
REPRODUCTION AND SEXUAL DIMORPHISM OF THE ENDEMIC ANDEAN GECKO *HOMONOTA ANDICOLA* (SQUAMATA: PHYLLODACTYLIDAE) FROM CENTRAL WESTERN ARGENTINA

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Abstract.—Studies of reproductive biology are essential to understanding the life history of species and contribute to determining their conservation status and future protection. The Andean Gecko (*Homonota andicola*) is a small lizard endemic to central western Argentina and occurs in Monte, Puna, and High Andes environments. Our objective was to determine the reproductive cycle of a population of *H. andicola* in the Calingasta Department of San Juan, Argentina, to establish its reproductive potential, and determine if the sexes are sexually dimorphic, and, if so, its relationship with reproduction. *Homonota andicola* started its reproductive activity in early spring. A single egg was produced, and we found that at least two clutches were produced per reproductive cycle. The gonadal cycle varied with the seasons. For males, testicular development exhibited no variation, demonstrating a continuous reproductive state throughout the activity season. We found that sexes were sexually dimorphic in head length and head width, with these variables being more pronounced in males. We attribute this dimorphism to sexual selection favoring males with larger heads. This study is the first contribution to the biology of the species and its conclusions should serve as a starting point for future research in both an ecological context and in terms of biodiversity conservation..

Key Words.—body size; reproductive cycle; South American gecko

INTRODUCTION

Reproductive patterns, survival, and growth rate are the main characteristics of the life history of an organism (Wootton 1993; Martori and Aun 2010), with reproductive attributes being basic parameters for understanding how species adapt to their environment (Tinkle et al. 1970). The reproductive strategy of lizard species is determined by a particular set of environmental conditions (Tinkle et al. 1970). Environmental factors such as rainfall, temperature, and photoperiod (Hernández-Gallegos et al. 2002) influence the relative times of various reproductive events such as gametogenesis, copulation, gestation, clutch, hatching, or birth (Ibargüengoytía 2008). In warmer tropical and less seasonal climates, many lizards repeatedly reproduce throughout the season, producing smaller clutches during each reproductive episode (Mesquita et al. 2016b) than lizards from colder and seasonal climates, which tend to have clutches at lower frequencies but with larger sizes. In temperate regions, reproduction is usually seasonal and follows temperature

and day length patterns, with low temperatures in winter being a limiting factor for reproduction (Fitch 1970; Mesquita et al. 2016b). Oviparous species from habitats with seasonal environments show maximum reproductive activity in spring-summer. With this pattern, gonadogenesis occurs in the spring with subsequent courtship, copulation, and ovulation (Fitch 1970; Cuellar and Cuellar 1977). On the other hand, plasticity in lizard life-history traits is also influenced by genetic factors (Dunham et al. 1988; Mesquita et al. 2016a). For example, clutch size is a phylogenetically conserved attribute in geckos (Vitt 1986) and most species produce only one or two eggs at a time (Mesquita et al. 2015, 2016b), which is a relatively small number compared to most other lizard families (Mesquita et al. 2016a).

Lizards can present sexual dimorphism in body size as well as in the size of body parts (e.g., head, abdomen, and limbs; Herrel et al. 2001; Juri et al. 2018). The morphological variation between sexes has been explained by two main hypotheses (Cox and John-Alder 2007): male-biased dimorphism by sexual selection,

which gives advantages in male-male competition for territory and access to females for reproduction (Endler and Houde 1995), and female-biased dimorphism explained by fecundity advantage, where larger females are favored because litter/clutch size tends to be larger for larger females than smaller females (Pincheira-Donoso and Hunt 2017). A third hypothesis is that of niche divergence, where differential use of one or several resources by one sex can promote morphological differentiation between sexes (Schoener 1967; Hierlihy et al. 2013). This hypothesis, though, has been considered a consequence of sexual selection because some structures, such as the head and size of limbs, are associated with combat between males (Kuo et al. 2009; Juri et al. 2018) as well as with the use of resources, such as food or microhabitats. Therefore, in addition to the difference in size, analysis of the shape of different morphological attributes is a crucial component to consider when evaluating sexual dimorphism (Butler and Losos 2002; Kuo et al. 2009) and can be informative regarding morphological variation between sexes and the selective pressures imposed (Pianka 1986).

