

## Sexual Size Dimorphism and Age in *Odontophrynus* cf. *barrioi* (Anura: Odontophrynidae) from the Monte Desert, Argentina

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**ABSTRACT.**—Current knowledge on sexual dimorphism and population structure in the genus *Odontophrynus* is limited. We studied age structure, age at maturity, and longevity in *Odontophrynus* cf. *barrioi*, with skeletochronology. We also determined whether sexual dimorphism in body size exists in this species, and evaluated its relation to demographic life history traits. We found that females were larger in four variables corresponding to the morphology of the head. In addition, females of *O.* cf. *barrioi* have a longer tibia-fibula and femur than males. Nevertheless, *Odontophrynus* cf. *barrioi* shows no sexual dimorphism in snout-vent length. We suggest the possibility that sexes have different growth trajectories after the onset of reproduction, as they are exposed to different selection pressures, or even predation rate, because of size differences.

Anurans exhibit secondary sexual dimorphism (SSD), with disparity in body size as one of the most common features (Duellman and Trueb, 1994). This is usually explained by Darwin's theory of sexual selection. In most species of anurans, adult females exceed adult males in body size. However, in some cases males are larger than females or there is no SSD (Shine, 1979). The larger size of females is often explained by an increased body size favoring an increase in fertility (Duellman and Trueb, 1994). Moreover, there are two hypotheses that can explain the smaller size of males. The first proposes the selective predation on larger males (Shine, 1979). The second attributes the cessation of growth in males at reproductive maturity (Woolbright, 1989), as reproductive behavior is energetically costly for males. Calling and defense of breeding sites are the main causes of energy expenditure for males during this period.

Often SSD in body size reveals that females have longer snout-vent lengths (SVL); however, males can still be larger in other size variables. Such is the case for male *Rhinella marina* that are shorter than females in SVL, but have larger muscle mass on the fore and hind legs, which helps resist attack by other males during amplexus (Lee, 2001; Lee and Corrales, 2002). Quiroga et al. (2004) showed in *Rhinella arenarum* that spines on the dorsal skin are found only in males and can be important during interactions between males during amplexus. Dimorphisms, such as gender differences in the size of the head, limbs, and other features, have been linked to food niche segregation, heat, space, and pre- and postmaturation, among other characteristics (Perez-Mellado and De La Riva, 1993; Herrel et al., 1999; Butler and Losos, 2002; Smith and Roberts, 2003). This variation can also be attributed to differential age at maturity, growth rate, and/or longevity (Monnet and Cherry, 2002; Marangoni et al., 2011); therefore consideration of these factors is essential in the study of amphibian sexual size dimorphism.

Skeletochronology is based on the presence of cyclic annular bone growth, which can be visualized in cross-sections of the bone (Castanet, 1982; Castanet and Smirina, 1990). This method of counting the number of lines of arrested growth (LAGs) in cross-sections of phalanges, obtained by toe clipping, is the most

commonly used tool for evaluating age structure in amphibians and reptiles, providing age estimation through nonlethal means (Castanet and Smirina, 1990).

The genus *Odontophrynus* Reinhardt and Lütken 1862 is currently distributed in southern and eastern South America and includes 11 species (Frost, 2013). Sexual dimorphism and population structure of species belonging to this genus have not been studied thoroughly. No sexual dimorphism was found in populations of *Odontophrynus cordobae* and *Odontophrynus americanus* from central Argentina (Grenat et al., 2012) but Caramaschi and Napoli (2012) reported the presence of SSD in *Odontophrynus carvalhoi* and *Odontophrynus monachus*. Furthermore, Rosset (2008) mentioned the existence of sexual dimorphism in *Odontophrynus maisuma*. We must emphasize that the work of Caramaschi and Napoli (2012) and Rosset (2008) were not intended to test the existence of SSD, but they reported the possible existence of SSD caused by a trend in the size of females being larger than males.

