This is an Accepted Manuscript of an article published by Taylor & Francis in Studies on Neotropical Fauna and Environment on 10th July 2017, available online: http://www.tandfonline.com//doi/full/10.1080/01650521.2017.1356051.
Published in Studies on Neotropical Fauna and Environment. 57 (3): 244–247.

Cannibalism in the Andean lizard *Liolaemus orientalis*

Octavio Jiménez-Robles[a] and Ignacio De la Riva[a]

[a] Department of Biodiversity and Evolutionary Biology, Museo Nacional de Ciencias Naturales-Consejo Superior de Investigaciones Científicas (CSIC), Madrid, Spain

Corresponding author: Octavio Jiménez-Robles, octavio.jimenez.robles@gmail.com, Department of Biodiversity and Evolutionary Biology, Museo Nacional de Ciencias Naturales, Madrid, Spain

Abstract

Cannibalism is a recurrent behavior across the animal kingdom, with important ecological and evolutionary consequences due to its potential trade-offs on the fitness of involved individuals and demography dynamics. Cannibalism has been reported in eight species of several phylogenetic lineages within *Liolaemus,* a highly diverse genus of Neotropical lizards. Within the *Liolaemus montanus* series, two species are reported to eat juveniles in captivity. We observed a female *Liolaemus orientalis*, another *L. montanus* series member, which had ingested a juvenile of its own species in the wild. As it generally happens with other lizards, cannibalism in *Liolaemus* has been suggested to be performed by the larger sex, being *L. chiliensis* the only other case observed until now in which the cannibalistic individual was a female. The fact that females are slightly smaller than males in *L. orientalis*, converts our observation in an exception to previously observed trends. We suggest that there is a relation of this behavior with the presence of a masculine trait in the cannibalistic female: developed precloacal pores. We also discuss how refuge availability may influence demography and the probability of dispersing juveniles encountering adults, increasing the chances for cannibalism to play some role in population density regulation.

Resumen

El canibalismo es un comportamiento recurrente en el reino animal, con importantes consecuencias ecológicas y evolutivas, debidas a sus potenciales efectos sobre la eficacia biológica de los individuos implicados y las dinámicas demográficas. El canibalismo ha sido descrito en ocho especies de varios linajes filogenéticos dentro de *Liolaemus*, un género de lagartijas neotropicales altamente diverso. Dentro de la serie de *Liolaemus montanus*, se

conocen dos especies que comen juveniles en cautividad. Observamos una hembra de *Liolaemus orientalis*, otro miembro de la serie de *L. montanus,* que había ingerido un juvenil de su propia especie en estado salvaje. Al igual que ocurre generalmente con otros saurios, se ha sugerido que el canibalismo en *Liolaemus* es realizado por el sexo más grande, siendo hasta ahora *L. chiliensis* el único otro caso conocido en el que el individuo caníbal era una hembra. El hecho de que las hembras son ligeramente más pequeñas que los machos en *L. orientalis*, convierte nuestra observación en una excepción a las tendencias observadas previamente. Sugerimos que puede haber una relación de este comportamiento con la presencia de un carácter masculino en la hembra caníbal (poros precloacales desarrollados). También discutimos cómo la disponibilidad de refugio puede influir en la demografía y la probabilidad de que los juveniles en dispersión se encuentren con adultos, aumentando las posibilidades de que el canibalismo juegue algún papel en la regulación de la densidad poblacional.

Keywords: masculinized females; population dynamics; precloacal pores; predation; sexual dimorphism

Introduction

Cannibalism or predation of conspecifics is a widespread behavior in the animal kingdom with important ecological and evolutionary implications (Polis 1981). Although in some cases cannibalism happens as a stochastic event, selective pressures and fitness trade-offs may result in deterministic evolution of behaviors either favoring or avoiding cannibalism in different contexts (Rand & Andrews 1975; Polis 1981; Jenssen et al. 1989; Pfennig 1997; Lourdais et al. 2005). Cannibalism in reptiles is often regarded as an opportunistic result of encounters of different size classes, often with juveniles being the prey (Polis & Myers 1985). Hence, an important set of predators of juvenile lizards is constituted by adults of the same species (Siqueira & Rocha 2008). The highly diverse genus *Liolaemus*, with more than 250 species (Schulte et al. 2000; Abdala & Quinteros 2014) is not an exception, as cannibalism has been observed in six *Liolaemus* species in the wild and in two additional species in captivity (reviewed by Pincheira-Donoso 2012; Villarreal et al. 2012). The general lack of knowledge on natural history and behavior within *Liolaemus* (Halloy et al. 2013), the difficulty of observing intraspecific predation events in nature, and the occurrence of this behavior across different phylogenetic groups within *Liolaemus* (Pincheira-Donoso 2012), suggests that the extent of cannibalism in this genus might be underestimated.

