recorded the presence/absence of gravid females, frogs in amplexus, and calling males. We used Pearson's Product Moment Correlation coefficients (Zar 1996) to establish the relationship between the quantitative reproductive variables with SVL and net body mass for females using XLSTAT Pro 7.5 (Addinsoft, Paris, France Island, France).

Age-related parameters.—We used 53 specimens, comprising eight males (seven from S1, one from S2), nine females (all from S1), and 36 juveniles (all from S1) for age estimation using skeletochronology following standard laboratory procedures (Smirina 1972; Castanet and Smirina 1990) with minor modifications proposed by Marangoni (2006). This method, widely employed in studies of anuran species (Castanet and Smirina 1990; Tejedo et al. 1997; Cajade et al. 2013; Marangoni and Baldo

2023), involves assessing age based on cyclic annual and annular bone growth marks, visualized as LAGs in stained bone cross-sections (Castanet and Smirina 1990). We washed clipped digits in water for 30 min and then decalcified them in 5% nitric acid for 1–3 h. We then dehydrated the bone samples, paraffin-embedded them, and sectioned them using a rotation microtome (Arcano RMT-30, Instrumental Pasteur, Buenos Aires, Argentina) at 14–16 μm , and stained them with Harris haematoxylin. We recorded the presence/absence of a line of metamorphosis (LM) and LAGs from stained transverse sections (15 μm) of the third phalanx of a rear leg of each animal. We used a Leica ICC50HD camera mounted on Leica DM500 microscope (Leica Microsystems, Wetzlar, Hesse, Germany) to take digital images. We used the LAS EZ.INK software (Leica Application Suite Version 3.3, 2016; Leica Microsystems, Wetzlar, Hesse, Germany) to take and analyze the digital images. For each sex, we calculated the following age-related parameters based on information obtained through skeletochronology (*sensu* Leskovar et al. 2006): (1) median lifespan, defined as median of the age distribution; (2) age of sexual maturity (i.e., minimum reproductive age); (3) longevity, defined as the maximum age reached among individuals; and (4) potential reproductive lifespan, calculated as the difference between maximum age and minimum reproductive age. We determined age by counting the number of LAGs, where each LAG counted represents 1 y (age in LAGs henceforth) using three independent observers each counting LAGs following the approach described by Patón et al. (1991).

Growth patterns.—We employed nonlinear estimation using the STATISTICA 8 statistical package (StatSoft Inc., Tulsa, Oklahoma, USA) to calculate the von Bertalanffy (1938) growth model following Beverton and Holt (1957):

$$\text{SVL}_t = \text{SVL}_{\text{max}} (1 - e^{-k(t-t_0)})$$

where SVL_t is the expected or average SVL at time (or age) t , SVL_{max} is the asymptotic SVL, K is the growth rate coefficient, and t_0 is the time or age when the average SVL was zero. We fitted the von Bertalanffy (1938) growth model and estimated growth parameters (VBGPs) using nonlinear Least Squares Regression. We considered two estimated VBGPs to be significantly different when their 95% confidence intervals (CI) did not overlap. We used 36 postmetamorphic juveniles from S1 (0 LAGs) as the

zero age in the von Bertalanffy growth model.

Trophic ecology.—We examined stomach contents from 29 males (seven from S1, six from S2, 16 from S3), 14 females (nine from S1, one from S2, four from S3), and 36 juveniles (all from S1). We recorded the number of prey items per stomach for each prey category (defined below) and we estimated the volume of each prey item using the formula for an ellipsoid,

$$V = 4/3 \pi (1/2 L)(1/2 W)^2$$

where V is volume, L is length, and W is width (Dunham 1983). We calculated prey diversity using the Shannon Index (H' ; Shannon and Weaver 1949). To determine the importance of each prey category (I) in the diet, we used the formula:

$$I = (F\% + N\% + V\%) / 3$$

where, $F\%$ = occurrence percentage, $N\%$ = numeric percentage, and $V\%$ = volumetric percentage (Biavati et al. 2004). We calculated the importance of prey categories for pooled stomachs (IPS). Additionally, we calculated the niche breadth (N_b) of prey item and prey volume using Levins's Index (Levins 1968),

$$N_b = (\sum_{pij} 2)^{-1}$$

where pij represents the probability of finding the item i in the sample j .

