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Communal egg-laying and hatchling size in the pygmy gecko *Coleodactylus natalensis* (Squamata: Sphaerodactylidae) in an Atlantic Forest site of Brazil

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Abstract. Knowing the biology and natural history of a species is the first step to formulate conservation strategies. In this perspective, this study reports new data about the reproductive biology of *Coleodactylus natalensis*, an endemic and threatened species from Atlantic Forest remnants of Northeast Brazil. Our observations took place at the Floresta Nacional de Nísia Floresta, a protected area of Rio Grande do Norte state, during the months of March and April 2019. Along the 32 inspected quadrants (50 m^2 each), we recorded a total of 18 eggs of *C. natalensis* in six distinct egg sites, all of them found in the soil below the leaf litter layer. Considering that this species has a clutch size of a single egg, we found strong evidence of communal egg-laying in one site with 10 eggs close to each other; another three sites had two eggs each, and two eggs were found solitary in the leaf litter. Egg sites did not differ in temperature, humidity or leaf litter depth from random points without eggs along the quadrants. Fifteen of the 18 eggs hatched in the lab, with an average incubation time of 46.6 ± 18.5 days (range 15–73). In addition, an egg laid by a gravid female in the lab hatched after 65 days (relative clutch mass: 0.252). The average snout vent-length of hatchlings (n = 16) was 11.9 ± 0.4 mm (range: 11.1–12.3) and average hatchling mass was 33.1 ± 3.5 mg (range: 29.8–40.2). The hatchling size of *C. natalensis* is significantly smaller than that of *C. meridionalis*, its closer congeneric species.

Keywords. Communal nesting; clutch size; lizards; relative clutch mass; threatened species.

Introduction

Communal egg-laying is the behaviour of egg deposition by a female near the eggs of conspecific females, and is widespread among animals (Graves and Duvall, 1995; Doody et al., 2009). In reptiles, this phenomenon is identified as a clumped distribution of egg clutches at a scale visible to an observer, whereby it is highly likely that mothers would have detected the presence of conspecific eggs or conspecific mothers during oviposition site choice (Doody et al., 2009). Two basic types of communal egg-laying are often distinguished: "communal nesting" refers to mothers nonincidentally laying their eggs with those of conspecifics under or within structures such as rocks, logs, bark, vegetation, or crevices, whereas "colonial nesting" involves mothers utilizing common nesting areas, but, in this case, the eggs are generally buried and not deposited in the same nest cavity (Espinosa and Lobo, 1996). In the most recent review of communal egg-laying in reptiles and amphibians, Doody et al. (2009) documented the occurrence of this behavioural trait in 255 lizard species. Subsequently, new reports have increased the number of species known to deposit eggs in communal sites (e.g. Bezerra et al., 2011; Lima et al., 2011; Oliveira et al., 2014; Bernstein et al., 2016; Domingos et al., 2017; Doody et al., 2017). Although communal egg-laying usually involves conspecifics females, it may also occur among females of different lizard species sharing a single nest (e.g. Krysko et al., 2003).

Sphaerodactylidae (Squamata: Gekkota) is a family of lizards distributed in South and Central America, the Caribbean, eastern Asia, the Middle East, and North Africa (Vitt and Caldwell, 2014). Currently, 224 species and 12 genera are recognized (Uetz et al., 2019). Sphaerodactylids are tiny to moderate-sized geckos (20–60 mm adult snout-vent length – SVL) that

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occupy a wide range of habitats from lowland tropical rainforests to deserts, occurring on the ground, in leaf litter, or on tree trunks and limbs (Vitt and Caldwell, 2014). Among New World sphaerodactylids, the genus *Coleodactylus* Parker, 1926 is distributed in northeast South America and comprises a miniaturized species complex of diurnal leaf-litter geckos (SVL: 20–28 mm), currently composed of five species (Vanzolini, 1968; Ávila-Pires, 1995; Gonçalves et al., 2012). Knowledge about the reproductive biology of *Coleodactylus* is still incipient; available data is restricted to clutch size, which is constrained in one single egg in most populations (Vanzolini et al., 1980; Lisboa et al., 2008; Mesquita et al., 2016). In addition, a clutch size varying from one to two eggs is reported for *C. meridionalis* (Boulenger, 1888) (Mesquita et al., 2016).