Homonota is a genus of small lizards belonging to the Phyllodactylidae family and is currently composed of 13 species (Cacciali et al. 2018) distributed throughout South America, including southern Bolivia and western Paraguay, Uruguay, as well as the Brazilian state of Rio Grande do Sul. In Argentina, it can be found along the border with Bolivia (25°S) all the way south to the province of Santa Cruz (52°S). The Andean Gecko or *Matuasto* (*Homonota andicola*) in Argentina is an endemic species found from Uspallata in the province of Mendoza to the town of Calingasta in the province of San Juan (Acosta et al. 2017). In San Juan, it can be found in the Monte and Puna ecoregions starting at 1,000 m elevation. It is a small (45 mm) saxicolous lizard (Fig. 1) active at dusk and dark (Acosta et al. 2017).



FIGURE 1. The Andean Gecko (*Homonota andicola*), Calingasta Department, San Juan, Argentina. (Photographed by Juan Carlos Acosta).

The one study published on this species (Blanco et al. 2009) was done with a population of *Homonota* that is now considered related to another taxonomical group (*darwini*), based on a recent taxonomical revision using molecular data (Mariana Morando, pers. comm.). Much is still unknown about this species with respect to its biology and state of conservation. The habitat of the population we studied faces diverse anthropic pressures related both to the construction of tourism infrastructure in the region, including the removal and transportation of soil, and to mining activities carried out within the species range of distribution. Taking this into account, our objective was to describe both the reproductive cycle and the morphometric sexual dimorphism of *H. andicola* in an area of Monte in San Juan to provide the first relevant data on its biology.

MATERIALS AND METHODS

Study site and specimens.—We worked in the center of the Calingasta Department (31°20'20.05"S, 69°25'13.87"W), 170 km west of the city of San Juan, Argentina (Fig. 2), which belongs to the Monte Phytogeographical Province (Márquez et al. 2017). In the valley between the Cordillera and Precordillera, like in other piedmont areas, the Monte is influenced by altitude and drought, encompassing extensive areas with scarce precipitation (on average < 100 mm per year). Xerophilous plants adapted to the warm dry climate predominate, forming low scrublands made up mainly of *Jarilla* (*Larrea divaricata*), *Alpataco* (*Prosopis flexuosa* var *depressa*) and the verbenacea *Mulguraea echegrayi* (no common name; Márquez et al. 2014). The study site had numerous accumulations of abandoned rubble on the banks of the Calingasta River because of intensive open-pit extraction of aluminum, iron, and magnesium sulfates during the 1970s (Fig. 2). In 2015, the study site was greatly modified by anthropic activities related to the widening of the Calingasta River and the construction of a bridge and viewpoints, among other infrastructure projects (Fig. 2). This caused a significant decrease in the population of *H. andicola*, leaving relics of the species that may have survived in some sectors (unpubl. data)

We captured lizards manually in spring (October 2014), summer (December 2013–2014) and fall (March 2014), at nighttime hours while lizards were active. For each lizard we caught, we measured snout-vent length (SVL) using digital dial calipers (± 0.010 mm). We did not perform captures during the colder months because the lizards were not active. We considered the thermal seasons proposed by Poblete and Ruiz (2006) to analyze the seasonal variations of reproductive parameters, which established seasons as summer from 14 November to 10 March, fall from 11 March to 25

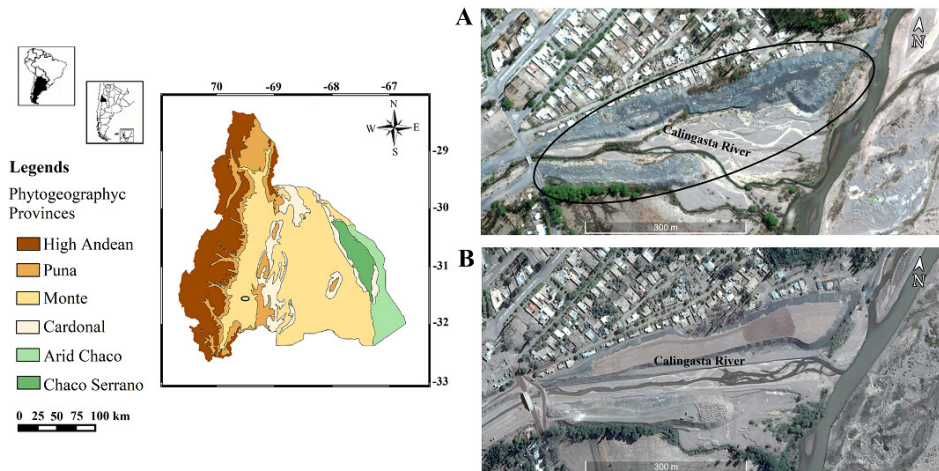


FIGURE 2. Map of the phytogeographic provinces of San Juan, Argentina, extracted from Los Reptiles de San Juan (Márquez et al. 2017). (A) Study site in the center of the Calingasta Department (ovoid outline) where we sampled the Andean Gecko (*Homonota andicola*) population (2013–2014). (B) Anthropogenic modifications made to the site where the samples were collected in 2015. (Satellite images taken from Google Earth).