Although there is a general tendency of female cannibalism in the animal kingdom (Polis 1981), Siqueira & Rocha (2008) showed that cannibalism in lizards is usually performed by the larger sex. Within *Liolaemus*, either gender can be the biggest, depending on the species (Pincheira-Donoso & Tregenza 2011; Cox & Kahrl 2014). In seven out of the eight known cannibalistic *Liolaemus* species, intraspecific predation happened in males. The only exception reported so far was *L. chiliensis,* in which females preyed on juveniles and are larger than males (Pincheira-Donoso 2012). Such female-biased sexual size dimorphism is the plausible reason for this exceptional case of female cannibalism in *Liolaemus* (Pincheira-Donoso 2012).

Herein, we report the first evidence of cannibalism in *Liolaemus orientalis* Müller, 1924, a viviparous species of the *Liolaemus montanus* series (sensu Schulte et al. 2000; Lobo et al. 2010). This lizard is known from several localities in the Cordillera Oriental of the Andes in southeastern Bolivia and northwestern Argentina (Dirksen & De la Riva 1999; Díaz Gómez 2007). In the studied population, we could observe that *L. orientalis* has some slight sexual dimorphism in size, coloration and the expression of precloacal pores. Males reach slightly larger sizes than adult females, although that difference is not statistically significant (O. Jiménez-Robles, unpublished data). Juveniles are born with a disruptive dorsal pattern with transversal dark gray bars, which fade as they grow. Females of *L. orientalis* retain a faded juvenile pattern while males change coloration ontogenetically, turning to plain nickel-gray on dorsum (O. Jiménez-Robles, pers. obs.). All males possess developed precloacal pores, while most females lack them (O. Jiménez-Robles, pers. obs.).

Material and methods

During November 2012–January 2013 and November 2013–January 2014, we conducted research on habitat use, distribution and thermal ecophysiology of *L. orientalis* in the vicinities of Arenales (21.854°S, 65.012°W, WGS84, 3600–4300 m asl, Municipality of Yunchará, Province of Avilez, Reserva Biológica Cordillera de Sama, Department of Tarija, Bolivia).

When the weather conditions allowed their activity, one observer surveyed lizards by slowly walking along 200 m transects. As *L. orientalis* may have escape distances of more than 15 m (O. Jiménez-Robles, pers. obs.), the observer carefully scanned visually all available surfaces in a radius of 20 m at least. Once a lizard was detected, it was approached cautiously with the intention to noose it with a modified 3 m fishing rod and to measure body temperature (with a hand-held thermometer a few seconds after capture), substrate

temperature, sex, body size (snout to vent length; SVL) and weight. We also recorded whether females had precloacal pores, and classified them as absent, vestigial or developed. After measurements were taken, individuals were released at the capture spot.

Results

On 26 December 2013, at 12:27 h and 4290 m asl, a female of *L. orientalis,* was found basking on a stone of less than 50 cm in length. Her intra-cloacal temperature was 32.5°C and substrate temperature was 27.3°C. While being handled, she vomited an immature male of her own species (Figure 1). It had been swallowed head-first being the head partially digested, while the posterior part of the body was still intact (except for the missing tail tip). The preyed individual had a SVL of 45 mm, tail length > 19 mm and weight of 2.5 g. The female size (81 mm of SVL, 96 mm of tail length, and 15.2 g of weight after vomiting) was slightly below the most frequent observed SVL for adult females in this population and conserved a fainted juvenile dorsal color pattern, suggesting that she was still growing. She had developed precloacal pores (Figure 1B).