The Natal's Pygmy Gecko (*Coleodactylus natalensis* Freire, 1999) is the smallest species of the genus (maximum SVL of 22 mm in males and 24 mm in females) and is endemic to Atlantic Forest remnants of Rio Grande do Norte, the northeastern most state of Brazil, having a very small extent of occurrence, less than 50,000 ha (Freire, 1999; Lisboa and Freire, 2012). *Coleodactylus natalensis* is a thermoconformer and microhabitat specialist, inhabiting the leaf litter of forest fragments surrounded by urban areas and depending on these shaded and mesic remnants to survive (Freire, 1996; Sousa and Freire, 2011; Lisboa and Freire, 2012). Its diet is composed of small invertebrates with relatively low abundance in the leaf litter, mainly isopods and spiders (Lisboa et al., 2012). Lisboa et al. (2008) reported a clutch size of one egg and hatchling size (SVL) of 11 mm based on one individual hatched in the lab; this study constitutes the only available data on the reproductive biology of *C. natalensis.* Lisboa and Freire (2012) identified a relatively small density of *C. natalensis* in its type locality when compared to the densities of other sphaerodactylids around the world. Due to all these ecological constraints and the process of habitat loss and fragmentation of the Atlantic Forest caused by urban expansion (Myers et al., 2000), *C. natalensis* has been added to the Brazilian list of endangered species, in the category "Endangered" (Brasil, 2014; MMA, 2018). Given that conservation measures are urgent for *C. natalensis* and that knowing the biology and natural history of a species is the first step to formulate conservation strategies (Primack and Rodrigues, 2001), this study reports new data about reproductive biology of *C. natalensis*. Our main questions were: (1) Do *C. natalensis* females lay eggs in communal sites? (2) Is hatchling size of *C. natalensis* smaller than in congeneric species? (3) Is relative clutch mass of *C. natalensis* comparable to other gecko species?

Materials and Methods

Study area.—The Atlantic Forest is the second largest tropical rainforest in the Americas; its biodiversity is remarkable and the region contains many endemic species of phylogenetically diverse groups (Myers et al., 2000). Originally, it extended along the Brazilian coast from the state of Rio Grande do Norte to the state of Rio Grande do Sul, continuing to the east of Paraguay and northeast Argentina. However, currently the Atlantic Forest has been severely fragmented, having lost about 93% of its original vegetation cover (Myers et al., 2000, Tabarelli et al., 2005). The Atlantic Forest is extremely heterogeneous and dominated by tropical pluvial forests that become more seasonal as one moves inland (Tabarelli et al., 2005).

The Floresta Nacional de Nísia Floresta (FLONA; 06.0878ºS, 35.1853ºW; datum: WGS84; 61 m a.s.l.) is a protected area located in the municipality of Nísia Floresta, near the coast in the state of Rio Grande do Norte. The climate is warm and humid (sensu Köppen) and the average annual temperature is 26°C (Pinto et al., 2012). The rainy season extends from March–July and the dry season from August to February, with annual mean rainfall and relative humidity 1455 mm and 76%, respectively (Pinto et al., 2012). The FLONA covers a total area of 175 ha of reserve, of which 45.2% represents stational semidecidual forest, 14.1% consist of tabuleiros vegetation (arboreal-shrubby and herbaceous strata), 39.7% are occupied by exotic vegetation derived from forest experiments, and 1% consists of housing, administrative buildings and nurseries of native plant species (Pinto et al., 2012).

Methodological procedures.—Our observations took place during a field study to investigate the population density of *C. natalensis* at the FLONA. During the months of March and April 2019, we delimited 32 quadrants of 50 m^2 each (50 x 1 m) in four different sites of the study area (eight quadrants in each site), starting from the edge to the centre of the forest fragment. The vegetation in all sampled sites consisted of stational semidecidual forest. Two researchers inspected each quadrant in the morning (08:00 h to 11:00 h) and afternoon (14:00 h to 17:00 h) by turning over all the leaf litter during one hour, totalling 32 hours of sampling effort divided in eight days (15 to 17 March, 22 to 24 March, 31 March and 29 April).