May, winter from 26 May to 31 August, and spring from 1 September to 13 November. We took these lizards to the laboratory and euthanized them by intraperitoneal administration of sodium thiopental anesthetics fixed in Bouin's solution for 24 h. We preserved each specimen in 70% ethanol and deposited all the specimens in the Scientific Herpetological Collection of the Facultad de Ciencias Exactas, Físicas y Naturales at the Universidad Nacional de San Juan, Argentina.

Reproduction.—For females, we registered the number of yolked follicles and the number of eggs in the oviduct, with the length and width of both being subsequently measured using a digital dial caliper (± 0.01 mm). To calculate their volumes, we applied the formula used to calculate the volume of an ellipsoid:

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

where L = length and A = width (Dunham 1983). We also evaluated the condition of the oviduct, being either widened or not. Females presenting both yolked follicles and oviductal eggs were considered as subsequent clutches. For males, we observed the coiled state of the epididymis (convoluted epididymides) as an indicator of sexual maturity (Anderson and Vitt 1990; Vitt 1991; Ramírez-Bautista et al. 2021) and measured both the width and length of the testicles to calculate their volumes with the formula of an ellipsoid sphere (Dunham 1983) as above.

Sexual dimorphism.—We measured 11 morphometric variables in adult males and females using a digital dial caliper (± 0.01 mm): snout-vent length (SVL); head length (HL); head width, length between the corners of the mouth (HW); maximum head height

(HH); distance of separation between front and back limbs (DBL); humerus length (HUL); radius-ulna length (RUL); femur length, from the groin to the knee (FL); tibia-fibula length (TFL); inter-ocular distance (IOD); and tail length (TL).

Statistical analyses.—To make comparisons between samples and sexes, we used Analysis of Variance (ANOVA) and Analysis of Covariance (ANCOVA), respectively. We analyzed the effects of seasons (spring, summer, and fall) on gonadal cycles using ANOVA, although when the assumptions of normality and/or homogeneity of variance were not met, we used the non-parametric Kruskal-Wallis (KW) test. To test for pair-wise differences if the KW test was significant, we used Dunn's test. To test morphological differences between sexes in terms of snout-vent length (SVL), we performed a Student's t -test (the assumptions of independence, normality, and equal variances were met). We tested for overall differences in morphology between sexes using Multivariate Analysis of Covariance (MANCOVA), with sex as factor and body size (SVL) as covariate. Furthermore, we performed ANCOVAs for each morphological variable independently to determine which variables differed between males and females. The variable TL was not included in our analysis of the morphological variation between sexes, as it was not available for all studied specimens. Significance levels for the tests of each ANCOVA were calculated using the Bonferroni adjustment of 10 comparisons with $P \leq 0.005$.

RESULTS

Reproduction.—We analyzed 45 individuals: 26 females and 19 males. The *H. andicola* we studied had an annual reproductive cycle, starting its reproductive

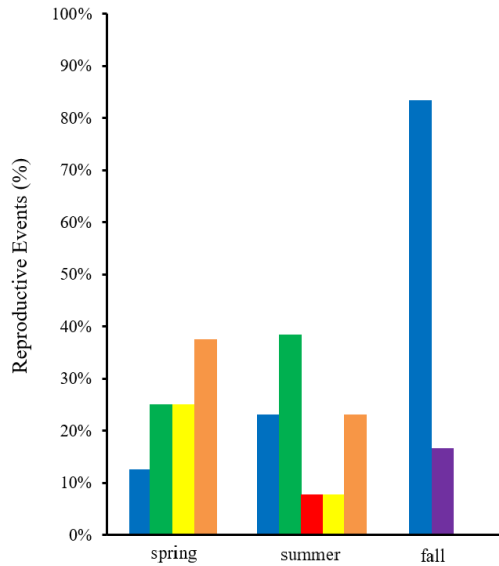


FIGURE 3. Percentage of reproductive events of the Andean Gecko (*Homonota andicola*) by season. Sample size for each season: spring = 8, summer = 13, fall = 5. Blue bars = non-reproductive, green bars = yolked follicles, red bars = yolked follicles, egg, and widened oviduct, yellow bars = egg in oviduct and yolked follicles, orange bars = egg in oviduct, and purple bars = widened oviduct.