We used Pearson's Product Moment Correlation coefficients (Zar 1996) to evaluate the relationship between the mouth width of frogs and mean prey volume. When assumptions of normality were not met (Shapiro-Wilk test), the data were transformed and normalized using natural logarithms (\ln). We present data for central tendency as mean \pm 1 standard deviation. We used significance level $\alpha = 0.05$ for all analyses.

RESULTS

Body size and sexual size dimorphism.—The SVL of females ranged from 19.18–24.99 mm (mean = 21.21 ± 1.54 ; $n = 15$) and net body mass ranged from 0.36–1.13 g (mean = 0.63 ± 0.18 ; $n = 15$). In males, SVL ranged from 15.67–21.28 mm (mean = 19.00 ± 1.17 ; $n = 35$) and total body mass ranged from 0.11–0.65 g (mean = 0.42 ± 0.11 ; $n = 35$). For juveniles, SVL ranged from 10.66–14.00 mm (mean = $12.09 \pm$

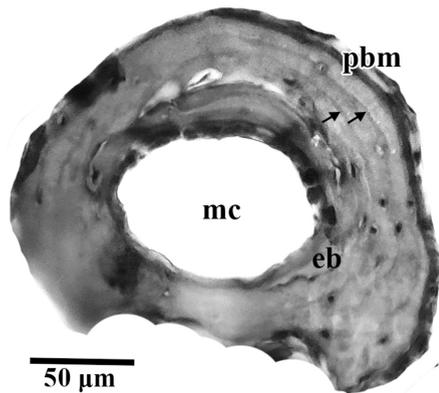


FIGURE 2. A cross-section through the diaphysis of the phalanx of a Snouted Treefrog (*Ololygon berthae*; male, 2 y old). Two lines of arrested growth (LAG) are visible in the periosteal bone (indicated by arrows). Abbreviations are medullary cavity (mc), endosteal bone (eb), and periosteal bone margin (pbm). (Photographed by Andrea I. Lezcano).

0.97 mm; $n = 36$) and total body mass ranged from 0.06–0.23 g (mean = 0.12 ± 0.03 g; $n = 36$). There were significant effects of sex on SVL and net body mass (Mean Squares (MS) = 51.76; $F = 30.73$; $P < 0.001$; Coefficient of Variation (CV) = 1.54%; $df=1$), indicating that body size was sexually dimorphic, with females averaging significantly longer (MS = 51.32; $F = 30.82$; $P < 0.001$; CV = 1.53%; $df = 1$) and heavier (MS = 0.43; $F = 23.09$; $P < 0.001$; CV = 0.14%; $df = 1$) than males.

Fecundity and reproductive field observations.—

From the material studied (15 females), five females lacked mature eggs (three from source 1 and two from source 3). The coloration of mature ova from gravid females was half dark brown and half light brown. The OD ranged from 0.12–1.13 mm (mean = 0.87 ± 0.11 mm; $n = 10$). The OM ranged from 0.02–0.19 g (mean = 0.087 ± 0.059 g; $n = 10$). The OC ranged from 88–730 (mean = 331.1 ± 188.62 ; $n = 10$). The RE ranged from 3.17–37.25 % (mean = $14.35 \pm$

