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POSSIBLE COMMUNAL NESTING IN TWO SPECIES OF *LIOLAEMUS* LIZARDS (IGUANIA: TROPIDURIDAE) FROM NORTHERN ARGENTINA

Robert E. Espinoza[1]
Department of Biology, Colorado State University, Ft. Collins, Colorado 80523-1878, USA
email: espin_r@unr.edu

Fernando Lobo
Instituto de Herpetología, Fundación Miguel Lillo, Miguel Lillo 251, San Miguel de Tucumán 4.000, Argentina

Resumen. Se reporta el hallazgo de nidos comunitarios en *Liolaemus alticolor* y *L. bitaeniatus* (Iguania: Tropiduridae). Un nido comunitario de *L. alticolor* contenía 30 huevos en incubación además dos nidos comunitarios de otros cuatro ya eclosionados. Se descubrieron además dos nidos comunitarios de *L. bitaeniatus* conteniendo 14 y 11 huevos cada uno. El nido de *L. alticolor* probablemente representa la oviposición de 5-7 hembras, mientras que los nidos de *L. bitaeniatus* representarían la puesta de 2-3 hembras. Existía importante variación en el grado de desarrollo de los huevos de un mismo nido sugiriendo que las puestas individuales fueron realizadas a lo largo de un período de días a semanas. Las dos especies son fenéticamente muy similares en morfología y comportamiento, ellas estarían estrechamente relacionadas y pertenecen al mismo grupo de especies. Debido a esto es posible que el comportamiento de formar nidos comunitarios haya evolucionado una sola vez en el antepasado común de estas especies más bien que independientemente en las mismas. No se encontró evidencia de limitaciones particulares de habitat en las localidades donde se hallaron los nidos, por lo que se podría postular que este comportamiento habría evolucionado debido a la perferencia de las hembras por lugares ya utilizados previamente. Estudios empíricos cuidadosos son necesarios para apoyar o desestimar cualquiera de las hipótesis existentes con relación a la evolución de los nidos comunitarios.

Communal nesting and colonial nesting have been reported in many lineages of squamate reptiles (see review in Graves and Duvall 1995); however, the terms are often used imprecisely to describe similar, yet distinct, behaviors. We define communal oviposition as the nonincidental deposition of eggs at a shared nest cavity by two or more conspecifics. This distinguishes communal oviposition from colonial nesting behaviors in which nests are constructed adjacent to one another, but the eggs are generally not deposited in the same nest cavity (e.g., Burger 1993; Mora 1989; Rand 1967; Wiewandt 1982).

Both communal and colonial nesting behaviors have been reported in several tropidurid lizards including: *Microlophus* (=*Tropidurus*) *albemarlensis* (Burger 1993; H. Snell, pers comm 1995), *M. delanonis* (Werner 1978), *M. grayi* (Burger 1993), *Tropidurus flaviceps* (Dixon and Soini 1986), *T. hispidus* and *T. oreadicus* (Vitt 1993), *T.* (=*Plica*) *plica* (Vitt 1990), *T.* (=*Platynotus* and *Tapinurus*) *semitaeniatus* (Vitt 1992; Vitt and Goldberg 1983), *T. spinulosus* (Pérez et al. 1991), and *T. torquatus* (Vitt and Goldberg 1983). To our knowledge, communal oviposition has not been reported for any members of the genus *Liolaemus*.

The genus *Liolaemus* includes more than 150 described species and subspecies (Etheridge 1995) of relatively small to moderately-sized (50-110 mm SVL) lizards that are distributed throughout most of arid and semiarid South America (Cei 1986, 1993; Donoso-Barros 1966). Despite the distribution and diversity of this group of lizards, few studies have examined aspects of their reproductive biology. In this paper we report evidence of communal nesting for two species of *Liolaemus* lizards from northern Argentina.

MATERIALS AND METHODS

Eggs of *Liolaemus alticolor* (*n*=30 developing

[1] Department of Biology/FA 314, University of Nevada, Reno, Reno, Nevada 89557-0015 USA.

and four egg shells) were collected on 23 January 1995 along the roadside of Ruta Provincia 47, 22 km S of Mina Capillitas, Departamento Andalgalá, Provincia Catamarca (27°27'S, 66°25'W, 2825 m elevation). We found the eggs in moderately moist, loamy-sand that had accumulated in a 5-10 cm wide fissure in an east-facing granite boulder. The eggs had been deposited 10-30 cm from the crack surface and were generally in contact with one another (i.e., a single nest cavity). The shells of the four previously hatched eggs were found near the bottom of the nest cavity below most of the developing eggs. The total area occupied by the eggs was approximately 300 cm^2. The soil temperature surrounding the eggs was 26.0 C.

Two nests of *Liolaemus bitaeniatus* eggs were found on 1 February 1995, 18 km W of the intersection of Rutas 310 and 306, Sierra Medina, Departamento Burruyacu, Provincia Tucumán (26°12'S, 65°04'W, 1565 m elevation). The first nest contained 14 developing eggs and 11 shells of hatched eggs, and was found under a small sandstone boulder on a south-facing hillside. The second nest was also found on a gently sloping, south-facing hillside approximately 0.5 km W of the first nest. At this site, 11 developing and two previously hatched eggs were unearthed from 5-8 cm of sandy soil partially covered by a 0.5 m^2 sandstone formation. Eight additional *L. bitaeniatus* neonates (and their eggshells) were uncovered at the same depth within 10 cm of the nest cavity that contained eggs. The temperature of the soil surrounding the *L. bitaeniatus* nests was not measured, but was estimated to be between 25 and 30 C.

