

Captive observations on reproduction of the Peak Tree Iguana, *Liolaemus monticola* (Squamata: Liolaemidae), an endemic species of Chile

Observaciones en cautiverio sobre la reproducción de la lagartija de los montes, *Liolaemus monticola* (Squamata: Liolaemidae), una especie endémica de Chile

Claudio Reyes-Olivares^{1,*}, Francisco Vidal², Nicol Quiroga², Esteban San Juan², Isidora Rivera³, Carlos Garín^{3,4}, Sebastián Jiménez⁵ & Carezza Botto-Mahan²

¹Escuela de Medicina Veterinaria, Facultad de Medicina Veterinaria y Agronomía, Universidad de Las Américas, Manuel Montt 948, Providencia, Santiago, Chile.

²Laboratorio de Ecología de Interacciones, Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Ñuñoa, Santiago, Chile.

³Departamento de Ecología y Biodiversidad, Facultad de Ciencias de la Vida, Universidad Andrés Bello, Santiago, Chile.

⁴Glauca Ambiental, Santiago, Chile.

⁵Laboratorio de Ontogenia y Filogenia, Departamento de Biología, Facultad de Ciencias, Universidad de Chile, Ñuñoa, Santiago, Chile.

*Corresponding author: creyeso@udla.cl

ABSTRACT

Liolaemus is a diverse genus of South American lizards whose reproductive biology remains poorly known in several species. We describe reproductive aspects of *Liolaemus monticola*, an endemic Chilean species, based on two gravid females that laid eggs in captivity. Both females produced four eggs, with different hatching success. The incubation period lasted 52–58 days. Measurements of size, mass, growth rate, and body mass index of hatchlings are reported. These data provide relevant information for future conservation actions.

Keywords: hatching, incubation, lizards, neonate, oviposition.

RESUMEN

Liolaemus es un género diverso de lagartos sudamericanos cuyo conocimiento reproductivo es limitado en varias especies. Se describen aspectos reproductivos de *Liolaemus monticola*, especie endémica de Chile, a partir de dos hembras grávidas que pusieron huevos en cautiverio. Ambas produjeron cuatro huevos, con distintas tasas de eclosión. El período de incubación fue de 52–58 días. Se reportan medidas de tamaño, peso, crecimiento e índice de masa corporal de los neonatos. Estos antecedentes aportan información relevante para futuras acciones de conservación.

Palabras clave: eclosión, incubación, lagartos, neonato, oviposición.

Liolaemus is a genus of lizards with 290 species (Uetz *et al.* 2025) and is the third most taxonomically diverse among terrestrial tetrapods (Abdala *et al.* 2021; Moya *et al.* 2025). The species of this genus are widely distributed in the southern cone of South America, found latitudinally from the center of Peru to Tierra del Fuego, and from the Atlantic and Pacific ocean

coasts, from sea level to 5,400 m a.s.l. in the Andes (Abdala *et al.* 2021). Within *Liolaemus*, two clades are recognized, *Liolaemus sensu stricto* and *Eulaemus*, which are also known as the 'Chilean' and 'Argentine' clades, respectively, since most are found on the west (Chile) and east (Argentina) sides of the Andes (Esquerre *et al.* 2019). These clades include numerous

groups that present a variety of morphological, ethological, genetic, and ecological characteristics, as well as different reproductive modes, which have allowed them to colonize environments from moderate to extreme climatic conditions (Pincheira 2012; Esquerré *et al.* 2019; Abdala *et al.* 2021; Moya *et al.* 2025).

Remarkable reproductive characteristics are recognized in *Liolaemus*. This clade has a similar proportion of oviparous and viviparous species (Abdala *et al.* 2021), which results from different reversion events from oviparous to viviparous, and vice versa, throughout its evolution (King & Lee 2015; Esquerré *et al.* 2019). Interestingly, an example of reproduction by parthenogenesis is reported in this clade (Abdala *et al.* 2016). All these characteristics have made *Liolaemus* a model study group for the evolution of reproductive modes in tetrapods (Schulte *et al.* 2000; Cei *et al.* 2003; Pincheira-Donoso & Tregenza 2011; Pincheira-Donoso *et al.* 2013; Esquerré *et al.* 2019; Cruz *et al.* 2022). However, there are many unknown aspects about the reproductive biology of many *Liolaemus* species, principally those distributed on the western side of the Andes (Ibargüengoytía 2008). For example, of the approximately 100 Chilean species of *Liolaemus* (Ruiz de Gamboa 2020; Moya *et al.* 2025; Uetz *et al.* 2025), at least 15 have known reproductive cycles: *L. nigromaculatus* (Wiegmann, 1834), *L. pictus*, *L. signifier*, *L. tenuis* (Duméril & Bibron, 1837), *L. lemniscatus* Gravenhorst, 1838, *L. bibronii* (Bell, 1843), *L. bellii* Gray, 1845, *L. gravenhorstii* (Gray, 1845), *L. magellanicus* (Hombron & Jacquinot, 1853), *L. jamesi* (Boulenger, 1891), *L. leopardinus*, *L. nigroviridis* Müller & Hellmich, 1932, *L. zapallarensis* Müller & Hellmich, 1933, *L. sarmientoi* Donoso-Barros, 1973, and *L. puna* Lobo & Espinoza, 2004 (Donoso-Barros 1966; Lemus & Wacyk 1969; Lemus *et al.* 1981; Ortiz 1981; Leyton *et al.* 1982; Jaksic & Schwenk 1983; Leyton & Valencia 1992; Ibargüengoytía & Cussac 1996; Medina & Ibargüengoytía 2010; Fernández *et al.* 2015), while most of the other species present anecdotal and incomplete data on their modes of reproduction and reproductive cycles (Donoso-Barros 1966; Ibargüengoytía *et al.* 2002; Ibargüengoytía 2008; Valladares & Briones 2012; Demangel 2016; Mella 2017a, 2017b; Troncoso-Palacios & Labra 2017).