For each egg registered in the field, we measured leaf litter depth with a ruler, substrate temperature, air temperature (1 cm above the leaf litter layer) and relative humidity by positioning a temperature sensor (Instrutherm® model S- 02K) coupled with a digital thermohygrometer (precision of 0.1°C; Instrutherm® model HTR-350) at the egg site (Fig. 1A). We also measured these same variables in five random points of each quadrant; for this, we divided each quadrant in 800 small squares of 0.0625 m^2 each (0.25 x 0.25 m), and randomly selected 5 squares by using Google's random number generator (www.google.com).

The eggs were carefully collected together with substrate, measured (length and width) with a digital calliper (precision 0.01 mm), weighed using a digital scale (precision 0.1 mg), kept in terrariums (Fig. 1B) and observed daily at the Herpetology Lab of the Rio Grande do Norte Federal University, Natal municipality (distant about 40 km from the study area). The average temperature in the lab was 27.0 ± 0.9 ° C (range: 25.9–29.1), and air humidity was 53.1 ± 16.9 % (range: 28.0–87.0). We estimated egg volume by the prolate spheroid formula (Sales and Freire, 2016). We measured the SVL and weighed all neonate lizards immediately after hatching. In addition to eggs found in nature, we also monitored one egg laid by a *C. natalensis* female which was being kept temporarily in the lab; the female laid the egg after three days following her capture in nature. The neonate individuals were fixed in 10% formaldehyde, preserved in 70% ethanol, and deposited in the Herpetological Collection of Rio Grande do Norte Federal University.

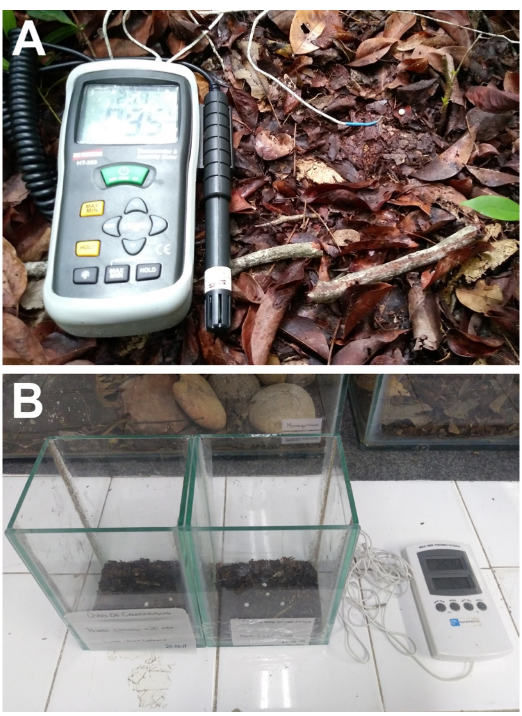

Figure 1. Methodological procedures for collection in the field and incubation of eggs of *Coleodactylus natalensis* in the lab. A: measurement of temperature and humidity in the egg site with a digital thermohygrometer. B: incubation of eggs in terrariums at the Herpetology Lab of the Rio Grande do Norte Federal University. Photos by Raul Sales.

We calculated relative clutch mass (RCM) for the female that laid the egg in the lab as ratio of the clutch mass (egg mass) to total maternal mass (clutch plus body) (Vitt and Price, 1982). We compared temperature (substrate and air), humidity and leaf litter depth between egg sites and random quadrant points by independent t-tests. We used this same test to compare the hatchling sizes of *C. natalensis* and *C. meridionalis* (the closest congeneric species) (Geurgas et al., 2008). We obtained data on *C. meridionalis* from the literature (Oliveira et al., 2014). All statistical analyses were performed using SPSS Statistics 20.0 (IBM) software for Windows ($\alpha = 0.05$). All variables were tested for normality and homoscedasticity of variances before performing parametric tests. Throughout the text, we report descriptive statistics as means ± 1 SD.

Results

Along the 32 inspected quadrants, we recorded a total of 18 eggs of *C. natalensis* in six distinct egg sites, all of them found in the soil below the leaf litter layer. None of the variables measured at egg sites differed from random points measured along the quadrants (Table 1).