Discussion

Our observation is the second reported case of female cannibalism in *Liolaemus.* Contrarily to the predictions of Siqueira and Rocha (2008) for lizards, and Pincheira-Donoso (2012) for the genus *Liolaemus*, cannibalism is not always performed by the larger sex. At least the exceptional case of female cannibalism in *L. orientalis* follows the common pattern observed in other animals (Polis 1981), where females are usually the cannibalistic sex.

However we could not discard that cannibalism in *L. orientalis* could be a behavior also carried out by males. In some lizards, several degrees of female masculinization have been observed both in aggressive behavior and physical traits (Viets et al. 1993: Hews & Quinn 2003; Swierk & Langkilde 2013). In the genus *Liolaemus*, males generally have precloacal pores, but there is variation in their occurrence in females; if present, they are always smaller and less numerous than those of males (Valdecantos et al. 2014). In the *L. orientalis* population of Arenales, the expression of fully developed precloacal pores in females was observed in this cannibalistic female and three other females (while we observed other 32 females with no pores and 16 with vestigial pores). Further evidences are needed to understand the biological meaning of the different expression of precloacal pores in females of *Liolaemus*, and to know if their presence has any relation with aggressive behavior and infanticide risk.

Previous observations of intraspecific predation within the *montanus* series took place in laboratory conditions with *L. huacahuasicus* (Halloy & Halloy 1997) and *L. forsteri* (Villarreal et al. 2012). Hence, our observation in *L. orientalis* confirms that cannibalism happens in nature in free-ranging members of the *Liolaemus montanus* series (sensu Schulte et al. 2000).

Cannibalism in the animal kingdom is usually conditioned by size differences. This explains its higher occurrence in large species (Polis 1981). Pincheira-Donoso (2012) detected that large species of *Liolaemus* were more likely to be cannibalistic, all the reports belonging to species in the far right range of body size frequency distribution for the genus, with the exception of *L. darwinii*, which has a medium size. The other cannibalistic species not included in that analysis, *L. huacahuasicus*, *L. forsteri*, and *L. orientalis*, would be also in the right side of size frequency distribution and reinforce the same conclusions.

The risk of cannibalism in the wild may be also affected by demographic factors (Polis 1980). *Liolaemus orientalis* in the Cordillera de Sama occurs at relatively low densities when compared with other lizards such as the smaller *Liolaemus* spp. that live below 3800 m of elevation in the study area (Jiménez-Robles, unpublished). Despite these low densities, the limited availabilities of refuges in its habitat may increase the chances of individual encounters. This means that dispersing juveniles could face some intraspecific predation risk by the relatively high probability of coming across an adult when seeking for a refuge. Under these habitat constraints, cannibalism may be a way of regulating population densities, especially when approaching carrying capacity.

Given the lower substrate temperature, the cannibalistic female was likely raising her body temperature mainly through heliothermy, although with the thigmothermic contribution of a substrate with high thermal inertia such as a stone. Probably she was trying to optimize digestion of her prey while basking. The juvenile, with approximately a sixth of the mass of the predator, did not even fit into her stomach, so the urgency of digesting it was even higher. Preying on such big items undoubtedly contributes great nutritive benefits but it also implies some costs like an urgent need to bask more time to accelerate digestion and a higher risk of predation or losing the stomach content after a stressing event (as it happened in the reported case).

Acknowledgements

José A. Alfaro, Edmundo Martínez and other rangers and managers of SERNAP (Servicio Nacional de Áreas Protegidas) provided logistic support in Reserva Biológica Cordillera de

Sama. James Aparicio (CBF-MNHN) helped with bureaucracy for research permits, which were provided by the Ministerio de Medio Ambiente y Agua of Bolivia (VMA-DGBAP 1866/2012). Nellsy A. Ohara lent her camera for taking the pictures, and she together with Ramiro Estrada-Núñez provided assistance during data collection. Anne Zillikens and three anonymous reviewers provided comments that improved the manuscript.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

Research costs were supported by the Spanish Ministry of Economy and Competitiveness project CGL2011-30393 (Principal Investigator, I. De la Riva). O. Jiménez-Robles was supported by a JAE-pre grant from the Spanish Scientific Research Council (CSIC).