The aims of this study were to present the first data on age structure, age at maturity, and longevity for another species of this genus, *Odontophrynus* cf. *barrioi*, with the use of skeletochronology. Furthermore, we determined whether sexual size dimorphism in body size exists, and evaluated it in relation to demographic life history traits. We also discussed the chronological formation of the LAGs in relation to reproductive activity patterns.

### MATERIALS AND METHODS

**Study Site and Collection Methods.**—*Odontophrynus* cf. *barrioi* (Fig. 1) is usually associated with arid and subarid environments of central and western Argentina and we selected a small stream in the Quebrada de Las Flores as our study site. This region, characterized by an arid climate, is part of the Monte Desert located 55 km east of the City of San Juan, in Caucete Department (31°31'S, 67°51'W, 800-m elevation). In the wet season, average maximum temperature reaches 30.7°C and average minimum temperature reaches 19.6°C, with a mean annual rainfall of 89 mm. In the dry season, average maximum temperature drops to 20°C and average minimum temperature to 6°C (Cabrera, 1976; Warner, 2004).

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DOI: 10.1670/13-216



FIG. 1. Amplexus of *Odontophrynus* cf. *barrioi* from Quebrada de las Flores, San Juan, Argentina.

The taxonomic status of the study population is unclear because a recent review of *O. barrioi* (Rosset et al., 2007) mentioned that the southernmost range of the species is in northeastern San Juan province; our study population is located about 105 km southwest of the more austral population of *O. barrioi* (Rosset et al., 2007). The toads in our study population have some features of their external morphology that resemble *O. barrioi* (Rosset, pers. comm.).

*Odontophrynus* cf. *barrioi* is a poorly known species that apparently changes its thermoregulatory strategies throughout the year (Sanabria et al., 2012). The breeding season of the study population begins in September after an aestivation period of approximately 3 mo (LBQ, unpubl. data). *Odontophrynus* cf. *barrioi* lays individual eggs on the bottom of streams like other species in the genus (Lavilla and Rouges, 1992). The tadpoles have a prolonged time to metamorphosis (about 7 mo), and reach 76 mm in stage 38–41 of Gosner (1960) similar to *O. barrioi* (Gonzalez et al., 2014). Recently González et al. (2013) described the nematode parasite *Falcaustra sanjuanensis* found in *O. cf. barrioi*.

We walked the study site randomly and collected individuals by visual encounter (Heyer et al., 2001). We surveyed the study site once a month (from November 2006 to November 2007) and each field survey lasted 5 h (starting at 2000 h), covering an area of approximately 150,000 m<sup>2</sup>.

**Individual Measurements.**—We collected 47 toads, including 40 adults (20 males and 20 females) and 7 juveniles. We collected either calling males or pairs in amplexus during chorusing nights to ensure that all individuals were mature and they were breeding. We sacrificed the toads by injecting 2 mL of anesthesia (Xylocaine 2%, 2% lidocaine HCl, AstraZeneca Lab) into their lymph sacs. Toads were then fixed in 10% formaldehyde for 3 days and preserved in 70% ethanol. We determined the sexual size dimorphism for 17 morphological variables, measured with a digital caliper (accuracy 0.01 mm). Morphological variables

measured include snout–vent length (SVL), head width between the commissure of the mouth (HW), height of the head at the commissure of the mouth (HH), length of the head from the posterior margin of atrial opening of naris (HL), internaris distance (IND), eye–naris distance (END), eye–snout distance (ESD), interorbital distance (ID), eye diameter (ED), radio-ulna length (RUL), humerus length (HuL), hand length (HL), femur length (FL), tibia–fibula length (TbFL), calcaneum length (CaL), foot length (FL), and length of finger four (LF4). All individuals were deposited in the herpetological collection of Fundación Miguel Lillo, Tucumán, Argentina (FML: 27132–27178).