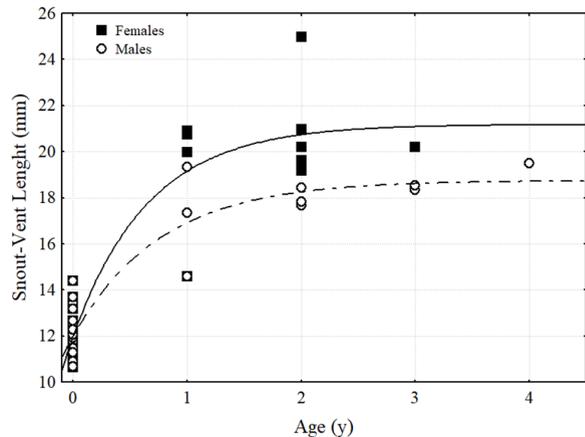


FIGURE 3. Growth curves fitted to the von Bertalanffy model for body size (snout-vent length) in nine male (circles) and eight female (closed squares) Snouted Treefrog (*Ololygon berthae*) from Corrientes Province, Argentina. Juveniles are indicated by open squares.

10.05%; $n = 10$). The OSF was 13.54 ($n = 10$). We found no significant correlation between SVL and OC, OM, or RE, nor between net body mass and OM or RE ($n = 10$ in all cases). By contrast, net body mass was significantly correlated with OC ($r = 0.76$; $t = 3.39$; $P = 0.009$; $n = 10$). We observed two periods of reproductive activity of *O. berthae*. We recorded gravid females, frogs in amplexus, or calling males (Fig. 1) during spring (22–25 September and 15–18 October 2012) and during summer (22–25 February and 12–16 March 2013).

Age-related parameters.—

We found well-defined LAGs in the periosteal bone in all adult specimens that were analyzed, and they were relatively easy to count to assess individual age (Fig. 2). Endosteal resorption never interfered with age estimation because we observed the metamorphosis lines in all specimens. For both males and females, the mode and median values were 2 y of age (Table 1). The age frequency in females was most often represented

Table 1. Age-related traits of adult Snouted Treefrogs (*Ololygon berthae*) from Corrientes province, Argentina ($n = 9$ females and eight males). Traits are mean age (\pm standard deviation [SD] in y), modal age (y), median age (y), frequency age (y; sample size in parentheses), age at maturity (i.e., the minimum age, in years [= LAGs]), longevity (maximum age, y); potential reproductive lifespan (PRLS, y), mean snout-vent length (SVL) at age of maturity (AM) \pm SD in mm, and maximum (Max) SVL and the age (y) of first-year breeders. For sex, M = males and F = females.

Sex	Mean age	Modal Age	Median Age	Frequency Age	Age at Maturity	Longevity	PRLS	Mean SVL at AM	Max SVL(age)
M	2.25 ± 1.03	2	2	1(2), 2(3), 3(2), 4(1)	1	4	3	18.33 ± 1.41	21.28 (at 3 y)
F	1.77 ± 0.66	2	2	1(3), 2(5), 3(1)	1	3	2	20.53 ± 0.48	24.99 (at 2 y)

Table 2. Estimated von Bertalanffy growth parameters of nine females and eight for the Snouted Treefrog (*Ololygon berthae*) in Corrientes Province, Argentina. Abbreviations are R = coefficient of determination, SVL_{max} = average maximal body size (mm), S_0 = average juvenile body size (0 LAGs; mm), K = growth rate coefficient, defining the shape of the growth curve, M = males, and F = females. For each variable, standard error is in parentheses and 95% confidence interval is below the point estimate.

Sex	R (n)	SVL_{max}	S_0	K
M	0.931	18.75 (0.60)	12.02 (0.17)	1.31 (0.44)
		17.53–19.97	11.69–12.36	0.41–2.20
F	0.933	21.18 (0.92)	12.02 (0.23)	1.51 (0.57)
		19.33–23.03	11.56–12.48	0.36–2.67

by 1–2 y (eight of nine individuals), while in males the frequency was mostly 1–3 y (seven of eight individuals; Table 1).