activity in early spring. Reproductive activity in females varied over time. Ninety percent of females were reproductively active in spring and 75% in summer, with no reproductive activity in fall (Fig. 3). Minimum reproductive size of females was 31.6 mm SVL. A single egg was produced with evidence of double clutching based on the simultaneous occurrence of yolked follicles, egg, and a widened oviduct (Fig. 3). We observed smaller individuals (young) in October and December, corresponding to spring and summer, which indicates that hatching takes place during this period.

Gonadal activity in females varied significantly over time ($H = 8.65$, $df = 2$, $P = 0.010$; Fig. 4), with

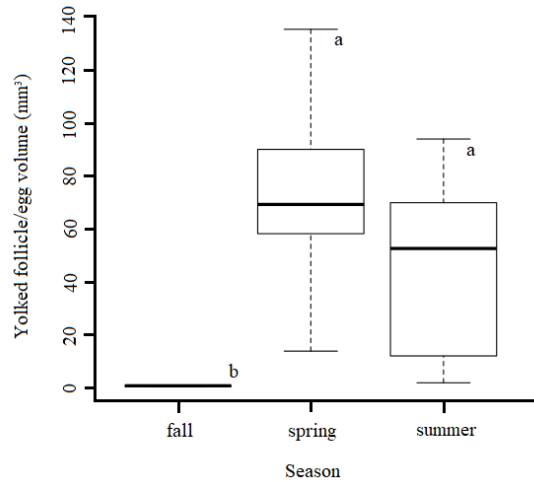


FIGURE 4. Variation in female reproductive activity based on the number of yolked follicles per egg volume of the Andean Gecko (*Homonota andicola*) by season: spring, summer, fall. Sample size for each season: spring = 8, summer = 13, fall = 5. Different letters (a, b) indicate significant differences.

fall showing significantly less activity compared to spring and summer ($P < 0.050$ for both comparisons). For males, minimum reproductive size was 29 mm SVL. Testicular development was synchronous with the female gonadal cycle; however, testis volume did not differ significantly between seasons ($F_{2,16} = 0.020$, $P = 0.980$; Fig. 5).

Sexual dimorphism.—Snout-vent length between males and females were not significantly different ($t = 1.240$, $df = 43$, $P = 0.221$). All morphometric variables, except for tail length (TL), were positively related to increasing SVL (Table 1). Significant differences in body shape occurred between sexes (Wilks' $\lambda = 0.633$, $P = 0.027$). Two morphological variables differed significantly between males and females: head length (HL) and head width (HW), with these variables being

TABLE 1. Analysis of sexual body size dimorphism in adult Andean Geckos (*Homonota andicola*) from San Juan, Argentina, showing the mean \pm standard error in millimeters. Comparisons were made with ANCOVA for each morphometric variable, with snout-vent length as the covariate. The degrees of freedom for each F value are 1 and 42. Asterisks (*) indicate significant difference between sexes ($n = 45$) with $P < 0.005$ using the Bonferroni adjustment method with 10 comparisons.

| Morphometric variable (mm) | Males | Females | F | P |
|--|-----------------|-----------------|-------|--------|
| Head length (HL) | 7.31 \pm 0.11 | 7.26 \pm 0.09 | 9.554 | 0.003* |
| Head width (HW) | 5.16 \pm 0.11 | 4.96 \pm 0.09 | 5.470 | 0.001* |
| Maximum head height (HH) | 3.38 \pm 0.07 | 3.39 \pm 0.05 | 0.775 | 0.383 |
| Distance of separation between limbs (DBL) | 15.2 \pm 0.33 | 15.9 \pm 0.29 | 1.519 | 0.224 |
| Humerus length (HUL) | 3.38 \pm 0.07 | 3.39 \pm 0.05 | 0.597 | 0.443 |
| Radius-ulna length (RUL) | 3.24 \pm 0.11 | 3.22 \pm 0.06 | 1.041 | 0.313 |
| Femur length (FL) | 3.96 \pm 0.08 | 3.90 \pm 0.07 | 2.044 | 0.160 |
| Tibia-fibula length (TFL) | 3.51 \pm 0.07 | 3.53 \pm 0.07 | 0.330 | 0.568 |
| Inter-ocular distance (IOD) | 3.08 \pm 0.10 | 2.97 \pm 0.08 | 3.244 | 0.078 |

