BRILL *Behaviour (2021)* DOI:10.1163/1568539X-bja10065 **Behaviour** brill.com/beh

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

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Received 6 May 2020; initial decision 28 July 2020; revised 19 December 2020; accepted 28 December 2020

Abstract

Predation prompts the evolution of antipredator traits, molds behaviour, and can lead to the evolution of parental care. We investigated parental care and predator-avoidance behaviour of neonates in the social lizard *Liolaemus leopardinus*. We used clay models to quantify bird predation pressure on *L. leopardinus*. Predation was significantly greater on small models and models in open habitat. Late-term pregnant females left their social groups on rock outcrops and gave birth in solitary underneath flat rocks in vegetated microhabitat. Mothers stayed with their litters inside natal chambers for at least 24 h and when they left, sealed the neonates inside. Mothers remained close to their natal chamber and neonates when neonates emerged. Neonates and young yearlings moved significantly less and occupied vegetated microhabitat significantly more than older age classes. We suggest that the maternal behaviour and secretive behaviour of neonates may be related to the heavy avian predation on neonates.

Keywords

anti-predation, birds, clay models, group living, parental care, reptile.

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1. Introduction

Predation is a selective force that molds behaviour and prompts the evolution of antipredator traits, for example, nest guarding, direct repulsion, startle response, crypsis, etc. (Krebs & Davies, 1993; Lanham & Bull, 2004; Huang & Pike, 2011; Davies et al., 2012). Among those traits, cryptic colouration (i.e., background matching) and cryptic behaviour (i.e., remaining still or moving little; Cooper et al., 2008; Webster et al., 2009; Vignieri et al., 2010; Stevens & Ruxton, 2019) are two very effective techniques animals use to avoid visually oriented predators (Lima & Dill, 1990; Capodeanu-Nägler et al., 2016). Animals may also reduce predation pressure through a shift to safer habitats (Dickman, 1992; Pierce, 1998; Winandy et al., 2016). This strategy is especially important for juveniles since small, young conspecifics tend to have more predators than their adult counterparts (Reznick, 1996; Costelloe & Rubenstein, 2015). This disproportionate predation pressure decreases over time as young individuals achieve a certain size threshold as shown in amphibians (Caldwell et al., 1980; Smith, 1983), mammals (Longland & Jenkins, 1987), fishes (Reznick, 1996) and crustaceans (Moksnes et al., 1998).

Strong predation pressures can also lead to the evolution of parental care, defined here as any form of behaviour expected to increase the successful production of progeny (Clutton-Brock, 1991; Balshine, 2012; Smiseth et al., 2012). Parental care has evolved independently in a broad range of taxa, and has been well documented in mammals and birds, groups in which the behaviour prevails through long term parent-offspring associations and social interactions. Interactions like burrow or nest sharing and nutritional provisioning promote parent-offspring associations and make parental care possible (Clutton-Brock, 1991; Costelloe & Rubenstein, 2015).

It has long been thought that reptiles lack sociality and, consequently, lack parental care (Somma, 2003a; Balshine, 2012; Doody et al., 2013; While et al., 2014). However, parental behaviour has been described in more than 140 reptile species of the more than 9500 known living species (Somma, 2003a, b; Huang, 2006; Doody et al., 2013 and references therein). Therefore, it is plausible that many more yet undocumented cases of parental behaviour in reptiles exist. Reptile parental behaviour is mainly expressed in rather simple forms (e.g., guarding or defense of nests/burrows, eggs, or offspring; Somma, 2003a; Huang, 2006; While et al., 2014). Nevertheless, complex

forms and degrees of parental care have been described for the group, especially in relatively long-lived lizard species (Gans, 1996; Chapple, 2003; Balshine, 2012; Doody et al., 2013). Research on parental care of squamate reptiles (lizards and snakes) is still in its early stages (While et al., 2014). Many species of reptiles are elusive and secretive, making it difficult to locate their oviposition and birth sites, therefore parent-offspring associations and parental behaviour are challenging to observe and document in-situ (While et al., 2014). Thus, in many instances, contributions to our knowledge of parental behaviour in reptiles are anecdotal observations (Lemos-Espinal et al., 1997; Masters & Shine, 2003; Rismiller et al., 2010; While et al., 2014). Despite these shortcomings, reptiles serve as a good general model for discerning the selection pressures that develop parental care and drive its complexity because parental care is not as predominant as in fish, birds and mammals; parental care in reptiles, especially lizards, is only now emerging as an important natural history trait (While et al., 2014).

Liolaemus leopardinus (Müller & Hellmich, 1932) is a medium-to-large lizard endemic to temperate central Chile. The geographic range of the species is limited to a narrow altitudinal band above timberline at 1800–3000 m (Pincheira-Donoso & Núñez, 2005; Pincheira-Donoso et al., 2008). Low temperatures and seasonal scarceness of resources are characteristic of the habitat. Lizards are active during austral spring, summer, and fall, and inactive during the extreme austral winter. Individuals of the species are long-lived and their life span can exceed a decade (Santoyo-Brito et al., 2018). The species is highly social; at times groups on rock outcrops are formed by two adults (male and female) and one to three juveniles (Fox & Shipman, 2003), and at other times larger groups of up to 6–10 (or more) adults and juveniles on open rock outcrops and within crevices are observed (Santoyo-Brito, 2017). Despite their cryptic colouration, individuals basking or moving on the open rock are relatively conspicuous. High genetic relatedness among individuals within these social groups is common (Santoyo-Brito, 2017). Although pregnant females are sometimes found within the social groups, results of a pilot study conducted in 2005 indicated that neonates are not found within the groups; we again observed this during two field seasons in the late spring and summer of 2011–2012 and 2012–2013 (Santoyo-Brito, 2017). Female *L. leopardinus* appear to reproduce on a yearly basis, giving birth to only 2–4 neonates (Santoyo-Brito et al., 2017).