Growth.—The patterns of growth for body size fit well for both male and females (i.e., $R = 0.931$ and 0.933 , respectively; Table 2) with a von Bertalanffy’s growth model (Fig. 3, Table 2). The SVL_{max} estimated for the model (Table 2) was similar to the mean SVL measured for each sex (estimate/measured SVL : 21.18/21.21mm for females and 18.75/19.00 mm for males). Females attained higher asymptotic size

(SVL_{max}) and had higher growth coefficients (K; Fig. 3, Table 2), although the differences for both variables were not significant (i.e., CI values overlapped; Table 2).

Trophic ecology.—Only 27.9% of adult specimens (three of 29 males and nine of 14 females) had identifiable stomach contents. The remaining 72.1% of adult specimens did not provide suitable information to be analyzed (19 specimens had empty stomachs and 12 specimens had undifferentiated contents). For juveniles, 63.8% (23 of 36) had identifiable stomach content, whereas the remaining 36.2% could not be analyzed because they had empty stomachs (3) or unidentifiable stomach content (10). Because we did not detect obvious differences in diet between adults and juveniles, we provide the diet analyses for all specimens combined.

The mean number of prey consumed per individual of *O. berthae* was 2.2 (± 1.84 ; range of values 1–8; $n = 35$) and the modal number was 1. The diet of *O. berthae* consisted of 13 types of item prey (Table 3). Considering IPS, the most important prey were Diptera, Araneae, Hemiptera, and Collembola (Table 3). Prey diversity (H') was 1.95 and niche breadth

TABLE 3. Diet of the 35 Snouted Treefrog (*Ololygon berthae*) in Corrientes Province, Argentina based on number prey items by prey type, volume of prey items by type, and frequency of prey types among frogs. Abbreviations are n = number of prey items and IPS = the importance value of prey type for pooled stomachs.

Prey Type	n	%	Volume (mm ³)	Volume (%)	Frequency	Frequency (%)	IPS
Insecta							
Coleoptera	4	3.74	0.64	2.01	4	12.50	6.08
Diptera	39	36.45	1.44	4.54	12	37.50	26.16
Collembola	18	16.82	0.15	0.47	9	28.13	15.14
Hemiptera	17	15.89	0.89	2.83	17	53.13	23.95
Larvae (insect)	2	1.87	0.72	2.27	2	6.25	3.46
Hymenoptera	5	4.67	4.14	13.1	5	15.63	11.13
Thysanoptera	1	0.93	0.10	0.33	1	3.13	1.46
Lepidoptera	1	0.93	0.28	0.90	1	3.13	1.65
Formicidae	2	1.87	0.15	0.46	2	6.25	2.86
Chelicerata							
Araneae	7	6.54	15.46	48.9	7	21.88	25.77
Pseudoscorpionida	2	1.87	2.52	7.97	2	6.25	5.36
Acarina	8	7.48	0.29	0.91	6	18.75	9.04
Malacostraca							
Isopoda	1	0.93	4.84	15.3	1	3.13	6.45
Total	107	100	31.61	100			

of prey number and prey volume were 4.97 and 3.44, respectively. The mean frog body length and mouth width were 14.74 ± 4.14 mm and 4.62 ± 1.21 mm, respectively. The mean frog body mass was 0.53 ± 1.59 g. The mean ln prey volume was significantly correlated with mouth width ($r = 0.66$; $n = 35$; $t = 4.99$; $P < 0.001$).