**Skeletochronology.**—Laboratory protocols followed the standard methods for skeletochronology (e.g., Smirina, 1972). Clipped digits from preserved specimens were washed in water for 30 min and then decalcified in 5% nitric acid for 30–45 min. The samples were then dehydrated, paraffin embedded, sectioned (14–16  $\mu$ m, Arcano<sup>®</sup>, Model RMT–30, rotation microtome), and stained by the Harris eosin–hematoxylin method. We took digital images, with a high-resolution camera SONY<sup>®</sup> SSC–DC50AP attached to a microscope Olympus BX50, from those diaphyses with the minimum medullar cavity and the maximum perimeter of bone. Cross sections were measured with the use of the computer package Image-Pro Plus Version 4.5 (Maryland, USA) and calibrated with the use of a standard micrometer. We recorded the presence/absence of the line of metamorphosis (LM) (line deposited when the aquatic larvae metamorphose to terrestrial juveniles), and lines of arrested growth (LAGs). The presence of the line of metamorphosis ensures there was no loss of the internal LAGs by reabsorption, which could lead to an underestimation of age. In those toads with no remnant of the line of metamorphosis, we estimated the degree of reabsorption by osteometrical analysis (Sagor et al., 1998; Tomašević et al., 2008). We then discriminated annual growth marks (LAGs, sensu stricto) from nonannual ones (irregular interruptions during

TABLE 1. Basic statistics for morphometric variables (for abbreviations see Materials and Methods section) of *Odontophrynus cf. barrioi*. Asterisks indicate significant differences between sexes in ANCOVA and ANOVA analyses.

Trait	Male (N = 20)	Female [N = 20]	P	Juvenile [N = 7]
	Mean $\pm$ SD (mm)	Mean $\pm$ SD (mm)		Mean $\pm$ SD (mm)
SVL	51.46 $\pm$ 4.64	52.42 $\pm$ 4.13	0.494	38.78 $\pm$ 3.91
HW	23.72 $\pm$ 2.20	24.90 $\pm$ 2.62	0.162	15.94 $\pm$ 2.21
HH*	10.47 $\pm$ 1.04	11.60 $\pm$ 1.14	0.001	8.48 $\pm$ 0.76
HL	17.65 $\pm$ 1.66	18.72 $\pm$ 2.11	0.108	13.75 $\pm$ 1.00
IND*	3.35 $\pm$ 0.34	3.82 $\pm$ 0.50	0.002	2.58 $\pm$ 0.22
END*	4.08 $\pm$ 0.45	4.94 $\pm$ 0.76	0.001	3.51 $\pm$ 0.41
ESD	9.31 $\pm$ 0.86	9.85 $\pm$ 1.66	0.294	5.47 $\pm$ 1.16
ID*	7.28 $\pm$ 0.71	8.00 $\pm$ 0.72	0.001	3.82 $\pm$ 0.81
ED	6.30 $\pm$ 0.68	6.64 $\pm$ 0.77	0.205	4.90 $\pm$ 0.46
RUL	11.22 $\pm$ 0.96	11.83 $\pm$ 1.23	0.096	7.98 $\pm$ 0.98
HuL	8.41 $\pm$ 1.31	7.98 $\pm$ 1.04	0.075	6.38 $\pm$ 0.74
HL	16.78 $\pm$ 1.28	17.64 $\pm$ 2.02	0.139	12.38 $\pm$ 1.71
FL*	22.66 $\pm$ 2.23	24.53 $\pm$ 2.97	0.022	17.01 $\pm$ 1.87
TbFL*	20.12 $\pm$ 1.28	21.06 $\pm$ 1.49	0.016	14.14 $\pm$ 1.86
CaL	9.56 $\pm$ 1.37	9.80 $\pm$ 1.54	0.901	7.02 $\pm$ 1.56
FL	28.32 $\pm$ 2.20	29.70 $\pm$ 2.52	0.069	21.10 $\pm$ 2.32
LF4	14.58 $\pm$ 1.43	14.97 $\pm$ 1.81	0.672	11.04 $\pm$ 1.44

inactivity periods), by the method described by Sinsch et al. (2007). Age was determined by two of us (FM and EAS), who counted LAGs independently to reduce bias. The age of maturity was defined as the lowest age recorded in a reproductive toad found in amplexus. We measured the longest and shortest perpendicular axes of bone perimeter (hereafter, BP, to the nearest micrometer) of two diaphyseal sections per specimen, following the methods of Hemelaar (1985). We determined the average diameter of bone perimeter by calculating the square root of the product of the two axis measurements.