At the high elevations where *L. leopardinus* lives, visually oriented predators that prey on lizards (especially smaller individuals) are two abundant species of shrike-tyrants, *Agrionis montana* and *Agrionis livida*, the less abundant American Kestrel, *Falco sparverius* (Ridgely & Tudor, 1994), and the very common Rufous-banded Miner, *Geositta rufipennis* (Santoyo-Brito et al., 2014). During March-April, when females give birth, *A. montana*, *A. livida*, and *G. rufipennis* are abundant at El Colorado, our study site in central Chile. Thus, bird predation on small neonate *L. leopardinus* appears to be intense (Santoyo-Brito et al., 2018). Another potential predator is the saurophagous snake *Tachymenis chilensis* (Greene & Jaksic, 1992). At our high-elevation site, however, *T. chilensis* is very rare and likely has minimal impact on total predation pressure. Likewise, cannibalism by larger *L. leopardinus* or predation by sympatric lizard species *L. bellii* and *L. nigroviridis* have not been reported and can probably be ruled out. Therefore, we suggest that high predation risk by visually oriented birds has caused neonates to seek more vegetated, protected habitat than the open habitat where the conspicuous social groups of the species live. A similar ontogenetic shift in habitat use has been reported in crayfish, fish, birds, and mammals. Young individuals inhabit a more protected habitat when compared to the open habitats occupied by adults (Laegdsgaard & Johnson, 2001; Gow & Wiebe, 2014; Costelloe & Rubenstein, 2015; Dyer et al., 2016).

During the austral fall of 2012 at our study site in central Chile, we employed clay lizard models to quantify the predation pressure on individuals of different size classes of *L. leopardinus*. We hypothesized that avian predation would be stronger on models representing the neonate size class than on older juvenile and adult size classes, and predation would be weaker on those models under cover than in the open. If true, it is possible that strong size-specific predation pressure has favored *L. leopardinus* to evolve parental care (e.g., in the form of nest selection, placement of neonates in more protected microhabitat, and active protection against predators). We radiotracked pregnant mothers to document their movements and habitat use before and after giving birth and to locate birthing locations, and we used a flexible borescope to observe the mothers with their offspring inside natal chambers. Strong size-specific predation may also force neonates to both behave secretively and utilize a microhabitat secluded from large open rock outcrops where they would be more susceptible to predation by visual predators. This secretive behaviour of neonates might explain why no neonates

have ever been reported from the field. Such secretive and cryptic behaviour would be expected to be retained until the neonates attain a greater size, making them less susceptible to predation, just like in crayfish, tadpoles, fish, birds, and others (Stein & Magnuson, 1976; Caldwell et al., 1980; Smith, 1983; Reznick, 1996; Grol et al., 2014; Hoy et al., 2014). To document the proposed secretive neonate behaviour and how it changes with age, we used radiotelemetry to quantify neonate movements and habitat use, and compared that to adults and older juveniles at the same time of the year, and also compared movements and habitat use of 7–8 month-old juveniles early the next spring to that of adults and older juveniles then.

2. Materials and methods

Our study was conducted in the Andean cordillera of central Chile at El Colorado, 35 km northeast of Santiago at 2760 m (33°14′S, 70°16′W; Fox & Shipman, 2003; Santoyo-Brito, 2017). The climate is characterized by dry summers, snowy austral winters, and a Mediterranean pattern of rainfall (di Castri & Hajek, 1976). The bare rock outcrops characteristic of our study site are located in treeless habitat dominated by patches of dwarf shrub *Berberis* sp. *Liolaemus leopardinus* shows little sexual size dimorphism, although adult males (mean Snout-Vent Length (SVL) = 100.8 mm) are slightly larger than adult females (mean SVL = 99.6 mm; Fox & Shipman, 2003; Santoyo-Brito et al., 2018). Free-ranging neonates are much smaller ($N = 6$; mean SVL = 40.9 mm).

In austral fall (mid-March of 2012), we estimated predation pressure from placement of 108 clay models of three size classes (neonate, juvenile, and adult; $N = 36$ models/size class) in three microhabitats (open rock faces, open soil, and under bushes; $N = 36$ models/microhabitat) for four days for a total of 432 model days. All three microhabitats were commonly used by lizards. Snout-vent length of each size class (40, 60, and 90 mm SVL, respectively) was determined from a pilot study conducted in 2005 and from Fox & Shipman (2003). Models were made of one hatchling *Crotaphytus collaris*, and one juvenile and one adult *L. leopardinus* deposited at the Collection of Vertebrates (COV) at Oklahoma State University prior to our fieldwork in Chile. At the time, we did not have access to neonates of the species, and hatchlings of *C. collaris* are similar in body size and morphology to *L. leopardinus* at this young age. Lizard specimens were arranged in a basking position and covered with silicone (Dragon Skin® Series; Smooth-On, Macungie,

Figure 1. Comparison of a live lizard and typical model made with custom-mixed modeling clay to estimate predation pressure of three size classes (neonate, juvenile and adult) of *Liolaemus leopardinus* during mid-March of 2012 at El Colorado, Chile.

PA, USA). Once hardened, the silicone was cut open and the lizard removed, leaving a detailed inverse mold. Molds were filled with custom-mixed modeling clay matching the background colour of the lizards, and after removal of the models, black dots and a line resembling the dorsal vertebral line were painted over the body to match the colour pattern of live animals (Figure 1). To prevent predators from carrying away the models, models were tied to a bush or rock in the appropriate microhabitat using a clear monofilament fishing line. Models were placed 3 m or more from each other. We also used six camera-traps (2 Stealth Cams, GSM Outdoors, Grand Prairie, TX, USA, and 4 Moultrie Bird Cams (Models WSCA02 and 03), EBSCO Industries, Birmingham, AL, USA), each one placed at an approximate distance of 1 m from six different clay models (2 of each model size) located in either open soil, open rock, or under vegetation. The camera (set to high sensitivity for motion triggering) was positioned horizontally at substrate level or above

the model using a tripod. The camera was used to document the species that made attacks and time of attack.