Liolaemus monticola Müller & Hellmich, 1932 (Fig. 1) is an endemic species to Chile, whose information about its reproductive biology is almost nil and has been reported only as anecdotal observations. It is an oviparous species whose females deposit 3-4 eggs with developed embryos (Donoso-Barros 1966). Its copulation period occurs in October (spring in the southern hemisphere), and its pregnancy is from November to January (spring-summer) (Donoso-Barros 1966;

Ibargüengoytía 2008). Notably, information on temperature and humidity requirements for the eggs, incubation/hatching time, and biometric data for neonate growth remains unknown. In this work, from two gravid females who laid eggs in captivity, we describe reproductive aspects for the first time.

Liolaemus monticola is distributed latitudinally from the Coirón mountain range, Coquimbo Region (31°57' S; 70°45' W), to Alto de Vilches, Maule Region (35°36' S; 71°05' W), and between 300-2500 m a.s.l. (Mella 2017a; Abdala *et al.* 2021). It is a saxicolous lizard, occupying a rocky habitat with shrubs on slopes and hills, preferably xeric (Mella 2017a), and it has an insectivorous diet specialized in eating ants (Jara & Muñoz-Pedreros 2018). This lizard presents apparent sexual dimorphism where females have a slender appearance, less blackish and reddish flanks, and grayer backs with less obvious light blue scales than males (Fig. 1), and only males have two precloacal pores (Mella 2017a).

In November 2022, during an ongoing study of *L. monticola*, we captured by noosing a total of seven adult females (mean snout-vent length, $SVL \pm SD = 51.93 \pm 5.31$ mm), four from Chacabuco ($SVL \pm SD = 53.19 \pm 6.34$ mm), and three from Pillo Pillo ($SVL \pm SD = 50.26 \pm 4.10$ mm), both from Valparaíso Region. We verified the estimated age and sex of each individual by observation of the base of the cloaca and by other morphological characteristics (e.g., presence or absence of precloacal pores), and transported them in voile bags inside individual plastic boxes (volume: 0.7 L; 17 x 12 x 6 cm) to the vivarium of the Laboratory of Ecology of Interactions, Faculty of Sciences, University of Chile, located in Santiago. Upon arrival, all specimens were relocated to individual terrariums (volume: 16 L; 35 x 20 x 23 cm) containing Kraft paper as a substrate, a shelter, and a couple of rocks. Water was provided with sprinklers for the first week, and then *ad libitum* dispensed in water containers (3 ml). Individuals were fed thrice weekly with larvae of *Tenebrio molitor* Linnaeus, 1758, and adults of *Drosophila melanogaster* Meigen, 1830 (Curly phenotype), sprinkled with vitamins and calcium (SERA Reptimineral C). The terrariums were placed in an indoor vivarium with conditions mimicking those recorded in the field site during normal spring days, photoperiod 14:10 h light: dark, temperatures between 25 °C and 30 °C, and continuous ventilation. Temperature and light were provided with an artificial UV/IR bulb (Exo Terra Solar Glo 125 W) placed 30 cm above the terrarium base. Relative humidity (RH) and temperature were measured using a Hygro-thermometer (Extech 445715, United States; Humidity: 10 to 99% RH; Temperature: -10 to 60 °C; Accuracy: ±4% RH, ±1 °C).



FIGURE 1. Adults (A) female and (B) male of *Liolaemus monticola*. / Hembra (A) y macho (B) adultos de *Liolaemus monticola*.

In the laboratory, we visually noticed that two of the seven females were gravid: LmCH09, captured on November 17, 2022, in Chacabuco (from now, F1; SVL = 54.8 mm; weight = 4.4 g), and LmPP04, captured on November 29, 2022, in Pillo Pillo (from now, F2; SVL = 51.9 mm; weight = 4.4 g), so an up-side down small container (volume: 0.25 L) filled with leaf soil was added to their terrarium so they could lay their eggs in them.

