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On the oviposition of *Homonota aff. darwinii* in the Puna region of the Central Andes of Argentina

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Abstract: Communal nest egg-laying refers to females laying their eggs with those of their conspecifics under or within artificial or natural structures. *Homonota aff. darwinii* is a recently discovered species that has not yet been formally described. The objective of this work is to characterise the oviposition of this species in the Puna region in the Central Andes of Argentina. We recorded the type and surface of the rocks where the eggs were laid, the temperature of the substrate, and the temperature of the rock surface facing the substrate. In addition, we recorded the daily temperature variation that a randomly selected potential spawning site would experience based on the characteristics of the rocks where the eggs were observed and the higher frequency of encounters with adult individuals. In January we found a nest with four hatched eggs under a rock. Later, in March we found two nests under two different rocks. One of the nests contained an unhatched egg, while the other nest contained an unhatched egg along with a hatched egg. Both unhatched eggs weighed 0.4 g and had a volume of 164.93 and 220.84 mm^3. The embryo of one of the eggs was in an advanced stage of development, close to hatching. The rocks where the eggs were deposited were granitic and greyish. Each rock had a surface area of 768 and 1392 cm^2, substrate temperature of 38.8 and 23.2 °C, and rock temperature of 35.5 and 24.9 °C, respectively. The potential nesting site registered a thermal amplitude of 15 °C (15–30 °C). It has been observed that *H. darwinii* in Patagonia has a one-egg clutch and an annual-biennial reproductive cycle, therefore, we hypothesize that the encounter of a nest with at least two unhatched eggs could indicate the occurrence of communal nests.

Keywords: Extreme environments, gecko, reproduction, Phyllodactylidae

In oviparous species without parental care, females can influence their offspring's survival, phenotype, and aptitude by selecting the best available sites for oviposition (Resetarits, 1996; Pike et al., 2011). In this sense, oviposition site selection influences the likelihood of eggs being predated and improves the development of the embryos, reducing the effect of critical environmental conditions (Resetarits, 1996; Doody et al., 2009). However, environments which are thermally challenging, maternal oviposition behaviour could be limited by the restricted availability of adequate oviposition sites (Pike et al., 2010). Laying eggs in communal nests refers to females who lay their eggs alongside those of their conspecifics under or inside structures such as rocks, trunks, bark, vegetation, or crevices (Graves and Duvall, 1995; Espinosa and Lobo, 1996; Doody et al., 2009; Sales et al., 2020). Many reptiles living in rocky environments do not dig their nests but rather lay their eggs within natural structures such as crevices or under rocks (Ackerman and Lott, 2004). Covariation between average temperatures and daily thermal amplitude at such locations presents a problem in selecting a nesting site because high or low average temperatures could be lethal for the eggs (Huey et al., 1989; Webb and Shine, 1998). For this reason, females should select nesting sites favouring egg development reducing exposure to extreme thermal conditions (Pike et al., 2010). Doody et al. (2009) documented the occurrence of communal nests in 255 lizard species. More recently, new studies on Neotropical geckos have increased the number of known species which lay their eggs in communal nests (Domingos et al., 2017; Sales et al., 2020, Lima et al., 2022). 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, 2016a),

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a relatively small number compared to most other lizard families (Mesquita et al., 2016b). In the Phyllodactylidae family, communal laying behaviour has been recorded in 21 species belonging to 7 different genera (see Domingos et al., 2017).

Homonota aff. darwinii (Figure 1A) is a recently discovered species that has not yet been formally described, but is in the process of taxonomic revision (L. Avila, pers. comm.). Therefore, there is a lack of knowledge of the basic biology and the ecological aspects of this new species. Currently, the genus is comprised of 13 species (Cabral and Cacciali, 2021) including three valid groups, *whitii*, *borelli*, *horrida*, where the *Homonota whitii*, *Homonota andicola*, *Homonota williamsii,* and *Homonota darwinii* species belong to the *whitii* group (Cacciali et al., 2018). Therefore, it would follow that *H. aff. darwinii* would also belong to this group (L. Avila, pers. comm.). The objective of this study is to characterise *Homonota aff. darwinii* oviposition in the Puna region of the Central Andes of Argentina, describing the structural and thermal characteristics of the nesting site.

The study area is located at approximately 3100 m above sea level (hereafter a.s.l.) in the Cordillera Frontal in the province of San Juan and belongs to the phytogeographical Province of the Puna, Argentina. High-Andean environment is characterised by extreme climate conditions being cold and dry with a great daily and seasonal range of air temperature (–20 to 30 °C throughout the year), prolonged periods of drought with average annual precipitation between 100 and 200 mm, low partial pressure of oxygen, strong winds, great solar radiation and frozen soil and thawing depending on the time of year (Márquez et al., 2018). Vegetation includes brush and an herbaceous layer, conditioned by precipitation of snow and hail during the winter months between June and September (Figure 1B; Márquez et al., 2018).