To document the pre- and postpartum behaviour of pregnant females during our second field season, we attached radio-transmitters (model: BD-2H, 0.9–1.04 g, internal antenna; Holohil Systems, Carp, ON, Canada) to the tail base of nine adult pregnant females. During late December to early April, we attempted to radiolocate all radio-tagged subjects at least two times a day from approximately 10:00 am to 6:00 pm. In late April of 2013, we fortuitously captured two free-ranging neonate *L. leopardinus*; this presented us with the opportunity to glue a miniature radio-transmitter (model BD-2x, 11.5 by 5.3 by 2.8 mm; 0.25 g, external antenna; Holohil Systems) to the dorsum of each one to study their behaviour. In November 2013 (early austral spring) we revisited our field site to capture and radio-tag three 7–8-month-old juveniles (hereinafter young yearlings) with the same model of radios (data on radiotelemetry in Table A1 in the Appendix). To locate all radio-tagged subjects, we used a hand-held, three-element Yagi antenna and a radio-receiver (Model R-1000; Advanced Telemetry Systems, Isanti, MN, USA). When the subject (mother, neonate, or young yearling) was radio-located underneath a rock or within a rock crevice, we removed the co-axial cable from the antenna and used that end of the cable to pinpoint the exact location. To observe and video-record behaviour of refuged lizards, we used a Rigel digital video borescope (Medit, Winnipeg, MB, Canada) with a 360-degree, two-way articulating probe (4 mm in diameter and 2 m long). All lizards were part of an intensive, two-year behavioural study. Thus, in addition to the radio-transmitter on a subset of lizards ($N = 15$), all subjects ($N = 62$) were permanently marked by both a unique toe-clip and a dorsal colour code combination of non-toxic latex paint dots, which allowed recognition of individual lizards from a distance without the need for recapture. Lizards were initially captured via noosing, SVL measured with a ruler, and sex determined by the presence (males) or absence (females) of precloacal pores when a hemipenal bulge was not observed (Santoyo-Brito et al., 2018).

On our study site, we placed scattered, numbered flags on top of prominent rocks, which could be seen from a distance. The location of each flag was recorded using a handheld GPS (Datum WGS84). We used this geographic information to create scale maps of our study site, implementing ArcMap v10.1. Maps were ground-truthed in the field and adjusted when

needed. We collected spatial data of marked *L. leopardinus* by visual sightings, capture and recapture of lizards when necessary (e.g., subject missing paint dot colours), scan sampling (focal observation via binoculars; Frost & Bergman, 2012), and radio-transmitter locations (attached to pregnant females, neonates, and young yearlings; data in Table A1 in the Appendix). To do this we walked slowly through the study area while recording the spatial location of marked lizards on a hardcopy map of our study site. The flags aided us to position the location of sightings to ± 1 m by triangulation. Spatial data collection took place from approximately 10:00 am to 6:00 pm.

It is not likely that our activities on the study site influenced the behaviour of the lizards. During radio-tracking surveys, the radio signal (i.e., beeping sound) of the radio-transmitters attached to subjects could be detected by the radio-receiver as far away as 60–70 m, but more commonly at 30–40 m even when radio-tagged individuals were in crevices 10–28 cm deep (Santoyo-Brito & Fox, 2012, 2015). The signal increased in strength as the antenna and receiver got closer to the radio-transmitter. The signal combined with our constant scan sampling in the direction of the strongest signal aided us to locate known individuals from a distance, making it unlikely that the lizard position was influenced by our presence. We also know that maximal distances of radio-signal detection exceeded by far the distance at which *L. leopardinus* seeks refuge when threatened by a human simulating a predator (Santoyo-Brito et al., 2020). The observed individuals were never intentionally flushed to seek refuge.

From late March through April 2015, we measured temperatures of the microhabitat underneath flat rocks similar to natal chambers during night (8:00 pm to 6:00 am) and day (10:00 am to 6:00 pm). We placed 8 pairs of iButtons (iButtonLink, Whitewater, MI, USA), one of each pair underneath a flat rock and the other underneath a nearby bush and recorded temperatures once an hour for 41 days.

2.1. Statistical analyses

To analyze predation pressure from placement of clay models, we used log-linear models in Multiway Frequency Analysis (MFA) that included model size, microhabitat, and attack frequency to calculate and test for significant two-way associations in the data. In this MFA, we pooled adjacent categories in the contingency table so as not to violate the assumptions of the analysis: no more than 20% of expected values less than five and no expected

value less than one (Tabachnick & Fidell, 2013). We pooled medium and large lizard models and compared them to small ones as our size variable (because our hypothesis was that small models would sustain more attacks than larger ones), and pooled the open microhabitats of rock and ground and compared them to the closed microhabitat of beneath bushes as our microhabitat variable (because our hypothesis was that models in the open would sustain more attacks than those under protective cover). Our resulting binary variables of model size, microhabitat, and attacked or not did not violate the MFA assumptions.

To compare the distances moved by different age classes of lizards, we first determined the average distance between consecutive locations of each marked lizard using the Haversine formula to calculate the linear distance in meters (Curry, 2014; Taylor et al., 2019). Because we had too few neonates and young yearlings to perform traditional statistical analyses, we used randomization tests (1000 iterations) to evaluate (1) differences between neonates and adults/juveniles and (2) differences between young yearlings and adults/juveniles in the average distance between consecutive locations. We first calculated the mean distance between consecutive locations for all neonates or all young yearlings, then counted the number of times out of 1000 iterations the mean of the same number of subjects pulled randomly from the set of adults and juveniles was equal to or smaller than the mean of the neonates or young yearlings. A count less than 50 was considered statistically significant, with the conclusion that the neonates or young yearlings moved less.

To test for statistical difference in habitat (i.e., off and on open rock outcrops) of 1) neonates versus adults/juveniles, and 2) young yearlings versus adults/juveniles, we used in each case a χ^2 test of independence of number of locations of lizards in the two habitats. For both the randomization and the chi-squared tests, we limited the analyses to the spatial data recorded during March-April and November-December. These are the months when adults/juveniles and neonates, and adults/juveniles and young yearlings, overlap, respectively.