**Demographic Life History Traits.**—Five life history variables were measured for each sex (sensu Leskovar et al., 2006): 1) age at maturity—the minimum number of LAGs counted in mature individuals collected during breeding activity; 2) longevity—the maximum number of LAGs counted in breeding individuals; 3) potential reproductive life span—the difference between longevity and age at maturity; 4) median life span—median age distribution; and 5) size at maturity—the average snout-vent length of all first breeders with the minimum number of LAGs.

**Statistical Analysis.**—All variables were log transformed to meet normality and homoscedasticity assumptions. We used multi- and univariate analyses of variance to test for differences in body size and diameter of bone perimeter between the sexes. We carried out ANCOVAs, using age as a covariate, to account for the effect of age on SVL. We also estimated sexual size dimorphism with the Lovich and Gibbons (1992) sexual dimorphism index (SDI): SDI = (size of larger sex/size of smaller sex)  $\pm$  1 (+1 if males are larger or  $-$ 1 if females are larger), and arbitrarily defined as positive when females are larger than males and negative for the contrary. We used linear regressions to test the association between body size (SVL and BM) and either age or diameter of the bone perimeter. All analyses were carried out with type III general linear models with the use of the PAST version 9.4 (Hammer et al., 2001) statistical packet, and a significance level of  $\alpha = 0.05$ .

## RESULTS

**Sexual Size Dimorphism.**—Of the 17 morphological variables measured, 6 showed differences between the sexes (Table 1). Four

variables were related to head size with females significantly larger than males (ANCOVA: HH:  $F_{1,37} = 12.13$ ,  $P = 0.001$ ; IND:  $F_{1,37} = 11.31$ ,  $P = 0.001$ ; END:  $F_{1,37} = 17.86$ ,  $P = 0.0001$ ; ID:  $F_{1,37} = 15.61$ ,  $P = 0.0003$ ; Cov.: SVL). Females also had significantly larger hind limbs than males (ANCOVA: FL:  $F_{1,37} = 5.71$ ,  $P = 0.02$ ; TbFL:  $F_{1,37} = 6.32$ ,  $P = 0.01$ ; Cov.: SVL). Females were larger in BP than males (Table 1), but ANOVA showed no significant effects of sex on BP ( $F_{1,36} = 0.50$ ,  $P = 0.48$ ). The sexual dimorphism index (SDI) in body size was 0.019 (SVL). In specimens of age 1–3 yr, where sample size allowed estimation (age = number of LAGs observed, see discussion), variation in SDI was (age of specimens/SDI) 1/0.019, 2/ $-$ 2.002, 3/ $-$ 2.009 for SVL. Note that females were larger than males in average SVL only in age 1. Nevertheless, in all three ages there were no significant effects of sex on SVL ( $P = 0.77$ , minimum value found in the three ANOVAs).

**Skeletochronology.**—Of 47 samples, 44 sections (18 males, 20 females, 6 juveniles) showed recognizable bone structures that allowed age determination. In these sections, well-defined lines of arrested growth (LAGs) were found in the periosteal bone and were relatively easy to count in order to assess individual age (Fig. 2). The line of metamorphosis was visible in 84% ( $N = 37$ ) of the samples. Moreover, even in those specimens where the metamorphosis line had been replaced during the formation of the endosteal bone, the first LAG was never completely removed. Therefore, endosteal reabsorption did not prevent age estimation. Annuli (Peabody, 1958) were distinguishable easily from actual LAGs. They always stained more faintly and were often broader, as described previously by Leclair et al. (2005), Sinsch et al. (2007), and Marangoni et al. (2009, 2011) in temperate and subtropical species.