DISCUSSION

Body size and sexual size dimorphism.—We found sexual size dimorphism in *O. berthae*, with females significantly larger (SVL) and heavier (net body mass) than males. Sexual size dimorphism has been recorded in about 90% of anuran species, with females being larger than males (Shine 1979; Kupfer 2007). Sexual dimorphism among *Ololygon* species has been poorly documented. With over 52 species in the genus, sexual size dimorphism has been studied only in Rio Mutum Snouted Treefrog (*O. argyreornata*; Teixeira and Rödder 2007), Rio Doce Snouted Treefrog (*O. carnevalli*; Silva Guedes Folly 2017), and Kautsky's Snouted Treefrog (*O. kautskyi*; Pereira-Ribeiro et al. 2020) and in all three species, females were significantly larger than males. Several non-mutually exclusive factors can contribute to sexual size dimorphism in anurans, including faster growth rates and delayed reproduction in females or restrictions on the growth of males because of the energy demand linked to reproductive activity (Woolbright 1989). The larger size of females has also been explained as an adaptative result of selection favoring larger female body size to allow the production and accommodation of larger mature gametes (ovocytes; Crump 1974; Shine 1979). This seems unlikely in the case of *O. berthae*, however, because we did not find a correlation between SVL and OC. On the other hand, the sexual size dimorphism in *O. berthae* could possibly be explained by a faster growth rate of females, as our data suggest.

Fecundity and reproductive field observations.—Although a correlation between SVL of females and ovarian complement has been recorded for other related species (*O. carnevalli*; Silva Guedes Folly 2017), we did not find a significant correlation between SVL and ovarian complement for females of *O. berthae*. We found, however, a significant positive correlation between the net body mass and ovarian complement. The relationship between ovarian complement and ovum diameter provides a conceptual framework to understand the reproductive strategies

in anurans (Crump and Duellman 1974). The high value of ovarian size factor (13.54) for *O. berthae* relative to those described for other hyliid species (e.g., 7.05 in Bokermann's Tarauaca Treefrog, *Dendropsophus bokermanni*; 4.42 in Crump Treefrog, *Dendropsophus brevifrons*; Crump and Duellman 1974) is consistent with a reproductive strategy of low investment per egg. This is evidenced by the production of many small eggs by *O. berthae* and an extended period of time for reproduction during spring-summer (this study; Basso 1990) with at least two periods of reproduction in contrast to other hyliid species (above mentioned) that produce fewer and larger eggs in relation to body size and reproduce once per year (Crump and Duellman 1974). Considering similar reproductive strategies, the ovarian complement and ovocyte size of *O. berthae* are fewer and smaller on average than the number of eggs per clutch and egg size recorded, respectively, for other congeners such as *O. trapicheroi* (Rico et al. 2004). On the other hand, *O. berthae* differs from other *Ololygon* species such as Coastal Snouted Treefrog (*O. littorea*), Bandeirantes Snouted Treefrog (*O. perpusilla*), and Forest Snouted Treefrog (*O. v-signata*), which have the reproductive strategy of laying only a few, large eggs in bromeliads (Alves-Silva and da Silva 2009). Although no data about reproductive effort is available for other *Ololygon* species, future comparisons with other species could reveal interesting patterns associated with different reproductive strategies. Even terrestriality in the genus, as is evidenced for *O. berthae* (this study) or other species (Teixeira and Rödder 2007), could be a future area of research, when considered as a potential factor affecting the trade-off of between fecundity and egg size (Pupin et al. 2010; Pereira and Maneyro 2012).

Age-related parameters and growth.—Our results provide the first information available about age in the genus *Ololygon*. The periodicity of LAG formation by skeletochronology has been studied in many subtropical anuran species and has been explained by intrinsic genetic factors and extrinsic factors, such the bone growth detention due to periods of low temperatures (Kumbar and Pancharatna 2002; Marangoni et al. 2009; Jovanovic and Vences 2010; Cajade et al. 2013; Marangoni et al. 2018). These studies show linear relationships among age at maturity and growth, reproduction, and sexual size dimorphism. Our analyses show that males and females both reach the sexual maturity at 1 y old. These results are consistent with the lack

of significant differences between male and female growth rates. As we observed, however, there is a tendency for faster growth rate for females, which could imply a greater energy investment by females, and is a hypothesis that should be tested in future studies. Although females seem to be more short-lived than males by one year, the lifespan allows for at least 3 y of reproductive activity for females, which provides an intermediate reproductive potential in comparison to the higher potential lifespan (4–6 y) recorded for other subtropical anuran species (Cajade et al. 2013; Marangoni et al. 2018, 2019; Marangoni and Baldo 2023). Additionally, because we observed *O. berthae* to reproduce at least two times during spring-summer, the shorter longevity of females in comparison to males could be compensated for by improving reproductive success by having more than one reproductive period per year