To compare the locations of known mothers in relation to the respective natal chamber of each for the prepartum, parturient, and postpartum time periods, we tallied the number of sightings less than and greater than 5 m from each mother's natal chamber in each time period (all days before giving birth (prepartum), birth day plus five days (parturient), and all days after the

six-day parturient period (postpartum)) for each mother. We pooled counts of the three mothers less than and greater than 5 m from each mother's natal chamber and performed an overall Chi-squared test of heterogeneity across the three time periods. To test if individual mothers showed non-random proximity to the natal chamber across the three time periods, we conducted a randomization test. We made 1000 iterations of randomly scrambling all of each mother's distances from the natal chamber and randomly placing them into the three time periods, retaining the respective sample sizes of sightings for each mother in each time period, and tallied the number of times all three mothers changed their behaviour as did the three mothers over the actual three time periods, i.e., how many times over the 1000 iterations did randomized sightings of all three mothers show a decrease in distances from prepartum to partutient and an increase in distances from parturient to postpartum. A count less than 50 was considered statistically significant, with the conclusion that individual mothers followed the same pattern over the three time periods observed for mothers' sightings combined.

To analyze the late fall temperatures below flat rocks and within nearby bushes and to ensure that we did not inflate the sample size by pseudoreplication, we first averaged the maxima of all the hourly day and nighttime readings over the 41 days of data collection for each iButton and then used paired t-tests to compare the mean maximal temperatures under a rock and within a bush for the day and night intervals. Before conducting the paired t-test, we tested if the distributions of paired differences were normal with the Kolmogorov-Smirnov test. We performed all statistical analyses using SPSS (v21.0, IBM, Armonk, NY, USA).

3. Results

Small clay models were attacked more often and medium and large clay models less often than expected by chance (Table 1). Models in the open (rock and ground) were attacked more often and those under bushes less often than expected by chance (Table 2). The two-way association of size and attack frequency (partial $\chi^2 = 7.86$, df $= 1$, $p = 0.005$) and of microhabitat and attack frequency (partial $\chi^2 = 12.05$, df $= 1$, $p = 0.001$) were statistically significant. There was no significant association of size and microhabitat (partial $\chi^2 = 0.85$, df $= 1$, $p > 0.05$). Marks left on the models indicated bill strikes from predatory birds. We observed large numbers of the

Table 1.
Clay models, by size, attacked by birds during mid-March of 2012 at El Colorado, Chile.

Size	Observed attacked	Observed not attacked	Total
Large	8	28	36
Medium	13	23	36
Small	20	16	36
Total	41	67	108

Small models were attacked significantly more often than medium and large models (loglinear partial $\chi^2 = 7.86$, df $= 1$, $p = 0.005$).

Table 2.
Clay models, by habitat, attacked by birds during mid-March of 2012 at El Colorado, Chile.

Habitat	Observed attacked	Observed not attacked	Total
Rock	14	22	36
Ground	21	15	36
Bush	6	30	36
Total	41	67	108

Models in protected habitat under bushes were attacked significantly less often than those in the open habitat on rock or ground (loglinear partial $\chi^2 = 12.05$, df $= 1$, $p = 0.001$).

most suspected species, shrike-tyrants and miners (*Agriornis* and *Geositta* spp., respectively) at the study site. We did not capture any images of those species attacking models, but 12 pictures showed *Geositta* sp. in close proximity to the models.

After radiotracking females for almost four months, we discovered that pregnant females mostly remained with their social group, but in late-term frequently took solitary refuge beneath large, flat rocks in brushy microhabitats situated 10–50 m from the open rock outcrops. This behaviour contrasts with that observed for non-pregnant adult and juvenile females (and males) who, in the course of two field seasons, were rarely seen in brushy microhabitats (Santoyo-Brito, 2017). Most importantly, we discovered that females gave birth in solitary underneath such rocks (i.e., natal chambers) largely covered by dense low vegetation (*Berberis* sp.). Radiotracking information indicated that mothers stayed inside the natal chambers with their 3–4 newborns for at least 24 h after parturition.

While observing a pregnant female underneath a flat rock through the borescope, we recorded an agonistic behaviour, the female bit the tip of the

borescope at least six times. We had never observed this agonistic behaviour in any other context (including 150–200 borescope observations of adults in solitary and group refuges). To our surprise, the female was giving birth to three neonates at that exact moment in this natal chamber. It was possible to observe the newborns still moving inside their clear, compacted, marble-like embryonic sacs, and the immediate substrate in contact with the embryo was visibly moist. This was the first scientific record of a *L. leopardinus* mother giving birth in the field. We do not know if mothers help the neonates escape from their tight embryonic sacs. However, in the video, it is possible to see the mother biting at what seems to be an embryo still in its embryonic sac (see Video 1 at 10.6084/m9.figshare.13522652). In separate, laboratory situations, we sometimes had to help neonate *L. leopardinus* escape from their embryonic sacs or they died.

We discovered a total of three natal chambers and placed a motion-sensitive camera pointing to the entrance of all three chambers to document any parental behaviour by the mother and the behaviour of neonates. Radiotracking information, borescope observations, and video-recordings suggested that during the first 24 h, mothers and neonates did not leave the natal chamber. Some 20 h post-parturition, we video-recorded a recent mother, who was located facing outward partially in an entrance of the natal chamber. With all four limbs in contact with the ground, she vigorously moved both front and hind legs to move surrounding soil into the entrance, piling up soil at the entrance (see Video 2 at 10.6084/m9.figshare.13522652). Interestingly, on three different instances we observed packed soil heaped up against the entrance of other natal chambers. Although we did not video-record the females moving the soil and pebbles to close the entrance in these other cases, the marks on the substrate suggested this behaviour. Our observations indicated that mothers closed the entrances to the natal chamber with soil when they left, sealing the neonates inside, possibly to prevent the young, susceptible neonates from prematurely leaving the protection of the natal chamber. We confirmed the presence of the neonates inside sealed chambers 24 h after parturition via borescope observations. Video-recordings and borescope observations indicated that neonates continued to occupy the chambers without their mother inside for 2–5 days. During the first 2–3 days after parturition, the mothers were radio-located and observed basking at the entrance or nearby their natal chambers and nearby their neonates when they emerged, possibly to protect them. Before and after parturition the mothers