Because this species has a clutch size of a single egg, we found strong evidence of communal egg-laying in one site with 10 eggs (Table 2): four of the ten eggs were very close to each other (three of them just 1 cm apart, and the fourth one 2.5 cm distant of the other three; Fig. 2A); another four eggs were positioned 16 cm northeast from the other four described above (2 to 8 cm apart; one of them visible in Fig. 2A); finally, two more eggs were about 60 cm northwest from the first four eggs. The other three sites had two eggs each (not more than 10 cm apart), and two eggs were found solitary in the leaf litter.

Fifteen of the 18 eggs hatched in the lab. The first egg hatched after 15 days of incubation, and the last one after

Table 1. Average values (and ranges) of temperature (air and substrate), humidity and leaf litter depth measured at egg sites and at random points along sampled quadrants at Floresta Nacional de Nísia Floresta, state of Rio Grande do Norte, northeast Brazil.

Variables	Egg sites (n = 18)	Random points (n = 160)	Statistic
Air temperature (°C)	27.4 ± 1.2 (25.3–29.4)	28.0 ± 1.8 (24.7–35.1)	t = -1.203, df = 174, p = 0.231
Substrate temperature (°C)	27.9 ± 0.8 (26.5–29.3)	27.9 ± 1.3 (24.6–33.0)	t = -0.022, df = 174, p = 0.983
Relative humidity (%)	85.6 ± 4.3 (75.7–92.6)	87.1 ± 4.9 (67.4–94.3)	t = -1.218, df = 174, p = 0.225
Leaf litter depth (cm)	3.9 ± 1.3 (2.0–7.0)	4.0 ± 1.9 (1.0–10.0)	t = -0.462, df = 26.6, p = 0.648

Table 2. Dates of collection and hatch and morphometry of eggs and hatchlings of *Coleodactylus natalensis* from Floresta Nacional de Nísia Floresta, state of Rio Grande do Norte, northeast Brazil. SVL = snout-vent length.

Individual	Communal egg-laying	Date and hour of collection	Egg volume (mm^3)	Egg mass (mg)	Date of hatch (incubation time)	SVL (mm)	Mass (mg)
1	Yes (2 eggs)	22/03/2019 – 1640	56.0	55.4	–	–	–
2	Yes (2 eggs)	22/03/2019 – 1640	55.2	55.0	23/04/2019 (32 days)	11.5	31.2
3	Yes (2 eggs)	22/03/2019 – 1655	52.2	47.8	24/05/2019 (63 days)	12.4	32.3
4	Yes (2 eggs)	22/03/2019 – 1655	49.8	45.7	25/05/2019 (64 days)	11.6	32.6
5	No	24/03/2019 – 0945	45.9	36.4	–	–	–
6	Yes (10 eggs)	24/03/2019 – 0953	58.5	56.9	19/05/2019 (56 days)	12.0	37.8
7	Yes (10 eggs)	24/03/2019 – 0953	57.5	56.0	08/05/2019 (45 days)	12.5	36.2
8	Yes (10 eggs)	24/03/2019 – 0953	57.2	55.6	07/05/2019 (44 days)	12.5	34.7
9	Yes (10 eggs)	24/03/2019 – 0953	56.7	52.0	09/05/2019 (46 days)	12.3	33.0
10	Yes (10 eggs)	24/03/2019 – 0953	56.3	52.0	22/04/2019 (29 days)	11.9	32.7
11	Yes (10 eggs)	24/03/2019 – 0953	54.1	51.7	22/04/2019 (29 days)	11.7	32.6
12	Yes (10 eggs)	24/03/2019 – 0953	52.9	50.4	10/04/2019 (17 days)	11.9	31.8
13	Yes (10 eggs)	24/03/2019 – 0953	52.4	50.2	23/04/2019 (60 days)	12.1	31.6
14	Yes (10 eggs)	24/03/2019 – 0953	52.1	50.2	08/04/2019 (15 days)	11.3	31.3
15	Yes (10 eggs)	24/03/2019 – 0953	50.8	47.6	26/05/2019 (63 days)	11.1	29.8
16	No	31/03/2019 – 1110	39.7	30.1	02/06/2019 (63 days)	12.3	40.2
17	Yes (2 eggs)	29/04/2019 – 1550	41.2	32.3	11/07/2019 (73 days)	11.7	25.2
18	Yes (2 eggs)	29/04/2019 – 1550	51.0	46.9	–	–	–
19*	N/A	03/04/2019	55.9	56.2	07/06/2019 (65 days)	11.7	37.2

* Gravid female collected on 31 March 2019 laid the egg in the lab on 3 April 2019.