We summarized the demographic life history traits (Table 2) and age structure (Fig. 3) of adult *O. cf. barrioi*. The minimum number of LAGs (=age) counted in reproductive individuals was one for both sexes (Table 2). Females were larger at maturity than males, but the differences between sexes in body size at maturity (SVL) were not significant (age 1 yr for both sexes, Mann-Whitney  $U$ -test = 7,  $P = 0.25$ ).

In males, maximum body size was measured at 1 yr of age, whereas in females it occurred at 4 yr. We found sexual differences in longevity (3 yr for males and 4 yr for females). Thus, the difference in potential reproductive life span (PRLS) between sexes was 2 yr. Average age of collected individuals tended to be higher in females than in males (Table 2), but it did not differ significantly (Mann-Whitney  $U$ -test = 172,  $P = 0.80$ ).

Age of *O. cf. barrioi* was correlated positively with SVL and BP. However, significant correlation between age and SVL was only observed in females ( $r^2 = 0.29$ ,  $P = 0.01$ ,  $N = 20$ ).

## DISCUSSION

We tested the sexual dimorphism of 17 morphological body variables of *O. cf. barrioi* from the Monte Desert, San Juan, Argentina. We found that females were larger in four variables corresponding to head morphology, which may be caused by different ecological conditions for the sexes (Smith and Roberts, 2003). Sexual dimorphism in head size has been observed in other groups such as snakes (Shine, 1991) and turtles (Lindeman, 2000; Butl  et al., 2008). Females have different energy requirements than males because the cost of egg production is high (Slatkin, 1984). Furthermore, trophic requirements of female *O. cf. barrioi* are apparently different from males because females consume larger prey on average than males (LBQ,