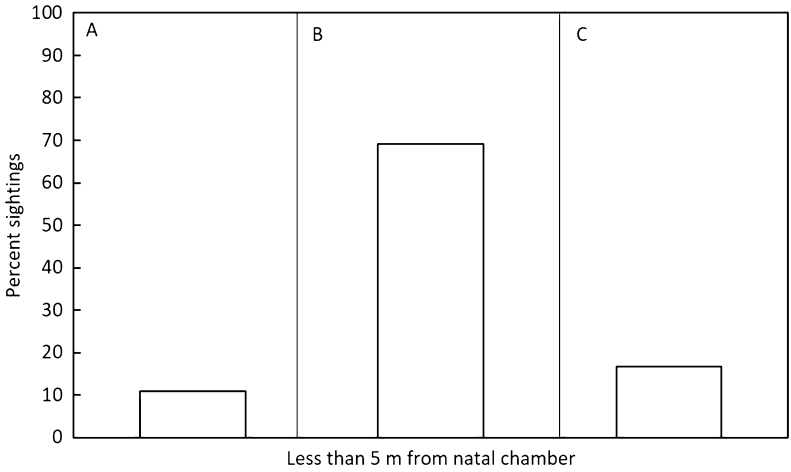

Figure 2. Percent sightings less than 5 m from the mother's natal chamber for (A) prepartum mothers (46 sightings), (B) parturient mothers for birth day plus 5 days after (13 sightings) and (C) postpartum mothers greater than 5 days after giving birth (18 sightings) at El Colorado, Chile, during austral summer 2013.

were located more often on the rock outcrops distant from their natal chambers (Figure 2). This change in behaviour was significantly different among prepartum, parturient, and postpartum mothers when combined sightings of mothers were analyzed by a Chi-squared test of heterogeneity ($\chi^2 = 20.47$, df $= 2$, $p < 0.001$). All three individual mothers showed the same significant pattern. In only 29 of the 1000 iterations did all three mothers show the same pattern of proximity to the natal chamber as in Figure 2 when all distances from the natal chamber of each mother were randomly scrambled across the three time periods, while retaining the same sample size per mother per time period (randomization test, $p < 0.05$).

After the capture and subsequent radiotracking of two neonates in late summer (and visual resightings of a third one without a radio), we observed that neonate *L. leopardinus* are solitary and very secretive. They can be found — rarely — in the open, but mostly they remain concealed under flat rocks covered by dense bushes (*Berberis* sp.). Neonates were radiotracked for a total of 40 lizard-days, and were found mainly underneath flat rocks similar to their natal chambers. Only occasionally did they move into a bush. Up to the end of our field season in late April, neonates spent a couple of days in a torpid state under a flat rock, and then moved to another flat rock usually <1–2 m distant and remained under that rock for a day or two

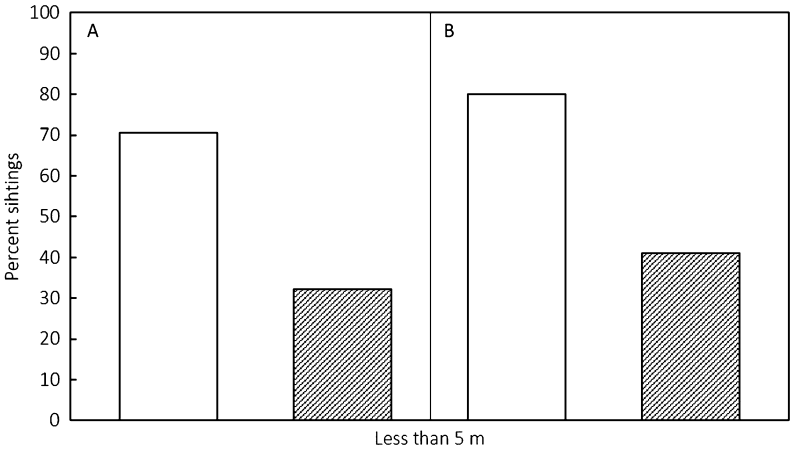

Figure 3. Percent sightings in which distance moved between consecutive sightings was less than 5 m, comparing (A) neonates (open bar) with pooled adults and older juveniles (shaded bar) during the same time of the year, March and April, 2013 and (B) young yearlings (open bar) with pooled adults and older juveniles (shaded bar) during the same time of the year, November and December, 2013, both at El Colorado, Chile.

even on clear and sunny days. The randomization test indicated that neonates ($N = 3$, mean distance between consecutive points = 3.5 m, SD = 3.0 m) traveled much shorter distances than adults and juveniles ($N = 26$, mean distance between consecutive points = 25.7 m, SD = 26.7 m) during the same time of the year (March-April): in only 13 cases out of 1000 random draws of the mean distances between consecutive locations of adults and juveniles pooled was the mean as small or smaller than the mean distance travelled by neonates ($p = 0.013$). Figure 3A shows the basis of this significant difference in movement of neonates vs. adults and older juveniles when consecutive distances moved less than 5 m are plotted. With respect to habitat use, neonates were never found on rock outcrops, whereas pooled adults and juveniles from the same time period mostly were ($\chi^2 = 146.51$, df = 1, $p < 0.001$).

It seems feasible that the neonates overwinter solitarily underneath large flat rocks in brushy habitat. Temperatures underneath such rocks with microhabitat similar to that used by neonates offered thermoregulatory advantages, especially at night. The mean maximal overnight temperature (8:00 pm to 6:00 am) underneath flat rocks (mean = 12.5°C; SD = 1.14) was warmer than that under a nearby bush (mean = 9.5°C; SD = 1.11; paired t-test, $t = 5.87$, df = 7, $p = 0.001$). Mean maximal daytime temperatures under

the rock and bush were not significantly different (paired t-test, $t = -1.198$, df $= 7$, $p = 0.27$). The Kolmogorov–Smirnov test indicated that the distributions of paired differences between mean maximal temperature under flat rocks and under nearby bushes for both the day and night intervals were not different from the normal distribution ($p = 0.998$ and 0.972, respectively).