73 days (average: 46.6 ± 18.5 days). In addition, the egg laid by the female in the lab hatched after 65 days (Fig. 3). Before oviposition, the gravid female weighed 222.8 mg, and the egg laid weighed 56.2 mg, thus the RCM of this female is 0.252.

Average egg volume (n = 19) was 52.4 ± 5.3 mm^3 (range: 39.7–58.5) and average egg mass was 48.9 ± 7.9 mg (range: 30.1–56.9). The average SVL of hatchlings (n = 16) was 11.9 ± 0.4 mm (range: 11.1–12.3) and average hatchling mass was 33.1 ± 3.5 mg (range: 29.8–40.2). Data for individual eggs and hatchlings are in Table 2. The hatchling size of *C. natalensis* is significantly smaller than that of *C. meridionalis* (t = -6.164, df = 29, p < 0.0001; Fig. 4).

Discussion

The choice of egg-laying site can be an important component of fitness, especially in animals without parental care. Environmental conditions critical to developing embryos, such as temperature and humidity, and risk of egg predation may be determinant factors in the choice of egg-laying sites by females (Doody et al., 2009). Communal egg-laying has evolved independently several times during the history of squamates (Doody et al., 2009), but appears to be prevalent in geckos (Graves and Duvall, 1995; Doody et al., 2009). In Brazil, for instance, communal egg-laying has been documented in several native gecko species such as *Hemidactylus agrius* Vanzolini, 1978, reported by

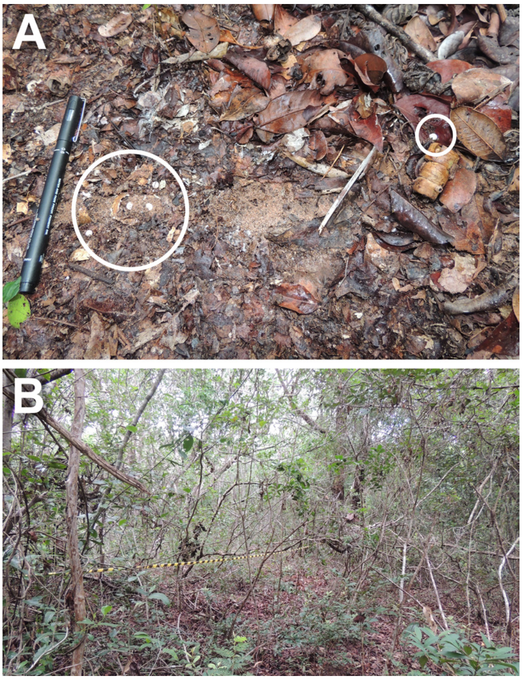

Figure 2. Communal egg-laying in *Coleodactylus natalensis* at Floresta Nacional de Nísia Floresta, state of Rio Grande do Norte, northeast Brazil. A: Partial view of the largest communal oviposition site, with five of the ten eggs visible (the leaf litter layer was artificially turned over). B: general view of the vegetation in the site where the eggs were found (stational semidecidual forest). Photos by Raul Sales.

Bezerra et al. (2011); *Phyllopezus periosus* Rodrigues, 1986, reported by Lima et al. (2011); *P. pollicaris* (Spix, 1825), reported by Domingos et al. (2017); *Gonatodes humeralis* (Guichenot, 1855), reported by Oda (2004); *Coleodactylus meridionalis*, reported by Oliveira et al. (2014); and also in the invasive alien gecko *Hemidactylus mabouia* (Moreau de Jonnès, 1818), reported by Sousa and Freire (2010). We found strong evidence of this phenomenon in *Coleodactylus natalensis*, since we registered one site with ten eggs and three sites with two eggs each. Given the proximity of the eggs in the field, the invariant clutch size of one egg in the species (Lisboa et al., 2008), and the fact that the eggs were not buried, we argue that it is highly probable that different *C. natalensis* females used the same sites to oviposit, and that they detected the presence of conspecific eggs during oviposition site choice. Furthermore, we prefer to use the term "communal egg-laying" rather than "communal nesting" for *C. natalensis* (see Doody et al., 2009) because we found no evidence of construction or utilization of a nesting cavity (we found all eggs in the soil below the leaf litter layer). We also found solitary eggs, suggesting that communal egg-laying is not obligatory in *C. natalensis*. Most species that exhibit communal egg-laying are also known to lay eggs in isolation, and this dichotomy often occurs within the same population (Vitt et al., 1997; Doody et al., 2009; Oliveira et al., 2014).