Trophic ecology.—The trophic ecology of *O. berthae* was characterized by a high percentage of empty stomachs, the consumption of few prey items per individual, and the lack of a large proportion of any one type of prey. This represents a generalist diet and a site-and-wait predator model, as occurs in many other hyloid species (Sole and Pelz 2010; Blanco Torres et al. 2017). In addition, the positive correlation between mouth width and prey volume suggests that *O. berthae* is non-selective for prey size. As recorded in other closely related species (e.g., *Oloolygon carnevalli*; Silva Guedes Folly 2017), Dipterans and Araneans were well-represented and important in the diet.

The importance of the foraging frequency on ground-dwelling prey (28.5% of *O. berthae* frogs preyed on collembolans or/and isopods) was particularly striking, suggesting a strategy combining scansorial foraging behavior with terrestrial foraging behavior for *O. berthae*. A terrestrial foraging behavior is not expected for scansorial species that inhabits the vegetation above to the ground. Terrestrial foraging in *O. berthae*, however, was also evidenced by the high capture rate of 52 specimens at S1 (seven males, nine females, and 36 juveniles) using pitfall traps placed outside the wetland habitat used for reproduction compared to only a few or no specimens of other hyloid species during the surveys using traps and most common at the same study site: three Montevideo Treefrogs (*Boana pulchella*), no Snouted Treefrogs (*Scinax fuscovarius*), *Scinax nasicus*, *Scinax squalirostris*, or Cochran's Snouted Treefrogs (*Scinax similis*). Likewise, most of the *O.*

berthae specimens captured with pitfall traps were found with prey items in their stomachs (three males, nine females, 33 juveniles). A strong representation of ground-dwelling prey was recorded for the closely related species *O. argyreornata*, where in the analysis of contents of 265 stomachs, 415 prey items were recorded, with 72% of them being ground-dwelling prey (Teixeira and Rödder 2007).

Regarding trophic ecology and reproductive behavior, all the males (16) and females (four) we collected during a reproductive activity event (S3 locality) had empty stomach contents, suggesting that both males and females do not feed during reproductive activity. A study of five hyloid species showed a positive relationship between the length of the reproductive period and the number of males with prey items in their stomachs (Sole and Pelz 2010). This pattern was also recorded in the closely related species Catharina Snouted Treefrog (*O. catharinae*; Mendonça et al. 2020). According to Sole and Pelz (2010), males that have short periods of reproduction have different feeding and calling habitats, and when they arrive to water bodies for reproduction, they focus on reproductive activity and not on feeding activity. We found *O. berthae* reproducing during two periods of reproductive activity in spring-summer, apparently shorter in time than for the hyloid Chaco Treefrog (*Boana raniceps*; Sole and Pelz 2010) where males call for two months and have prey items in their stomachs. The abundance of terrestrial prey we found in stomachs of *O. berthae* and the high capture rate outside the reproductive aquatic habitat suggests differences between feeding and reproductive habitat, in agreement with the observations of Sole and Pelz (2010) for frogs with short reproductive periods.