Neonates were not found in larger social groups until the next active season when they became yearlings. In November (early austral spring) of 2013, we captured four and radio-tagged and followed three young yearling lizards and radiotracked them for a total of 31 lizard-days. These were bigger (mean SVL = 48.75 mm) and more agile than the neonates from the fall before (mean SVL = 40.6 mm), and located in transitional habitat. Mostly they hid under dense *Berberis* bushes growing at the base of the large rock outcrops, sometimes for several days at a time. Young yearlings were sometimes found solitary and sometimes with older conspecific juveniles and adults at or near the large rock outcrops. When located under bushes, young yearlings remained immobile and were very hard to spot. They occasionally made brief forays up onto the outcrops or back to their vegetated natal habitat. One young yearling was found in a small crevice where it stayed overnight with three adults: two males and one female. All four lizards emerged healthy and unharmed the next morning. These young yearlings, like the neonates of the fall before, moved very little compared to adults and juveniles at the same time of the year. The randomization test indicated that young yearlings ($N = 3$, mean distance between consecutive locations = 6.42 m, SD = 2.75 m) traveled significantly shorter distances than adults and juveniles ($N = 16$, mean distance between consecutive locations = 24.81 m, SD = 17.59 m) during November-December: in only 6 cases out of 1000 random draws of the mean distances between consecutive locations of adults and juveniles pooled was the mean as small or smaller than the mean distance traveled by young yearlings ($p = 0.006$). Figure 3B shows the basis of this significant difference in movement of young yearlings vs. adults and older juveniles when consecutive distances moved less than 5 m are plotted. With respect to habitat use, young yearlings were found in brushy habitat away from the rock outcrops significantly more frequently compared to adults and juveniles, who were mostly found on the open outcrops ($\chi^2 = 30.64$, df = 1, $p < 0.001$).

4. Discussion

We hypothesized that avian predation would be stronger on models representing the neonate size class than on older juvenile and adult size classes, and predation would be weaker on models under cover than in the open. Our results support those hypotheses. During March-April, when females give birth, birds are abundant at our study site and it was very common to see foraging *Geositta* and *Agriornis* spp., known predators of neonate *L. leopardinus* (Ridgely & Tudor, 1994; Santoyo-Brito et al., 2014). Neonate-sized models, simulating newborn *L. leopardinus*, were more often attacked by avian predators than larger models. Other studies have shown that small individuals in relation to conspecific adult-sized ones tend to suffer greater predation (Janzen, 1993; Rivas et al., 1998; Kacoliris et al., 2013).

While it is true that a larger prey provides a bigger meal for the predator and therefore a greater nutritive benefit (optimal foraging theory), consumption of very large items requires longer handling, sustains processing costs, and increases risk of injury (Cooper & Stankowich, 2010). In fact, there is often a prey-size threshold above which specific prey are undesirable to predators because they are harder to capture, handle, and consume (Krebs & Davies, 1993; Scharf et al., 2000; Hawlena & Pérez-Mellado, 2009). Adult male and female *L. leopardinus* are fairly large (mean SVL = 100.8 and 99.6 mm, respectively) compared to neonates, young yearlings, and older juveniles (mean SVL = 40.6, 48.75, and 60.2 mm, respectively). Because birds do not chew and can only minimally reduce the size of their prey before ingestion by removal of wings, legs, etc., it is probable that due to gape-limitation, birds more often attacked neonate-sized models. In a similar example, the Izu Islands Thrush (*Turdus celaenops*), a gape-limited insectivorous bird, consumes only smaller juveniles of the abundant lizard, *Plestiodon latiscutatus* (Hasegawa, 1990; Brandley et al., 2014). It is possible that gape-limitation forces the South American Rufous-banded Miner (*G. rufipennis*) and the Black-billed Shrike-tyrant (*A. montana*) to consume mostly *L. leopardinus* neonates and not juveniles and adults. This could be particularly true for *G. rufipennis*, since it was previously known only as a ground-gleaning omnivore and until recently there was no record of predation on animals other than invertebrates (Santoyo-Brito et al., 2014).

Not surprisingly, models of *L. leopardinus* located on open rock or soil were more often attacked by birds than models under vegetative cover. A similar predation pattern has been described using models of hatchling

broad-headed snakes (*Hoplocephalus bungaroides*). Exposed models were attacked by birds significantly more than those under rocks (Webb & Whiting, 2005). It is likely that neonate *L. leopardinus* move little and mostly remain hidden under flat rocks in the habitat of the natal chambers through the fall because of the heavy avian predation pressure at this time. They tend to take refuge in places surrounded by dense bushes with long, sharp spines, making it nearly impossible to capture them. A similar behaviour has been reported in the green iguana (Henderson, 1974). Predation has been considered an important ecological pressure that determines habitat use of various lizard species in Chile (Jaksic & Simonetti, 1987). Neonate *L. leopardinus* show only minor differences in colour pattern when compared to juveniles or adults. Thus, we discard the hypothesis that the colouration of neonates makes them more visually attractive to predators (Martín & López, 1999; Stuart-Fox et al., 2003).

In oviparous species, oviposition-site selection is a non-random behavioural choice. In many instances the site selected by the mother may offer both direct and indirect benefits (e.g., reduced egg detection by predators, egg development in a suitable microclimate, and habitat safe from predators after hatching). All those benefits increase her fitness (Smiseth et al., 2012; Huang et al., 2013). Obviously, in viviparous species, the mother even more directly protects the developing embryos. It would seem that viviparity might generally evolve because of this increase in fitness from the mother's better protection, given that the cost to the mother is not prohibitive (Pincheira-Donoso, 2012). In fact, viviparity has evolved repeatedly from oviparity at least 100 times independently across squamate reptiles, notably in lizards (Shine, 2005; Blackburn, 2015). *Liolaemus leopardinus* is viviparous, so apparently fitness advantages of viviparity prevailed in its ancestors and probably still today are apparent in this species. But how do pregnant *L. leopardinus* females maximize the fitness of their young once they are born? We documented that mothers leave their social groups on open bare rock habitat in search of suitable natal chambers located in protected, brushy habitat (where neonate-sized models were less prone to predation by birds) to give birth to frail newborns who are not as agile and are less coordinated than older conspecifics (ESB, SPF, SFF, personal observations). The poor motor skills of the neonates contrast with the highly altricial recent newborns of sympatric lizard species *L. bellii* and *L. nigroviridis*, which can be seen running and hiding in the same brushy habitat. Mothers in many