During fieldwork carried out in January 2022, in an area of approximately 4 ha, three researchers conducted searches for rock microhabitats surrounded by vegetation over the course of three days, resulting in a total capture effort of 72 h per person. We discovered a nest with four hatched eggs on the ground under a rock but were unable to determine the species to which they belonged (Figure 2A). Subsequently, in March of the same year, while maintaining the same capture effort as in January, we found two nests under two different rocks (Figures 2B–2C). One of the nests contained an unhatched egg, while the other nest contained an unhatched egg along with a hatched egg (Figure 2D). Each unhatched egg was measured with a digital calliper (Lee Tools, 0.02 mm) and weighed with a 10-g spring scale (Pesola, 0.2 g). We estimated the volume of the unhatched eggs using the Dunham formula (1983) for an ellipsoid sphere $V = 4/3 \times (½ \times L) \times (½ \times W)^2$, where L = sphere length and W = maximum width of the sphere. We also recorded the type and surface of the rocks where eggs were deposited, the temperatures of the substrate, and the surface of the rock facing the substrate. Furthermore, we placed a datalogger under a randomly chosen rock for three days to record the daily temperature variation that a potential nest would experience. We collected and transported one of the unhatched eggs to the laboratory to identify the species and determine the stage of development of the embryo.

The embryo inside the egg was in an advanced stage of development, near hatching, with a snout-vent length of 18.44 mm (Figure 2E). Following Wise et al. (2009) and

Figure 1. Species and study area. A) *Homonota aff. darwinii* adult in the Cordillera Frontal of the province of San Juan, Argentina. B) General view of the environment in which *Homonota aff darwinii* exists in the Puna region of the Central Andes of Argentina.

Griffing et al. (2020), it can be inferred that the stage of embryo development approximately corresponds to stage 42 as defined by these authors. At this stage, it can be observed that the pigment resembles the final colour pattern of the nearly newborn animal, and the external nares open during this stage. Both rocks where the eggs had been laid were granite and greyish. In the region, in general, there is a predominance of Entisol soils, which are characterised by being stony soils of little development and depth with low organic matter content (Ortentes). The soils of this region are essentially lithic (stony) with fine sediments, often high in salt content and aeolian sandy sediments (Pereyra, 2012). Rock and egg measurements, as well as thermal data for the nest, are presented in Table. The potential daily temperature variation that *Homonota aff. darwinii* will experience during egg laying is illustrated in Figure 3.

From our observations, the question arises of whether *Homonota aff. darwinii* truly lays its eggs in communal nests, as reported for *Homonota uruguayensis* (Gudynas, 1986) and *Homonota borelli* (Godoy and Pincheira-Donoso, 2009), or if another explanation exists. For example, it is possible that the hatched eggs correspond to the same female that choose the same oviposition site

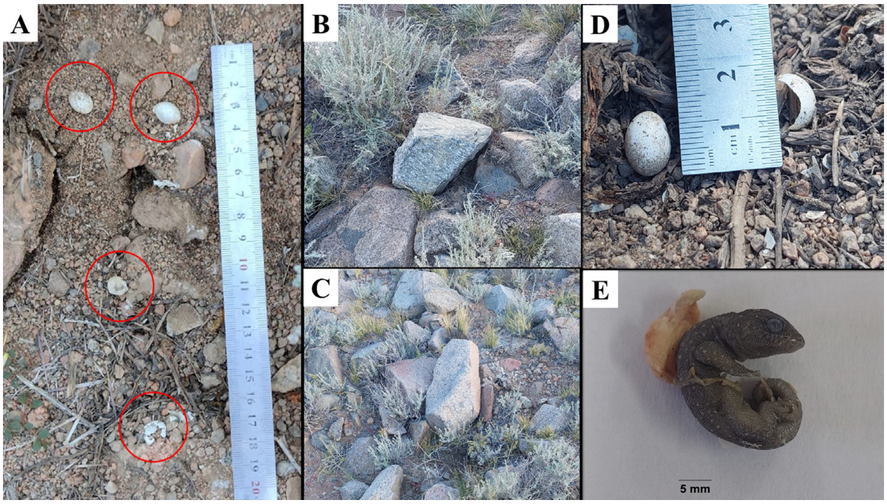

Figure 2. *Homonota aff. darwinii* oviposition in the Central Andes of Argentina. A) Laying of hatched eggs. B) Oviposition site for Egg 1. C) Oviposition site for Egg 2. D) Hatched and unhatched eggs. E) *Homonota aff. darwinii* embryo.