Immediately after we noticed oviposition, each egg was gently photographed on graph paper and weighted (g)

with a balance (Boeco, Germany; accuracy: 0.1 mg), and then transferred carefully inside a plastic container (0.5 L) filled with vermiculite (Fig. 2A) to an incubator (ZOOMED reptibator incubator; Fig. 2B), that maintained a mean RH of 80% and a mean temperature of 28 °C. Eggs were left in the dark and in the same position as they were initially and were not disturbed for the remainder of the incubation period until the hatching of the neonates, except when they were visually inspected each day.

The neonates were maintained under the same conditions

as the females, and we inspected them daily to assess their condition and record shedding events. We also weighed them with a balance (Boeco, Germany; Accuracy: 0.1 mg) once a week from hatching to week 32 in captivity to assess their growth.

We calculated the Hatching Rate (HR) using the formula $HR = \text{number of neonates}/\text{number of eggs}$. For the growth rate, we used the software ImageJ (version 1.x, Schneider *et al.* 2012), where individuals were measured weekly until week 32 in captivity using a photograph on graph paper, and the difference between consecutive measurements was calculated. We calculated the Body Mass Index (BMI), using the equation $BMI = M/SVL^2$ (Peig & Green 2010), where M is the mass of the lizard. All data are expressed as mean \pm standard deviation (SD).

Both gravid females laid four eggs (ALS = 4), F1 on November 29, 2022, and F2 on January 2, 2023. The eggs had smooth, oval, and white shells (Fig. 2A) and were buried underground. We did not observe any maternal care behavior during the incubation period.

Only one of the four eggs (HR = 0.25; egg weight = 0.54 g) laid by F1 hatched between January 23-26, 2023, having an incubation period of 55-58 days; the neonate was named N1 (SVL = 25 mm). Conversely, only three of the four eggs (HR = 0.75) laid by F2 hatched between February 22-23, 2023, reaching an incubation time of 52-53 days. We called neonates as N2 (SVL = 27.2 mm; weight = 0.70 g), N3 (SVL =

24.9 mm; weight = 0.63 g), and N4 (SVL = 23.6 mm; weight = 0.63 g) (Fig. 2C; Fig. 3).

At birth, all the neonates presented an opaque coloration in gray and brown tones, in addition to the typical dot design of the adult morph, but with less brightness (Fig. 2C). Remarkably, N2, N3, and N4 presented malformations in their tail, presumably caudal scoliosis (lateral curves of the spine, Bateman *et al.* 2022; Fig. 3).

All the neonates accepted tenebrionids and flies weekly, but N1, the one with high length and weight (Fig. 4), was a better eater than the others. N1 showed a progressive increase in weight from hatching until the seventh week, when it stopped eating and began to lose weight (Fig. 4); it died of unknown causes in the eighth week of life.

The other neonates (Fig. 3) also increased their body size: at week 25, they reached a SVL of 38.4 mm (N2), 33.2 mm (N3), and 33.1 mm (N4). Weekly average growth rate had a high interindividual variability, with a mean value of 1.54 (\pm 1.62) mm, 0.83 (\pm 1.34) mm, and 0.81 (\pm 2.26) mm for N2, N3, and N4, respectively. Besides, they progressively increased their weight, although N2 always outweighed N3 and N4 from week 7, reaching a maximum weight of 3.7 g at week 32 (Fig. 4). N3 and N4 reached a maximum weight of around 1.5 g at week 26, gradually decreasing in both neonates until week 32 (Fig. 4). The average BMI of N2, N3, and N4 for 32 weeks was 0.13 (\pm 0.022), 0.10 (\pm 0.008), and 0.09 (\pm 0.007), respectively.