ungulate species show changes in habitat preference during parturition and early lactation, sometimes choosing brushier, more concealing vegetation (Gosling, 1969; Jarman, 1976; Leuthold, 1977; Bongi et al., 2008; Ciuti et al., 2009; Roberts & Rubenstein, 2014). Mothers of *L. leopardinus* stay with their neonates in the natal chamber for at least the first 24 h after parturition. The mothers were radio-located and observed basking at the entrance or nearby their natal chambers and emerged neonates some 2–3 days after parturition, probably guarding them or the nest, an example of postpartum parental care. Although most reptiles are highly precocial to independent upon birth or hatching (Davis et al., 2013), postpartum parental care has been documented in at least 60 oviparous and viviparous lizard species from more than 10 families including Liolaemidae (Somma, 2003a; Halloy et al., 2007; While et al., 2014). We did not quantify the benefit to neonates from the maternal behaviour. However, it has been shown that even relatively simple forms of mother-offspring associations during early postnatal periods benefit the newborns by improving their antipredation behaviour, levels of activity, boldness, and exploration (Munch et al., 2018).

Borescope videos of very young newborn *L. leopardinus* in their natural natal chambers in the field and our manipulations with captive-born others revealed that neonates were frail and very vulnerable to harm. Field observations and video-recordings showed that when the mother left her natal chamber, she packed the entrances with soil, possibly to prevent neonates from leaving the chamber, and, thus, indirectly protecting them from predation. Video-recordings and radio-tracking data indicated that mothers were observed and located on several occasions close to the natal chambers, their neonates, and away from their social groups on bare rock outcrops. A similar behaviour has been reported in pregnant *Liolaemus elongatus*, another viviparous, high-elevation Andean lizard (Halloy et al., 2007).

The repetitive aggressive behaviour shown by one mother as she was giving birth in the field (gaping at, charging, and biting the tip of the borescope) might be a case of direct parental care, especially since this aggressiveness contrasts with the otherwise non-aggressive behaviour that characterizes this species (Fox & Shipman, 2003; Santoyo-Brito, 2017; Santoyo-Brito et al., 2017). It is possible that mothers show agonistic behaviour only during the time when the neonates are still inside their embryonic sacs, when their newborns are possibly the most vulnerable to predation. Likewise, staying with the neonates for a time inside the natal chambers and then later nearby

the chambers when the neonates venture outside a bit might be protective parental care by the mother. Other squamate species show aggression against predators and protective behaviour when their offspring are present (Greene et al., 2002; Sinn et al., 2008; Huang et al., 2013; Sherbrooke, 2017), and we have observed adult *L. leopardinus* showing protective guarding behaviour against us in the field (but not biting) when they were with older juveniles. We suggest that *L. leopardinus* may show parental care especially of neonates but even of older, free-ranging juveniles.

None of the radiotracked newborns were observed or located in proximity to conspecifics after they left the area outside the natal chamber. Neonates moved very short distances over the day, significantly less than adults and juveniles. They were located mainly underneath flat rocks similar to the natal chambers, and only occasionally moved to ground cover, but were never located on the rock outcrops inhabited by adults and juveniles. We suggest that the neonates' secretive behaviour is a strategy to decrease their vulnerability to predation by birds. After overwintering underneath flat rocks, the neonates emerged as bigger and more agile yearlings. They continued to behave very cryptically and moved around significantly less than adults or older juveniles at the same time of the year. Gradually these young yearlings moved toward the rock outcrops, but mostly stayed in bushes. Significantly fewer sightings of them were made on the open, rock outcrops compared to adults and older juveniles.

In a striking sense, *L. leopardinus* neonates behaviourally resemble one category of newborn ungulates, but in an extended temporal way. Relative to adults, ungulate infants are particularly vulnerable to predation due to their smaller size and poorer escape ability (Leuthold, 1977; Bleich, 1999; Barber-Meyer & Mech, 2008). Consequently, young bovids, cervids and equids adapt one adaptive anti-predator strategy or another; they can be divided into 'follower' and 'hider' species, depending upon their infant behaviour (Walther, 1965, 1969; Lent, 1974; Leuthold, 1977). Very young infants of 'hider' species spend more time in hiding in solitary away from their mother and other conspecifics, and then gradually transition to less hiding and more activity until they join the social herd (Costelloe & Rubenstein, 2015). Older transitional fawns are more susceptible to predation even though they are older and more agile because they are more detectable due to their change in behaviour (Fitzgibbon, 1990; Byers, 1997; Costelloe & Rubenstein, 2015). The young of 'follower' species stay with the mother and the social group

from birth on and rely on the group for protection from predators (Hamilton, 1971; Leuthold, 1977; King et al., 2012; Costelloe & Rubenstein, 2015). So neonate *L. leopardinus* are like 'hiding' species of ungulates, except that the mother does not return to the hidden neonate for nursing or other maternal care. Neonate *L. leopardinus* remain in their hiding phase to and through brumation (longer than in ungulates) and only the following spring begin to make the transition toward social life with the adults and older juveniles on the rock outcrops. Perhaps it is not wise to extend the comparison of lizards and ungulates too far, but there are other species of viviparous social lizards in which the neonates stay with the social groups from birth on, much like the 'follower' species of ungulates. Examples are *Xantusia vigilis* (Davis et al., 2011), *Egernia stokesii* (Duffield & Bull, 2002; Lanham & Bull, 2004; Gardner et al., 2016), *E. whitii* (Chapple & Keogh, 2006), and *E. striollata* (Duckett et al., 2012). We are unaware, however, if there are other examples of 'hider' social species of lizards, like *L. leopardinus*.