Remarks and future studies.—The ecology of *O. berthae* includes female age-related parameters that differ from males, possibly different growth rates between sexes, reproduction during spring-summer time, and a trophic ecology where individuals have a foraging strategy partially associated with terrestrial habits. Besides the new insights on the ecology of *O. berthae*, our study points out that unknown values for the ecology of a CAS species could lead to erroneous estimations by evaluators during conservation assessments (e.g., the maximum values of ovarian complement we recorded far exceeded the egg number arbitrarily assigned during the Argentinean conservation assessment; see Varia et al. 2012). Two main points of discussion should be considered as potential directions for future studies

in ecology and anuran conservation. First, the lack of ecological information was recognized by the amphibian conservation plan of Argentina (Dure et al. 2018) as a problem to address for future conservation assessments. Thus, the focus on the study of the life history and ecology of those species perceived as CAS should also be of interest for conservation biologists in addition to vulnerable and threatened species. This could provide a useful preventive approach, especially in those countries with a low percentage of threatened species or with a great number of CAS species. For example, 10% (16) of the anuran species and subspecies from Argentina have been arbitrarily assigned by the specialists to the Not Threatened conservation category. This decision was made after the conservation index value obtained for each species did not fit within any existing category (see Vaira et al. 2012). These species are easily recognized as CAS and could be a future focus of study. Second, there should be an increase in the effort devoted to the study of demographic life-history traits. Such studies could make these assessments more precise. For example, the reproductive traits of any species should be related to its lifespan, so to calculate the potential total of eggs produced by females, it is necessary to know the lifespan. Thus, more complete information would be obtained for the reproductive potential of any species, rather than a simpler variable such as egg number per clutch that is used by some indexes (e.g., SUMIN; Giraudo et al. 2012). For example, the continuity/validation of the SUMIN index for the amphibian categorization of Argentina (Dure et al. 2018) could be modified in the future to incorporate the ecological age-related parameters to improve the assessments.

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APPENDIX: Material examined of the Snouted Treefrog (*Oloolygon berthae*) from Corrientes Province, Argentina. UNNEC = Colección Herpetológica de la Universidad Nacional del Nordeste, Corrientes, Argentina.

Source 1: Santo Domingo Private Natural Reserve, Departamento de Paso de los Libres, Corrientes: 13867 UNNEC (5 August 2013, male); 13871 UNNEC (22 September 2012, male); 13875–13876 UNNEC (15 October 2012, male); 13881–13883 UNNEC (15 October 2012, male); 13868 UNNEC (5 August 2013, female); 13872–13874 UNNEC (15 October 2012, female); 13877–13880 UNNEC (15 October 2012, female); 13884 UNNEC (15 October 2012, female); 13885–13920 UNNEC (15 October 2012, postmetamorphic juveniles).

Source 2: 13056 UNNEC (5 August 2009, El Socorro, Mercedes, Corrientes, male); 6169 UNNEC (12 July 1999, Santo Tome, Corrientes, male); 13060 UNNEC (22 August 2012, Bonpland, Corrientes, male); 10059 UNNEC (24 April 2008, San Juan Mini, Concepción, Corrientes, male); 7353 UNNEC (27 October 2000, Gobernador Virasoro, Corrientes, male); 13059 UNNEC (20 October 2010, El Socorro, Mercedes, Corrientes, male); 13058 UNNEC (5 May 2010, El Socorro, Mercedes, Corrientes, male); 9627 UNNEC (25 August 2007, Laguna Galarza, Corrientes, male); 10046 UNNEC (28 April 2008, San Juan Mini, Concepción, Corrientes, male); 13057 UNNEC (5 August 2008, El Socorro, Mercedes, Corrientes, male); 13869 UNNEC (22 March 2013, Tres Cerros, Departamento de San Martín, Corrientes, male); 13870 UNNEC (1 September 2012, Tres Cerros, Departamento de San Martín, Corrientes, male); 9620 UNNEC (25 August 2008, Estancia San Lorenzo, Departamento de Santo Tome, Corrientes, female); 9407 UNNEC (2 April 2007, Estancia El Naranjal, Pellegrini, San Martín, Corrientes, female).

Source 3: 3 September 2018, Reserva Natural Rincón de Santa María, Ituzaingo, Corrientes: 13847–13850 UNNEC (male); 13851 UNNEC (female); 13852–13862 UNNEC (male); 13863–13866 UNNEC (female).



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