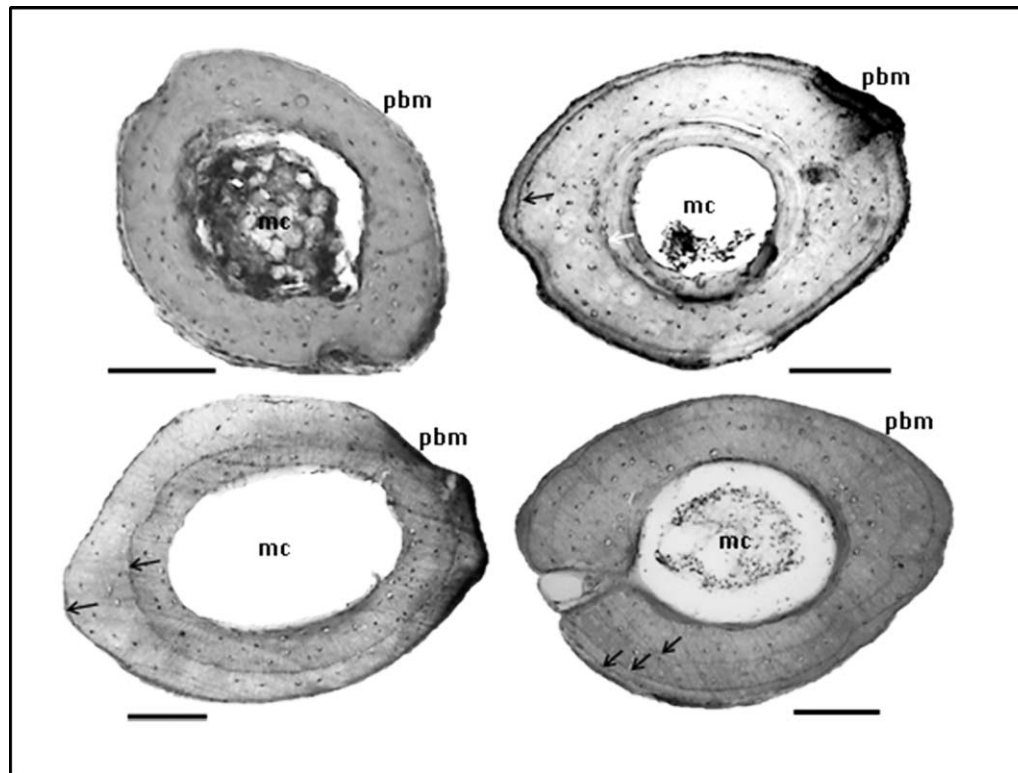


FIG. 2. Cross sections of phalanges stained with Ehrlich's hematoxylin of *Odontophrynus* cf. *barrioi*. Upper left: juvenile of 32.8-mm SVL, without LAGs formed. Upper right: male of 47.4-mm SVL and 1 yr. Lower left: male of 48.3-mm SVL and 2 yr. Lower right: male of 52.3-mm SVL and 3 yr. LAGs are indicated by black arrows. White arrow: line of endosteal resorption. eb: endosteal bone; mc: medullary cavity; pbm: periosteal bone margin. Scale bars: 100  $\mu$ m. All figures are at the same magnification.

unpubl. data). This supports the hypothesis that sexual dimorphism in the head dimensions of female *O. cf. barrioi* is related to food size selection (Slatkin, 1984). Bulté et al. (2008) also found that sexual dimorphism in the head of the temperate turtle species *Graptemys geographica* is related to differential selection of food items between the sexes. Sexual dimorphism in head size may be advantageous as related to individual fitness of *O. cf. barrioi* because of the obvious correlation between energetic (=food) intake and number or quality of offspring produced.

In addition, females had a longer tibia-fibula and femur than males, which may be related to their reproductive mode. *Odontophrynus* cf. *barrioi* lays its eggs singly on the bottom of water bodies (Lavilla and Rouges, 1992); therefore the longer limbs of females are beneficial for them as they move along the bottom of the pond depositing their eggs, with the male in amplexus. In *R. arenarum*, the metacarpal inner tuber and length of the humerus are larger in females than in males (Quiroga et al., 2004). The authors proposed that these differences help the female support her own weight and that of the male on her back when depositing eggs. Furthermore,

toads are often semisubmerged during amplexus, making locomotion more difficult for females. In male anurans, usually forelimbs are longer and more robust than those of females and young males. This provides advantages during amplexus, enabling males to withstand competitive attacks from other males (Lamb, 1984; Lee, 2001; Lee and Corrales, 2002).

Male and female *O. cf. barrioi* show similar SVLs. In amphibians, terrestrial postmetamorphic growth represents between 90 and 99.9% of total growth until average adult size is attained (Werner, 1986). Furthermore, this growth exhibits an indeterminate pattern with an exponential period that decreases considerably after the onset of reproduction, with the attainment of an asymptotic size (Hemelaar, 1988; Halliday and Tejedo, 1995). The main determinants of adult size variability in anurans (Monnet and Cherry, 2002; Hasumi, 2010; Sinsch et al., 2010) are related with differences in age at maturity, age structure, postmetamorphic growth rate, and sex-specific differences in mortality rate (Howard, 1981; Halliday and Verrell, 1988; Hemelaar, 1988), as well as restrictions on the growth of males because of the energy

TABLE 2. Populations life history traits of *Odontophrynus* cf. *barrioi*: AM = age at maturity of the youngest first breeders; PRLS = potential reproductive life span; SVL = snout-vent length.

Sex	N	Mean $\pm$ SE (LAGs)	Mode (Frequency)	Median life span (yr)	AM (LAGs)	Longevity (LAGs)	PRLS (yr)	SVL at AM $\bar{X} \pm$ SE (mm)	Maximum SVL (age) (mm)
Males	20	2.05 $\pm$ 0.20	2(7)	2	1	3	1	49.5 $\pm$ 3.12 (N = 5)	61.04 (at 1 LAGs)
Females	18	2.20 $\pm$ 0.21	2(9)	2	1	4	3	50.4 $\pm$ 0.94 (N = 5)	62.1 (at 4 LAGs)