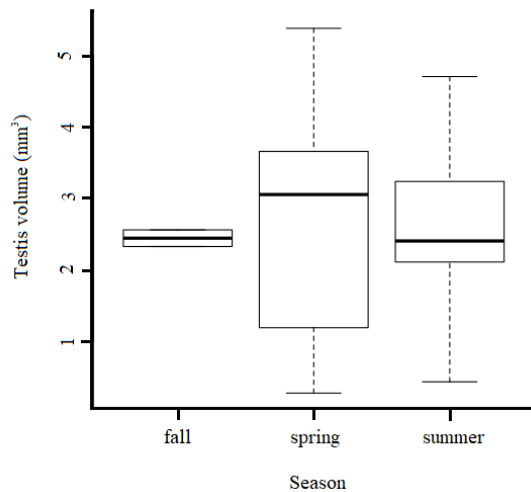


FIGURE 5. Variation in male reproductive activity based on testes volume of the Andean Gecko (*Homonota andicola*) by season: spring, summer, fall. Sample size for each season: spring = 8, summer = 9, fall = 2.

greater in males than in females (Table 1). There were no significant differences between males and females for other morphometric variables (Table 1).

DISCUSSION

Reproduction.—The beginning of the reproductive cycle in *H. andicola* in early spring agrees with those obtained for other species of the genus, such as the South American Marked Gecko or *Matuasto* (*H. horrida*; Aun and Martori 1994; Cruz 1994; Martori et al. 2002; Nieva et al. 2013; Pelegrin and Bucher 2015), the Borelli's Marked Gecko or *Matuasto* (*H. borelli*; Gomez and Acosta 1998), the Argentine Marked Gecko (*H. whithii*; Martori et al. 2002), the Underwood's Marked Gecko or *Matuasto* (*H. underwoodi*; Blanco et al. 2011), and *H. taragui* (no common name; Cajade et al. 2013). There were differences with those observed for Darwin's Marked Gecko (*H. darwinii*) in Patagonia, however. Females skip a year of reproduction, developing an annual-biennial cycle (Ibargüengoytía and Casalins 2007). *Homonota darwinii* is restricted to cold areas with reduced availability for daily and seasonal activity, which could explain the differences. Moreover, minimum reproductive sizes for *H. andicola* males and females are smaller than those of other species of the genus, such as *H. horrida* (39.1–40.1 mm SVL; Cruz 1994; Nieva et al. 2013) and *H. darwinii* (36.5 mm SVL; Ibargüengoytía and Casalins 2007).

All species of *Homonota* are oviparous, and for those for which the size of the clutch is known, it is typically a single egg (Gómez and Acosta 1998; Martori et al. 2002; Ibargüengoytía and Casalins 2007; Blanco et al. 2011; Nieva et al. 2013). We found that *H. andicola*

produced only one egg per reproductive bout. We found individuals with yolked follicles, an egg in the oviduct, and a widened oviduct simultaneously, which suggests that this species has at least two clutches in the annual reproductive cycle. Evidence of multiple clutches has been found in other studies of geckos (Vitt 2000; Kretzschmar and Abdala 2001; Nieva et al. 2013; Aurich et al. 2015; Pelegrin and Bucher 2015), which seems to be a generalized characteristic among species in Gekkonidae (Vitt 1986). The number of clutches seems to vary for other species of the genus, however. For *H. horrida* in the Semi-arid Chaco (Cruz 1994), the Arid Chaco (Pelegrin and Bucher 2015), and the Monte (Nieva et al. 2013), at least two clutches of one egg were reported per reproductive period, while for the same species in the Chaco Serrano, one (Aun and Martori 1994) and two clutches (Martori et al. 2002) by reproductive period were reported in two localities at approximately the same latitude. The differences recorded in the number of clutches for *H. horrida* could indicate an adaptive response to the variations in climate and availability of food from year to year (Fitch 1985; Pelegrin and Bucher 2015). On the other hand, completing various clutches per reproductive cycle could be related to strategies aimed at guaranteeing survival and success for at least one of the eggs in environments with severe risks of dehydration (Cruz 1994). In deserts of Africa and Australia, lizard reproduction is cyclical but extended, in some cases with more than one period of egg laying, and most species produce two eggs per clutch (Pianka and Pianka 1976; Pianka and Huey 1978). For *H. andicola*, we observed juvenile individuals in spring and summer, indicating that hatching takes place during these two seasons.