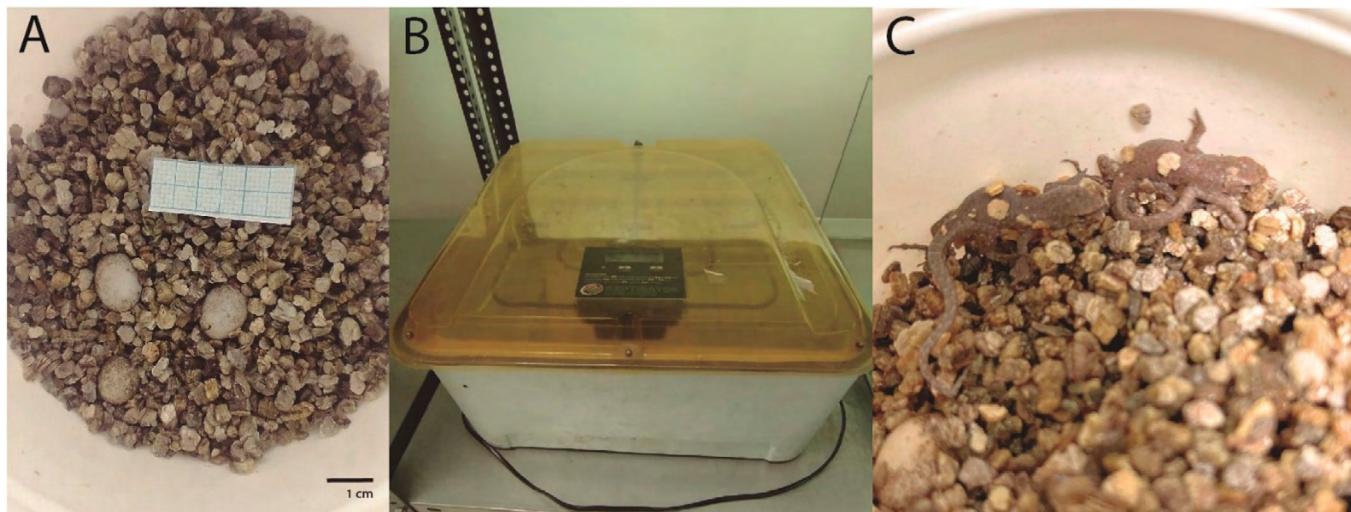


FIGURE 2. (A) Eggs of *Liolaemus monticola* were laid in the incubator. (B) ZOOMED reptibator incubator. (C) Neonates of *L. monticola* at the time of hatching. / (A) Huevos de *Liolaemus monticola* puestos en la incubadora. (B) Incubadora ZOOMED Reptibator. (C) Neonatos de *L. monticola* al momento de la eclosión.

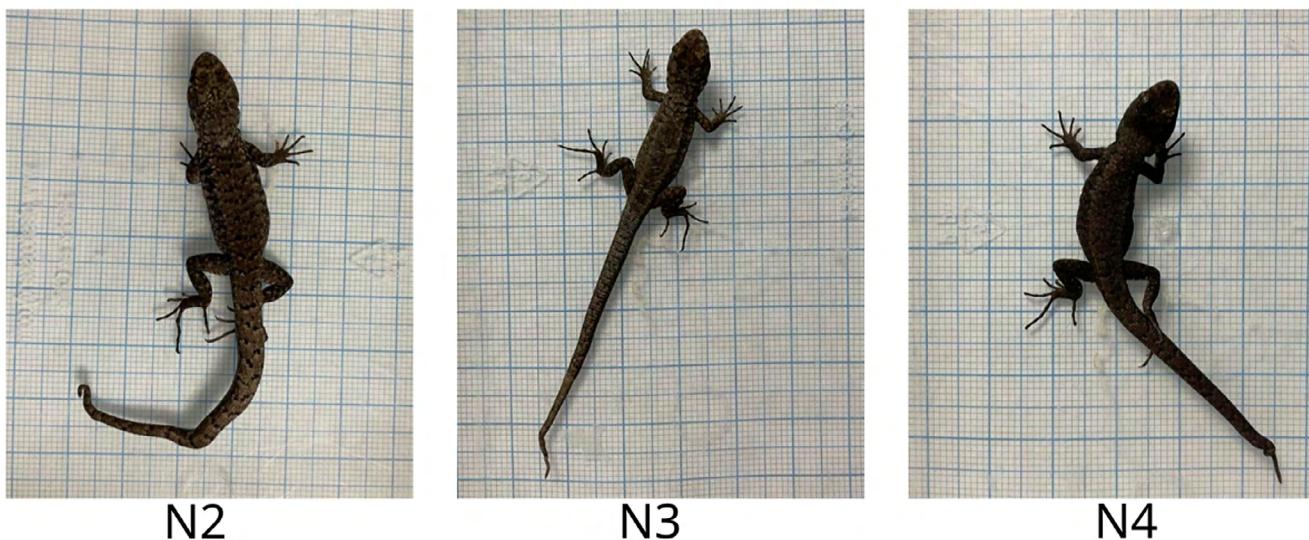


FIGURE 3. Juveniles N2, N3, and N4 of *Liolaemus monticola* at week 20. Note the malformations at the back end of his tail. / Juveniles N2, N3 y N4 de *Liolaemus monticola* en la semana 20. Nótese las malformaciones en el extremo posterior de su cola.