We removed the eggs from each nest, placed them into plastic bags with a layer of soil from the nest cavity, and returned them to the Fundación Miguel Lillo, San Miguel de Tucumán, for further examination. Eggs were numbered and their dimensions measured to the nearest 0.01 mm with electronic calipers. Egg mass was measured to the nearest 0.01 g on a triple-beam balance. All measurements were made within 24 h of collection.

Most of the eggs were subsequently fixed in 10% formalin, preserved in 70% ethanol, and the embryos staged according to Lemus et al. (1981) with the aid of a dissecting microscope (10-40X). Several (4-10) eggs were randomly selected from each nest and permitted to complete development in order to verify the identities of the species. These eggs were covered with 1-2 cm of slightly moistened wood shavings, placed in ventilated jars, and incubated at room temperature (approximately 25 C). Most of the eggs hatched within 1-3 weeks, but a few became moldy and shriveled during this period and were discarded. Upon completion of the study, the developing embryos and neonates were cataloged and deposited in the collection of the Fundación Miguel Lillo (FML 03495-03539).

RESULTS AND DISCUSSION

Mean (± 1 *SD*) egg dimensions (length x width) were 15.98 (0.89) x 10.56 (0.51) mm for the *Liolaemus alticolor* eggs, and 15.14 (0.88) x 9.68 (0.65) mm and 13.72 (0.62) x 10.04 (0.49) mm for the two nests of *L. bitaeniatus* eggs, respectively. Mean egg mass was 1.00 (0.13) g for eggs in the *L. alticolor* nest, and 0.83 (0.15) g and 0.77 (0.10) g for the eggs in the *L. bitaeniatus* nests. It is important to note that egg size may change appreciably after deposition (Packard and Packard 1988), so the values reported above likely provide only crude estimates of egg size at parturition.

We found a considerable range of embryonic development among the eggs within a nest for two of the three nest sites that were examined. Developmental stages ranged from 36 to 41 in the *Liolaemus alticolor* nest. This range represents a 36 day(d) difference in embryonic development of the closely related *L. tenuis tenuis* incubated at 22 C (Lemus et al. 1981). A similar range of development (39-42) was noted for embryos from the first *L. bitaeniatus* nest. Likewise, this range corresponds to a 38 d difference in development in *L. t. tenuis* (Lemus et al. 1981). Too few eggs from the second *L. bitaeniatus* nest were examined to provide a confident estimate of the range of embryonic development for the eggs within the nest, but the proximity of the eight neonates (stage 43) to their nest suggests similar patterns of variance. Collectively, these data suggest that several conspecific females deposited their clutches in each of these nest sites over a period of several days to several weeks.

Liolaemus alticolor and *L. bitaeniatus* are small lizards that rarely exceed 55 mm SVL or weigh more than 4-5 g. Clutch sizes for both species average 4-6 eggs (Ramirez Pinilla 1989, 1991). Thus, the nest of 30 *L. alticolor* eggs likely represents the clutches of 5-7 individuals. Likewise, the two nest of 14 and 11 *L. bitaeniatus* eggs could represent the combined progeny of 2-3 females. The additional previously hatched eggs, the range of embryonic development, and in one case, the newly emerged neonates adjacent to one of the nest sites, provide corroborating evidence for the use of shared nest cavities by conspecific females for both species. Assuming this information provides adequate evidence of communal nesting in *L. alticolor* and *L. bitaeniatus*, what is/are the mechanism(s) selecting for this behavior?

Numerous hypotheses have been proposed to explain the evolution of communal nesting and oviposition in squamate reptiles. Some investigators have suggested that communal nesting may be an adaptive response to life in environments where suitable nesting sites are rare (see Graves and Duvall 1995). Indeed, the cooler climates associated with the moderate to relatively high elevations and steep slopes in the region where these nests were found may limit the number of sites or the total area available for nesting. For example, females may share nest sites at higher elevations because fewer microenvironments provide the appropriate physical conditions required for successful incubation (e.g., hours per day at a specific minimum temperature, humidity, drainage, etc.). At our sites, microenvironments similar to those in which the nests were found, did not appear to be uncommon; however, we did not collect detailed information on these potentially alternative nesting areas.

Another possible explanation is that *Liolaemus alticolor* and *L. bitaeniatus* nest with conspecifics as a result of selection by female lizards for sites that have historically proven to be a successful environment for incubation. In practice, female lizards approaching the time of parturition could use olfactory cues to locate previously used nest sites. Eggshells remaining from the previous season could function as additional cues, informing the animal that the nest has historically provided a suitable nesting environment.

Lastly, *Liolaemus alticolor* and *L. bitaeniatus* are both members of the "*chiliensis*" group, a large unresolved but monophyletic assemblage within *Liolaemus* (Etheridge 1995). Thus, the use of communal nest sites may be the plesiomorphic condition for these taxa rather than a novel adaptation that has evolved independently within each species.

Until such hypotheses are empirically tested, the forces selecting for the evolution of communal nesting in these and other squamate reptiles will remain unresolved.

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