Radder and Shine (2007) discuss two different potential reasons for females to oviposit communally: (1) sites providing optimal conditions for eggs (i.e. temperature, humidity, shelter from predators) are scarce, so many females are forced to use the same site

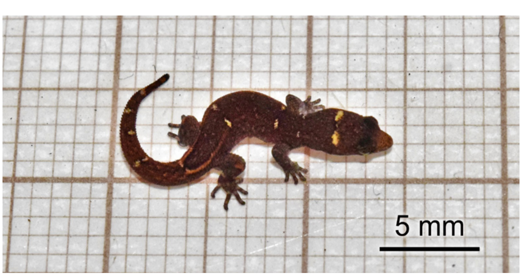

Figure 3. Neonate individual of *Coleodactylus natalensis* hatched at 7 June 2019 (specimen 19 in Table 2). Photo by Daniel Santos-Junior.

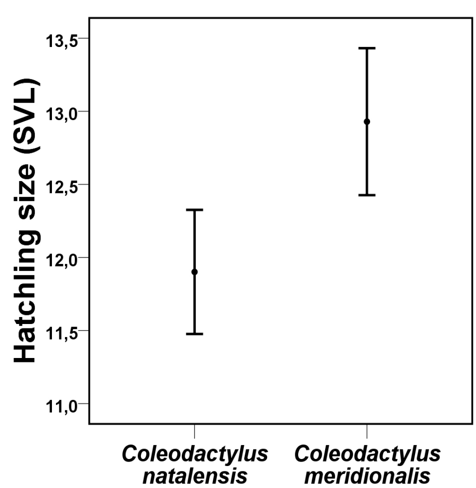

Figure 4. Hatchling sizes of *Coleodactylus natalensis* (source: this study) and *C. meridionalis* (source: Oliveira et al., 2014). Bars represent average values ± 1 standard deviation (SD).

for egg-laying (constraint hypothesis); or (2) there is a fitness benefit to eggs laid within a communal nest, or to females that aggregate for this purpose (adaptation hypothesis). These benefits could be related to less time spent searching and/or building a nest (Graves and Duvall, 1995), and to increased offspring performance and/or survivorship (Radder and Shine, 2007). These hypotheses are still controversial, but will be certainly better understood as more communal nesting records are described in the literature (Domingos et al., 2017). Our data for *C. natalensis* do not support the "constraint hypothesis" because the leaf litter is highly abundant in the study area, and the sites we found the eggs did not differ in temperature, humidity or leaf litter depth from random points without presence of *C. natalensis* eggs. Whether communal egg-laying has any adaptive advantage for *C. natalensis* remains unknown.

Geckos (clade Gekkota) have invariant clutch size, usually varying from one to two eggs, depending on the species (Fitch, 1970), and relative clutch masses (RCM) in these species are generally low when compared to other lizard families (Vitt and Price, 1982). The RCMs of 19 sphaerodactylid species available in the literature averages 0.158 ± 0.056, varying from 0.046 in *Lepidoblepharis xanthostigma* to 0.263 in *Sphaerodactylus elegans*, both from Central America (Mesquita et al., 2016). The single value of RCM for *C. natalensis* reported in this study (0.252) therefore falls into the upper range of RCM values in the Sphaerodactylidae, and is higher than average RCM of *C. meridionalis* (0.141) and *C. septentrionalis* (0.106) (Mesquita et al., 2016). *Coleodactylus natalensis* is the smallest species of the genus (Freire, 1999) and one of the smallest lizards in the world, and our data shows that hatchlings of this species are also smaller in body size than those of congeneric species.

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