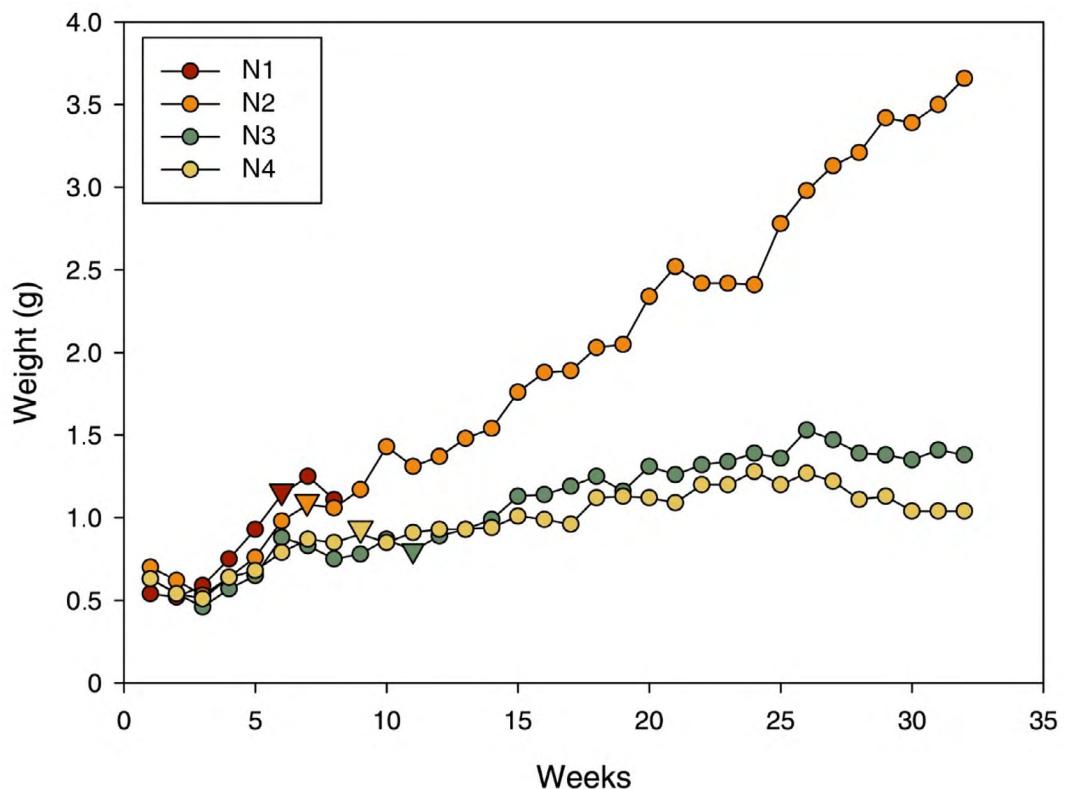


FIGURE 4. Weight (g) of four neonates (N1-N4) of *Liolaemus monticola* over 32 weeks. The triangle represents the first molting event. / Peso (g) de cuatro neonatos (N1-N4) de *Liolaemus monticola* a lo largo de 32 semanas. El triángulo representa la primera muda.

The first molt of each neonate was noticed during the fifth (N1), seventh (N3), ninth (N4), and eleventh (N2) weeks from hatching (Fig. 4). Neonates shed their skin in parts, so discrete shedding events could not be distinguished.

The reproductive biology of *L. monticola* is poorly understood. We know only that copulation and pregnancy occur between spring and summer and that females lay between 3 and 4 eggs (Donoso-Barros 1966; Ibargüengoytí 2008). In this work, we presented previously unknown information on incubation and hatching times, as well as biometric data for the growth of neonates of this species.

The observed incubation time for *L. monticola* is approximately 50 days, which is intermediate to that known in captivity for some of the other oviparous species of the genus. For instance, it is longer than that observed in *L. scapularis* (44 days; Lobo *et al.* 1995) and *L. quilmes* (45 days; Abdala *et al.* 1997), and shorter than that recorded in *L. tenuis* (72 days; Lemus *et al.* 1981). There are no records of the incubation time of *L. monticola* in the wild. However, it can likely be differentiated from that observed in captivity, considering that the duration of incubation in lizards is dependent on the environmental incubation temperature (Van Damme *et al.* 1992; Qualls & Shine 1998; Li *et al.* 2013; Raynal *et al.* 2022), including the genus *Liolaemus* (Medina *et al.* 2009), and on the geographic population variation (Smith *et al.* 2001; Ji *et al.* 2002; Li *et al.* 2013).

Liolaemus has a wide diversity of clutch sizes (see Cabrera 2021), which can be explained by different factors, such as the size and age of the female, or a progressive reduction in follicular atresia as the females grow and have greater abdominal capacity, among others (Leyton & Valencia 1992). Notably, *L. monticola* had an average egg-laying capacity (4 eggs) lower than many other *Liolaemus* species, including sympatric ones that have a similar body size, such as *L. lemniscatus* or *L. tenuis*, which lay on average 5.9 and 5.3 eggs, respectively (Cabrera 2021). Other factors, such as environmental variation or phylogenetic signal (Meiri *et al.* 2020), would determine the number of eggs laid for this species.

One of the neonates (N2) exhibited a higher growth rate than its siblings, and coincidentally, it was also the one with the highest weight at hatching. Lizard neonates born from the same clutch may show differences in phenotypic traits, such as early growth rate or body size (Overall 1994; Werner & Andrews 2002). These differences would depend on environmental factors, such as incubation temperature (Martínez-Caballero *et al.* 2017), humidity (Pandav *et al.* 2012), or food availability (Mugabo *et al.* 2010), as well as maternal and additive genetic effects (Noble *et al.* 2014). As the environmental conditions in captivity of this study were

the same for the clutches studied, we hypothesized that maternal and/or additive genetic effects would explain the individual differences observed in the growth of *L. monticola* neonates.