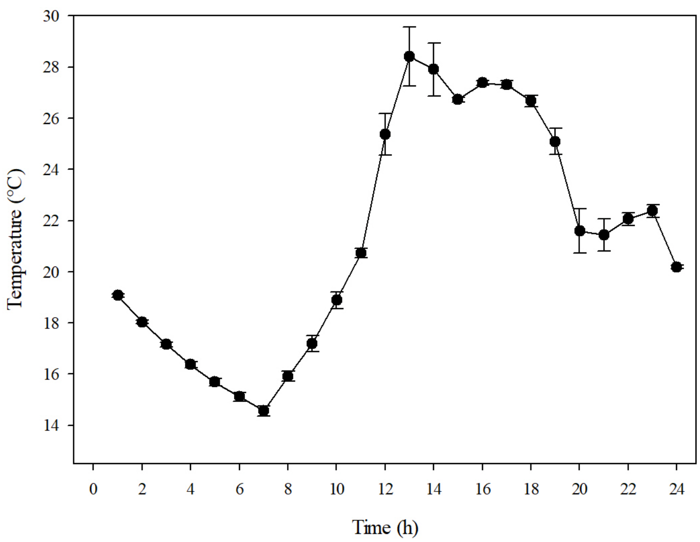

Figure 3. Daily temperature variation for a potential *Homonota aff. darwinii* nesting site. Average and standard errors are indicated.

each reproductive season (Magnusson and Lima, 1984; Johnston and Bouskila, 2007), which could be possible given the great longevity reported for *H. darwinii* in Patagonia, estimated to be 17 years (Piantoni et al., 2006). Thus, to confirm the communal nesting behaviour for this species, we would need to find a nest with at least two unhatched eggs along with the remains of the successfully hatched eggs.

Moreover, we can hypothesize that the egg-laying period for this species occurs at the end of spring and the beginning of summer since in January (early summer), we did find hatched eggs. In March (late summer), we also observed an increase in the proportion of hatchlings in the population (F.M. Valdez Ovallez, pers. obs.), indicating that hatchings would likely occur in this season. However, we cannot infer the timing of ovulation and mating, nor can we determine clutch size. Most of its congeners exhibit an annual reproductive cycle beginning in spring (Fernández et al., 2021). However, *H. darwinii* in Patagonia has a clutch of one egg and an annual-biennial reproductive cycle (Ibargüengoytía and Casalins, 2007). Likewise, within the genus, clutch sizes have been observed to be either one or two eggs, even for different populations of the same species (Fernández et al., 2021).

On the other hand, lizards that lay eggs in communal nests may be vulnerable to climate warming, especially if air temperature influences nest temperature (Dayananda et al., 2016). Additionally, it is predicted that in the future, summer heat waves will increase in frequency and duration, potentially leading to higher temperatures inside lizard nests (Dayananda et al., 2017; Abayarathna et al., 2019). In this regard, the eggs found inside the nests were subjected to high temperatures (Table), and significant daily thermal variations were recorded under the rocks that could potentially be used as nesting sites (Figure 3). It is therefore interesting to evaluate the impact of actual incubation temperature and projected future temperature increases on the offspring of this species. For instance, it has been observed that an increase in the incubation temperature of gecko eggs affects the cognitive abilities of the offspring (Abayarathna and Webb, 2020), leading to differences in morphology, locomotor performance, and survival (Dayananda et al., 2016, 2017) and altering their tolerance to critical temperatures (Abayarathna et al., 2019).

In this manner, we contribute the first set of knowledge to the natural history of *Homonota aff. darwinii*. Nevertheless, further studies on the basic biology of this species are necessary to gain a better understanding of how it thrives in harsh and restrictive environments like those of the Puna. Moreover, intensified efforts are required to search for additional nests of this species to confirm whether it engages in communal nesting. Future studies on the reproductive cycle and thermal biology, along with both field and developmental studies to determine how projected climate change may affect reproduction, thermal ecophysiology, and population viability, will make significant contributions to this field.

Table. Measurements of eggs, rocks and thermal data for the rocks where eggs were laid. The embryo recorded in the study corresponds to Egg 1.

	Egg weight (g)	Egg volume (mm^3)	Rock surface (cm^2)	Substrate temperature (°C)	Rock temperature (°C)
Egg 1	0.4	164.93	768	38.8	35.5
Egg 2	0.4	220.84	1392	23.2	24.9

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Conflicts of interest

The authors declare no conflicts of interest.

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