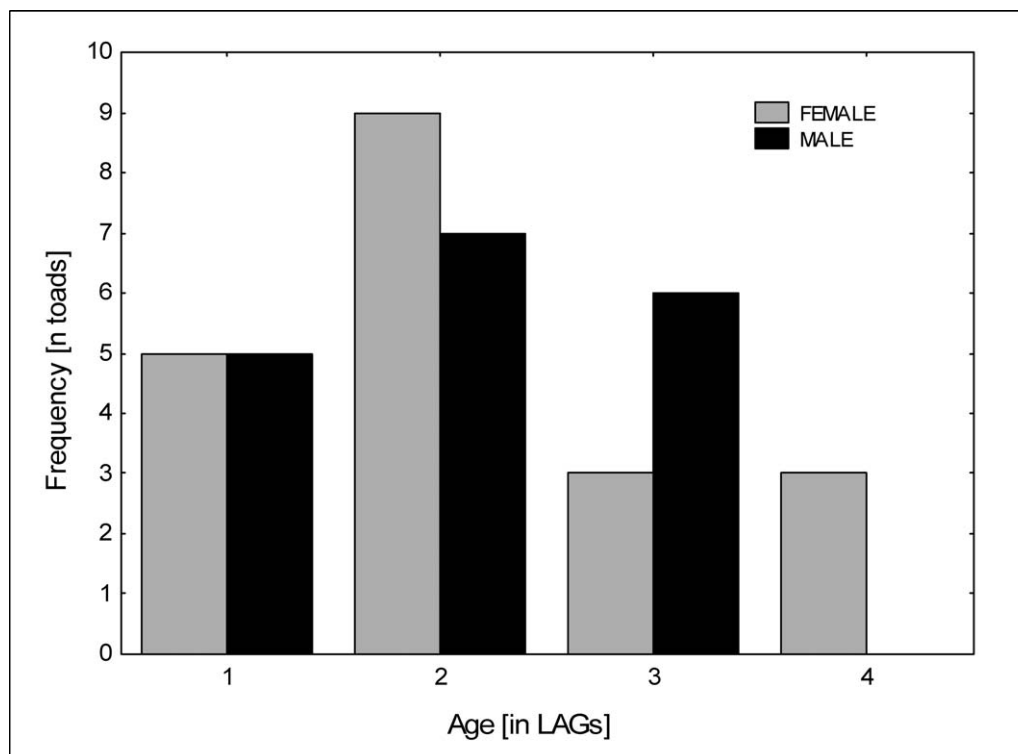


FIG. 3. Age distribution of *Odontophrynus cf. barrioi* from Quebrada de las Flores, San Juan, Argentina.

demand linked to reproductive activity and faster growth rates and delayed reproduction in females (Woolbright, 1989; Marangoni, 2006; Marangoni et al., 2008; Marangoni et al., 2011; Cajade et al., 2013). Thus, a possible explanation of the absence of sexual dimorphism in SVL observed in *O. cf. barrioi* could be the absence of sex differences in age at maturity, because both sexes reach maturity in 1 yr. Therefore, because there is no delayed reproduction in females, which could lead to differences in adult body size between sexes, they can devote the same time and energy to somatic growth (Stearns, 1992).

We found differences in longevity between sexes, with females living longer. Based on this, we suggest that both sexes may have different growth trajectories after the onset of reproduction, different selection pressures, or differences in predation rate by sex. Generally, the predation pressure on calling males is common during reproduction season (Woolbright, 1989). Future studies should address these questions to understand better the reasons behind the lack of sexual size dimorphism in some morphological traits of *O. cf. barrioi*.

*Acknowledgments.*—We are extremely grateful to anonymous reviewers for helpful corrections and constructive comments. We also thank M. Katzenberger and F. Hertel for correcting the English of this manuscript. We acknowledge J. M. Boeris for his assistance in sample processing. This project was partially supported by Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina.

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Accepted: 1 November 2014.

**Queries for hpet-49-02-13**

- 1. Author: This article has been lightly edited for grammar, style, and usage. Please compare it with your original document and make corrections on these pages. Please limit your corrections to substantive changes that affect meaning. If no change is required in response to a question, please write "OK as set" in the margin. Copy editor**