Although this study found that *L. monticola* eggs can develop at a specific temperature and humidity (28 °C and 80% RH), it remains unclear whether these values represent the environmental characteristics selected by females to lay eggs in their natural habitat. The environmental requirements and preferences for oviposition sites are unknown for many *Liolaemus* lizards, including *L. monticola*. However, in other oviparous lizard species, the behavior of selecting oviposition sites is not random and is subject to natural selection (e.g., the development of eggs in a suitable microclimate or protection against predators; Santoyo-Brito *et al.* 2021). This could occur for *Liolaemus*, considering that the temperature experienced by eggs in nature is a limiting factor for their development (Medina *et al.* 2009).

The causes behind the tail abnormalities observed in neonates are not clear. However, it has been observed in other reptiles that genetic and congenital factors, such as metabolic dysfunction in the mother, and/or environmental factors, such as extreme incubation temperature, habitat deterioration, agrochemical effects, or toxic pollution, could be involved in causing these malformations (reviewed by Bateman *et al.* 2022).

We hope that this report will encourage studies that enhance our understanding of the reproductive cycle of *Liolaemus* species (Ibargüengoytí 2008; Cabrera 2021), providing valuable information that could help with ex-situ conservation plans for species that may require it.

ACKNOWLEDGEMENTS

The study was authorized by the Servicio Agrícola y Ganadero (Resolución Exenta nº 3532/2023 and 12/2025) and the Comité Institucional de Cuidado y Uso de Animales (CICUA) of the Universidad de Chile (Certificate Nº 22553-FCS-UCH-e8). CR-O thanks the ANID Postdoctoral FONDECYT grant Nº 3230799 and CB-M to FONDECYT grant Nº 1221045.

REFERENCES

Abdala, C.S., Baldo, D., Juárez, R.A., Espinoza, R.E. 2016. The first parthenogenetic pleurodont iguanian: A new all-female *Liolaemus* (Squamata: Liolaemidae) from western Argentina. *Copeia* 104(2): 487-497.

Abdala, C.S., Laspiur, A., Scrocchi, G., Semhan, R.V., Lobo, F.,

Valladares, P. 2021. Las lagartijas de la familia Liolaemidae: Sistemática, distribución e historia natural de una de las familias de vertebrados más diversas del cono sur de Sudamérica. RIL editores-Universidad de Tarapacá, Santiago, Chile. 492 pp.

Abdala, F., Lobo, F., Scrocchi, G. 1997. Patterns of ossification in the skeleton of *Liolaemus quilmes* (Iguania: Tropiduridae). *Amphibia-Reptilia* 18(1): 75-83.

Bateman, P.W., Benken, R., Glowacki, R., Davis, R.A. 2022. A most unusual tail: Scoliosis in a wild Australian skink, and reported incidences and suggested causes of similar malformations amongst squamates. *Austral Ecology* 47(3): 723-728.

Cabrera, M.P. 2021. Reproducción en Liolaemidae: Ovíparos. In: Abdala, C.S., Laspur, A., Scrocchi, G., Semhan, R.V., Lobo, F., Valladares, P. (Eds.) Las lagartijas de la familia Liolaemidae. Sistemática, distribución e historia natural de una de las familias de vertebrados más diversas del cono sur de Sudamérica. pp. 312-316. RIL editores-Universidad de Tarapacá.

Cei, J.M., Videla, F., Vicente, L. 2003. From oviparity to viviparity: a preliminary note on the morphometric differentiation between oviparous and viviparous species assigned to the genus *Liolaemus* (Reptilia, Squamata, Liolaemidae). *Journal of Zoological Systematics and Evolutionary Research* 41(3): 152-156.

Cruz, F.B., Moreno Azócar, D.L., Perotti, M.G., Acosta, J.C., Stellatelli, O., Vega, L., Luna, F., Antenucci, D., Abdala, C., Schulte II, J.A. 2022. The role of climate and maternal manipulation in determining and maintaining reproductive mode in *Liolaemus* lizards. *Journal of Zoology* 317(2): 101-113.

Demangel, D. 2016. Reptiles en Chile. Fauna Nativa Ediciones, Santiago, Chile. 619 pp.

Donoso-Barros, R. 1966. Reptiles de Chile. Ediciones Universidad de Chile, Santiago, Chile. 458 pp.

Esquerré, D., Brennan, I.G., Catullo, R.A., Torres-Pérez, F., Keogh, J.S. 2019. How mountains shape biodiversity: The role of the Andes in biogeography, diversification, and reproductive biology in South America's most species-rich lizard radiation (Squamata: Liolaemidae). *Evolution* 73(2): 214-230.

Fernández, J.B., Medina, M., Kubisch, E.L., Manero, A.A., Scolaro, J.A., Ibargüengoytía, N.R. 2015. Female reproductive biology of the lizards *Liolaemus sarmientoi* and *L. magellanicus* from the southern end of the world. *The Herpetological Journal* 25(2): 101-108.

Ibargüengoytía, N.R. 2008. Estrategias reproductivas en reptiles. In: Vidal, M., Labra, A. (Eds.) *Herpetología de Chile*. pp. 391-425. Science Verlag, Santiago, Chile.