Female parturition occurs when nighttime temperatures grow colder, about two months before brumation. Nighttime temperatures were significantly warmer under flat rocks similar to natal chambers than inside bushes during this time. We suggest that the thermoregulatory advantage is an indirect benefit to the neonates from their mothers' nest-site selection in addition to the benefit of decreased risk of predation in the more vegetated habitat away from the open, rock outcrops. Neonates extend this advantage by selecting the same habitat until they enter brumation.

We discard the possibility of competition molding the described behaviour of *L. leopardinus* mothers and neonates. *Liolaemus leopardinus* is not agonistic toward conspecifics for access to resources. The species is passive and rarely fights or displays (Fox & Shipman, 2003). It likely uses chemical signaling in place of escalated visual communication (Fox & Shipman, 2003). Extensive home range overlap within and between sexes and the grouping behaviour during day and night clearly shows that lizards do not defend or compete for territories (Fox & Shipman, 2003; Santoyo-Brito, 2017). We have never observed any cannibalistic or aggressive behaviour by adults against neonates or young individuals in the field or laboratory (Santoyo-Brito et al., 2017). Although we did not measure food availability, apparently it was not a limiting resource during the period of our study; invertebrates and plant matter were abundant during the lizard active season, and we never observed intraspecific competition over food (Santoyo-Brito, 2017).

Our study calls for more extensive comparative research across populations of *L. leopardinus* experiencing different levels of avian predation pressure to more definitively determine that it is avian predation that is responsible for the parental behaviour of *L. leopardinus* mothers and the secretive, solitary behaviour of the neonates. It has been well established that both ecological and climatic (i.e., high predation pressure and harsh environmental conditions) can promote the expression of parental care (Clutton-Brock, 1991; Huang & Wang, 2008; Smiseth et al., 2012; Pike et al., 2015). This is true especially in species that inhabit cold-temperate environments, exhibit high reproductive effort (Halloy et al., 2007; Huang et al., 2013; Cabezas-Cartes et al., 2018), and have a limited supply of energy for reproduction. All these are characteristics of the high-elevation and highly social *L. leopardinus*. We hope our findings might stimulate other studies of neonate and maternal behaviour and avian predation pressure at high elevations in other species in other places.

Acknowledgements

We thank J. Grindstaff, M. Lovern and T. O'Connell for critically reading the manuscript and offering constructive input throughout the study. We thank field assistants D. Esquerré, M. Palma, N. Torres Achiles and J. Masseloux. Permission to conduct this research was given by Oklahoma State University IACUC according to ACUP AS-11-13, and by Servicio Agrícola Ganadero, Chile permit Nos 188 and 303. Conflict of Interests: The Authors declare that they have no conflict of interests. This study was funded by The National Geographic Society, Delta Foundation, the Southwestern Association of Naturalists, and Oklahoma State University.

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Table A1.
Tracking information (pooled radiolocations and visual sightings) of neonates and pooled adults and older juveniles in March and April, 2013, and of young yearlings and pooled adults and juveniles in November and December, 2013, at El Colorado, Chile.

Age and season	Individual	Age[1]	Sex[2]	Day observed		Total sightings
				First	Last	
Neonates in March and April	GOOG	N	–	28-Mar-13	25-Apr-13	9
	OOYY	N	2	16-Apr-13	26-Apr-13	9
	OYOO	N	1	19-Apr-13	27-Apr-13	2
Total						20
Adults and older juveniles in March and April	BBBW	J	1	12-Mar-13	26-Mar-13	3
	BBRB	A	2	4-Apr-13	4-Apr-13	13
	BGBG	A	2	8-Mar-13	13-Apr-13	7
	BWBW	A	2	2-Mar-13	11-Apr-13	21
	GGOG	A	1	26-Mar-13	16-Apr-13	3
	GGOO	A	1	5-Mar-13	12-Apr-13	2
	GOGO	J	2	12-Apr-13	17-Apr-13	2
	GOOO	J	1	12-Apr-13	20-Apr-13	2
	GRRG	A	1	21-Mar-13	23-Mar-13	2
	GWWW	A	1	16-Mar-13	27-Mar-13	2
	OGGO	A	1	6-Mar-13	8-Apr-13	2
	OOGG	A	1	2-Mar-13	13-Apr-13	4
	OWWW	J	1	5-Mar-13	27-Mar-13	2
	OYYO	A	1	17-Apr-13	18-Apr-13	2
	RBBB	J	2	26-Mar-13	6-Apr-13	2
	RRYR	A	1	12-Mar-13	24-Mar-13	2
	WBBB	A	2	24-Mar-13	29-Mar-13	2
	WOOO	A	1	16-Mar-13	8-Apr-13	3
	WOWO	A	2	14-Mar-13	12-Apr-13	11

Table A1.
(Continued.)

Age and season	Individual	Age[1]	Sex[2]	Day observed		Total sightings
				First	Last	
Adults and older juveniles in March and April (*Continued*)	WOWW	A	2	1-Mar-13	15-Mar-13	8
	WRWR	A	1	29-Mar-13	13-Apr-13	2
	WWWG	A	1	5-Mar-13	8-Apr-13	2
	YWWW	J	1	5-Mar-13	8-Mar-13	2
	YWWY	A	2	1-Mar-13	16-Mar-13	10
	YYYW	A	2	1-Mar-13	9-Apr-13	13
Total						124
Young yearlings in November and December	OORR	Yy	1	12-Nov-13	01-Dec-13	11
	ORRO	Yy	2	17-Nov-13	18-Nov-13	2
	ROOR	Yy	2	12-Nov-13	18-Nov-13	5
Total						18
Adults and older juveniles in November and December	BBBW	A	1	08-Nov-13	01-Dec-13	13
	BWWB	J	2	15-Nov-13	21-Nov-13	2
	GRRR	A	1	20-Nov-13	01-Dec-13	5
	GWGW	A	2	08-Nov-13	09-Nov-13	2
	RBRB	A	2	14-Nov-13	01-Dec-13	11
	RROO	A	2	15-Nov-13	30-Nov-13	3
	WWYY	A	1	08-Nov-13	01-Dec-13	9
Total						45

[1]Age: N, neonate; Yy, 7–8-month-old juvenile; J, older juvenile; A, adult.
[2]Sex: 1, Male; 2, Female.