The pattern of the reproductive cycle in *H. andicola* is similar to those observed in other congeners that inhabit different environments of Argentina at similar latitudes and elevations. Females reproduce annually, with ovulation and mating taking place in spring and egg laying and hatching happening in summer. They present one or two clutches per reproductive cycle. In contrast, *H. darwinii* is the southernmost gekkonid species, which lives at higher latitudes (35°S–52°S) with low average temperatures and reproduces annually or every 2 y (Ibargüengoytía and Casalins 2007). The reproductive cycle appears to be strongly affected by the shorter activity season that limits thermal and feeding opportunities, resulting in the inability to reproduce each year (Boretto et al., 2020). Therefore, these critical conditions select prolonged reproductive cycles and low reproductive production (Ibargüengoytía and Casalins 2007), where clutch size is influenced by the environment.

For males, there were no significant differences in testicular development among seasons. Male

reproductive activity seems to be continuous (Cruz 1994). These results coincide with those found for *H. darwini* (Ibargüengoytia and Casalins 2007) and *H. horrida* (Nieva et al. 2013). In *H. whittii* and *H. horrida* (Martori et al. 2002), however, testicular development differs among seasons.

Sexual dimorphism.—The sexual dimorphism that we found in the head dimensions of *H. andicola* could be attributed to sexual selection (Olsson et al. 2002; Cox and John-Alder 2007) favoring males with larger heads. These characteristics are particularly associated with intra and interspecies agonistic encounters (Hibbitts et al. 2005), forced copulation with females (Zuffi et al. 2011), defense of resources (Vitt and Zani 1996), and territorial acquisition and defense (Gruber and Henle 2004). The genus *Homonota* has one of the proportionally broadest snouts among gekkotans, with *H. darwini*, *H. borellii*, *H. uruguayensis*, and *H. andicola* being the most extreme (Daza et al. 2017). The significant sexual dimorphism in head length and width that we found for *H. andicola* males are similar to populations of *H. horrida* in Salta, Argentina (Cruz 1994), where males also exhibit sexual dimorphism in head dimensions. On the other hand, these results differ from those found in populations of *H. horrida* in San Juan, Argentina (Nieva et al. 2013), and populations of *H. darwini* in Patagonia, Argentina (Ibargüengoytia and Casalins 2007), though for different environments and latitudes. This could suggest that sexual dimorphism is perhaps not strongly fixed by phylogeny, but rather could depend evolutionarily on the recent history of each species and its current distribution. Larger head size in males than in females has also been observed for other Phyllodactylidae geckos (Atzori et al. 2007; Torki et al. 2010; Zuffi et al. 2011; De Fuentes-Fernández et al. 2016; Souza-Oliveira et al. 2017).

It is not known if there exist agonistic and territorial interactions in this population of *H. andicola*; however, male *H. horrida* have been observed in the dressée position (Abdala 1986), an intimidating posture in the presence of other individuals of the same or different species. We found no differences in SVL between the sexes, which is true for *H. horrida* (Cruz 1994; Nieva et al. 2013), but for *H. darwini* in Patagonia (Ibargüengoytia and Casalins 2007), females are larger than males. No differences in SVL between the sexes occur in some geckos in the family in New Zealand (Hare and Cree 2005), South Africa (Hibbitts et al. 2005), Brazil (Recoder et al. 2012), and Iran (Torki et al. 2010). Nevertheless, in other species belonging to the Phyllodactylidae family, males are larger than females (Johnston and Bouskila 2007; Torki et al. 2010; Zuffi et al. 2011; Nazarov et al. 2013; De Fuentes-Fernández et al. 2016) or females are larger than males (Vitt 1986,

1995; Colli et al. 2003; Souza-Oliveira et al. 2017).

Our study contributes the first data on the natural history of gecko species for which there are few ecological data, providing information on its reproductive biology and morphological traits associated with reproduction. Future studies would be useful to understand the biology of this species in depth and to be able to interpret the observed dimorphism and its relationship with reproduction, as well as with other aspects of its ecology (e.g., diet, behavior, etc.). Increased information on this species and for other species of the genus will allow for comparisons and interpretations in an evolutionary context.

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