Ibargüengoytía, N.R., Cussac V.E. 1996. Reproductive biology of the viviparous lizard, *Liolaemus pictus* (Tropiduridae): biennial female reproductive cycle? *Herpetological Journal* 6(4): 137-143.

Ibargüengoytía, N.R., Halloy, M., Crocco, M.C. 2002. El parto en el lagarto *Liolaemus kingii* (Iguania: Liolaemidae): observaciones etológicas. *Cuadernos de Herpetología* 16(2): 129-135.

Jaksić, F.M., Schwenk, K. 1983. Natural history observations on *Liolaemus magellanicus*, the southernmost lizard in the world. *Herpetologica* 39(4): 457-461.

Jara, M., Muñoz-Pedreros, A. 2018. Trophic ecology of the mountain lizard, *Liolaemus monticola* (Müller & Hellmich, 1932), an endemic species of the central Andes of Chile. *Australian Journal of Zoology* 65(6): 372-378.

Ji, X., Huang, H., Hu, X., Du, W. 2002. Geographic variation in female reproductive characteristics and egg incubation of *Eumeces chinensis*. *The Journal of Applied Ecology* 13(6): 680-684.

King, B., Lee, M.S.Y. 2015. Ancestral state reconstruction, rate heterogeneity, and the evolution of reptile viviparity. *Systematic Biology* 64(3): 532-544.

Lemus, D., Wacyk, J. 1969. Migration, settlement, differentiation and morphogenesis of the female gonade in *Liolaemus gravenhorsti*. *Archivos de Biología y Medicina Experimental* 6(1): 22-31.

Lemus, D., Illanes, J., Fuenzalida, M., De La Vega, Y.P., García, M. 1981. Comparative analysis of the development of the lizard, *Liolaemus tenuis tenuis*. II. A series of normal postlaying stages in embryonic development. *Journal of Morphology* 169(3): 337-349.

Leyton, V., Valencia, J. 1992. Follicular population dynamics: its relation to clutch and litter size in Chilean *Liolaemus* lizards. In: Hamlett, W.C. (Ed.) *Reproductive biology of South American vertebrates*. pp. 123-134. Springer-Verlag, New York.

Leyton, V.C., Veloso, A., Bustos-Obregón, E. 1982. Modalidad reproductiva y actividad cíclica gonadal en lagartos iguanídos de distintos pisos altitudinales del interior de Arica (lat. 18° 10' S). In: UNESCO (Ed.) *El hombre y los ecosistemas de montaña: 1- La vegetación y los vertebrados ectodérmicos del transecto Arica-Lago Chungará*. pp. 293-301. Oficina regional de Ciencias y Tecnología de la UNESCO para América Latina y el Caribe, Montevideo, Uruguay.

Li, H., Zhou, Z.-S., Ding, G.-H., Ji, X. 2013. Fluctuations in incubation temperature affect incubation duration but not morphology, locomotion, and growth of hatchlings in the sand lizard *Lacerta agilis* (Lacertidae). *Acta Zoologica* 94(1): 11-18.

Lobo, F., Abdala, F., Scrocchi, G. 1995. Desarrollo del esqueleto de *Liolaemus scapularis* (Iguania: Tropiduridae). *Bollettino del Museo Regionale di Scienze Naturali, Torino* 13(1): 77-104.

Martínez-Caballero, Y.T., Bock, B.C., Pérez, I., Ortega-León, Á.M., Páez, V.P. 2017. Incubation temperature and clutch effects on initial body sizes and growth rates in green iguana hatchlings (*Iguana iguana*). *Animal Biology* 67(3-4): 239-249.

Medina, M., Ibargüengoytía, N.R. 2010. How do viviparous and oviparous lizards reproduce in Patagonia? A comparative study of three species of *Liolaemus*. *Journal of Arid*

Environments 74(9): 1024-1032.

Medina, M., Gutierrez, J., Scolaro, A., Ibargüengoytí, N. 2009. Thermal responses to environmental constraints in two populations of the oviparous lizard *Liolaemus bibronii* in Patagonia, Argentina. Journal of Thermal Biology 34(1): 32-40.

Meiri, S., Avila, L., Bauer, A.M., Chapple, D.G., Das, I., Doan, T.M., Doughty, P., Ellis, R., Grismer, L., Kraus, F., Morando, M., Oliver, P., Pincheira-Donoso, D., Ribeiro-Junior, M.A., Shea, G., Torres-Carvajal, O., Slavenko, A., Roll, U. 2020. The global diversity and distribution of lizard clutch sizes. Global Ecology and Biogeography 29(9): 1515-1530.

Mella, J. 2017a. Guía de campo de reptiles de Chile. Tomo 1: Zona Central. Santiago, Chile. 308 pp.

Mella, J. 2017b. Guía de Campo de Reptiles de Chile. Tomo 2: Zona Norte. Santiago, Chile. 316 pp.

Moya, F., Mella-Romero, J., Simonetti, J.A. 2025. Do we have the necessary insights to classify species according to their conservation status? A case study in the world's southernmost lizard genus. Journal for Nature Conservation 83: 126766.

Mugabo, M., Marquis, O., Perret, S., Le Galliard, J.F. 2010. Immediate and delayed life history effects caused by food deprivation early in life in a short-lived lizard. Journal of Evolutionary Biology 23(9): 1886-1898.

Noble, D.W.A., McFarlane, S.E., Keogh, J.S., Whiting, M.J. 2014. Maternal and additive genetic effects contribute to variation in offspring traits in a lizard. Behavioral Ecology 25(3): 633-640.

Ortiz, J.C. 1981. Révision taxinomique et biologie des *Liolaemus* du groupe *nigromaculatus* (Squamata, Iguanidae). Thèse de Doctorat d'Étates Sciences Naturelles. Université Paris VII, France.

Overall, K.L. 1994. Lizard egg environments. In: Vitt, L.J., Pianka, E.R. (Eds.) Lizard ecology: historical and experimental perspectives. pp. 51-72. Princeton University Press.

Pandav, B.N., Saidapur, S.K., Shanbhag, B.A. 2012. Expression of phenotypic plasticity in hatchlings of the lizard *Calotes versicolor* (Squamata: Agamidae): influence of nest moisture. Phylomedusa: Journal of Herpetology 11(1): 13-20.

Peig, J., Green, A.J. 2010. The paradigm of body condition: a critical reappraisal of current methods based on mass and length. Functional Ecology 24(6): 1323-1332.

Pincheira, D. 2012. Selección y evolución adaptativa: Fundamentos teóricos y empíricos desde la perspectiva de los lagartos. Ediciones UC, Chile. 489 pp.

Pincheira-Donoso, D., Tregenza, T. 2011. Fecundity selection and the evolution of reproductive output and sex-specific body size in the *Liolaemus* lizard adaptive radiation. Evolutionary Biology 38: 197-207.

Pincheira-Donoso, D., Tregenza, T., Witt, M.J., Hodgson, D.J. 2013. The evolution of viviparity opens opportunities for lizard radiation but drives it into a climatic cul-de-sac. Global Ecology and Biogeography 22(7): 857-867.

Qualls, F.J., Shine, R. 1998. Geographic variation in lizard phenotypes: importance of the incubation environment. Biological Journal of the Linnean Society 64(4): 477-491.

Raynal, R.S., Noble, D.W.A., Riley, J.L., Senior, A.M., Warner, D.A., While, G.M., Schwanz, L.E. 2022. Impact of fluctuating developmental temperatures on phenotypic traits in reptiles: a meta-analysis. Journal of Experimental Biology 225: jeb243369.

Ruiz de Gamboa, M.R. 2020. Estados de conservación y lista actualizada de los reptiles nativos de Chile. Boletín Chileno de Herpetología 7: 1-11.

Santoyo-Brito, E., Perea-Fox, S., Núñez, H., Fox, S.F. 2021. Maternal care and secretive behaviour of neonates in the highly social lizard *Liolaemus leopardinus* (Squamata: Liolaemidae) from the central Chilean Andes may relate to size-specific bird predation. Behavior 158(3-4): 195-223.

Schneider, C.A., Rasband, W.S., Eliceiri, K.W. 2012. NIH Image to ImageJ: 25 years of image analysis. Nature Methods 9(7): 671-675.

Schulte, J.A., Macey, J.R., Espinoza, R.E., Larson, A. 2000. Phylogenetic relationships in the iguanid lizard genus *Liolaemus*: multiple origins of viviparous reproduction and evidence for recurring Andean vicariance and dispersal. Biological Journal of the Linnean Society 69(1): 75-102.

Smith, S.A., Austin, C.C., Shine, R. 2001. A phylogenetic analysis of variation in reproductive mode within an Australian lizard (*Saiphos equalis*, Scincidae). Biological Journal of the Linnean Society 74(2): 131-139.

Troncoso-Palacios, J., Labra A. 2017. New egg laying record for *Liolaemus chiliensis* (Lesson, 1830) (Iguania: Liolaemidae). Herpetology Notes 10: 529-531.

Uetz, P., Freed, P., Aguilar, R., Reyes, F., Kudera, J., Hošek, J. 2025. The Reptile Database, <http://www.reptile-database.org>. Accessed: April 2, 2025.

Valladares, P., Briones, W. 2012. Reproductive behavior in *Liolaemus manueli* (Reptilia, Liolaemidae) and its relevance in an ex situ conservation program. IDESIA (Chile) 30(3): 107-111.

Van Damme, R., Bauwens, D., Braña, F., Verheyen, R.F. 1992. Incubation temperature differentially affects hatching time, egg survival, and hatchling performance in the lizard *Podarcis muralis*. Herpetologica 48(2): 220-228.

Werner, D.A., Andrews, R.M. 2002. Laboratory and field experiments identify sources of variation in phenotypes and survival of hatchling lizards. Biological Journal of the Linnean Society 76(1): 105-124.

Received: 30.06.2025

Accepted: 01.10.2025

Editor: Fulgencio Lisón