References

Abdala CS, Quinteros AS. 2014. Los últimos 30 años de estudios de la familia de lagartijas más diversa de Argentina. Actualización taxonómica y sistemática de Liolaemidae. Cuadernos de Herpetología 28:55–82.

Cox RM, Kahrl AF. 2014. Sexual Selection and Sexual Dimorphism. In: Rheubert JL, Siegel DS, Trauth SE, editors. Reproductive Biology and Phylogeny of Lizards and Tuatara. Boca Ratón, Florida: CRC Press. Taylor and Francis Group. p 78–108.

Díaz Gómez JM. 2007. Reptilia, Iguania, Liolaeminae, *Liolaemus*, Puna, Prepuna, and mountain ranges, Northwestern Argentina. Check List. 3:105–118.

Dirksen L, De la Riva I. 1999. The lizards and amphisbaenians of Bolivia (Reptilia, Squamata): checklist, localities, and bibliography. Graellsia. 55:199–215.

Halloy M, Halloy S. 1997. An indirect form of parental care in a high altitude viviparous lizard, *Liolaemus huacahuasicus* (Tropiduridae). Bull Maryland Herpetol Soc. 33:139–155.

Halloy M, Robles C, Salica MJ, Semhan R, Juárez Heredia V, Vicente N. (2013) Estudios de comportamiento y ecología de lagartijas de los géneros Liolaemus y Phymaturus (Iguania: Liolaemini). Cuadernos de Herpetología 28:15–26.

Hews DK, Quinn VS. 2003. Endocrinology of Species Differences in Sexually Dichromatic Signals. In: Fox SF, McCoy JK, Baird TA, editors. Lizard Social Behavior. Baltimore, MD: The Johns Hopkins University Press. p 253–277.

Jenssen TA, Marcellini DL, Buhlmann KA, Goforth PH. 1989. Differential infanticide by adult curly-tailed lizards, *Leiocephalus schreibersi*. Anim Behav. 38:1054–1061.

Lobo F, Espinoza RE, Quinteros S. 2010. A critical review and systematic discussion of recent classification proposals for liolaemid lizards. Zootaxa. 2549:1–30.

Lourdais O, Brischoux F, Shine R, Bonnet X. 2005. Adaptive maternal cannibalism in snakes (*Epicrates cenchria maurus*, Boidae). Biol J Linn Soc. 84:767–774.

Pfennig DW. 1997. Kinship and cannibalism. BioScience. 47: 667–675.

Pincheira-Donoso D. 2012. Intraspecific predation in the *Liolaemus* lizard radiation: a primer. Anim Biol. 62:277–287.

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

Polis GA. 1981. The evolution and dynamics of intraspecific predation. Ann Rev Ecol System. 12:225–251.

Polis GA, Myers CA. 1985. A survey of intraspecific predation among reptiles and amphibians. J Herpetol. 19:99–107.

Rand AS, Andrews RM. 1975. Adult color dimorphism and juvenile pattern in *Anolis cuvieri*. J Herpetol. 9:257-260.

Schulte JI, Macey J, Larson A, Espinoza R. 2000. Phylogenetic Relationships in the Iguanid Lizard Genus *Liolaemus*: Multiple Origins of Viviparous Reproduction and Evidence for Recurring Andean Vicariance and Dispersal. Biol J Linn Soc. 69:75–102.

Siqueira CdC, Rocha CFD. 2008. Predation by lizards as a mortality source for juvenile lizards in Brazil. S Am J Herpetol. 3:82–87.

Swierk L, Langkilde T. 2013. Bearded ladies: females suffer fitness consequences when bearing male traits. Biol Lett. 9:20130644.

Valdecantos S, Martínez V, Labra A. 2014. Comparative morphology of *Liolaemus* lizards precloacal glands. Acta Herpetol. 9:147–158.

Viets BE, Tousignant A, Ewert MA, Nelson CE, Crews D. 1993. Temperature–dependent sex determination in the leopard gecko, *Eublepharis macularius*. J Exp Zool. 265:679–683.

Villarreal S, Aparicio J, Landívar CM, Guizada L, Pacheco LF, Dávila P. 2012. *Liolaemus forsteri* (ncn) cannibalism. Herpetol Rev. 43:70–71.

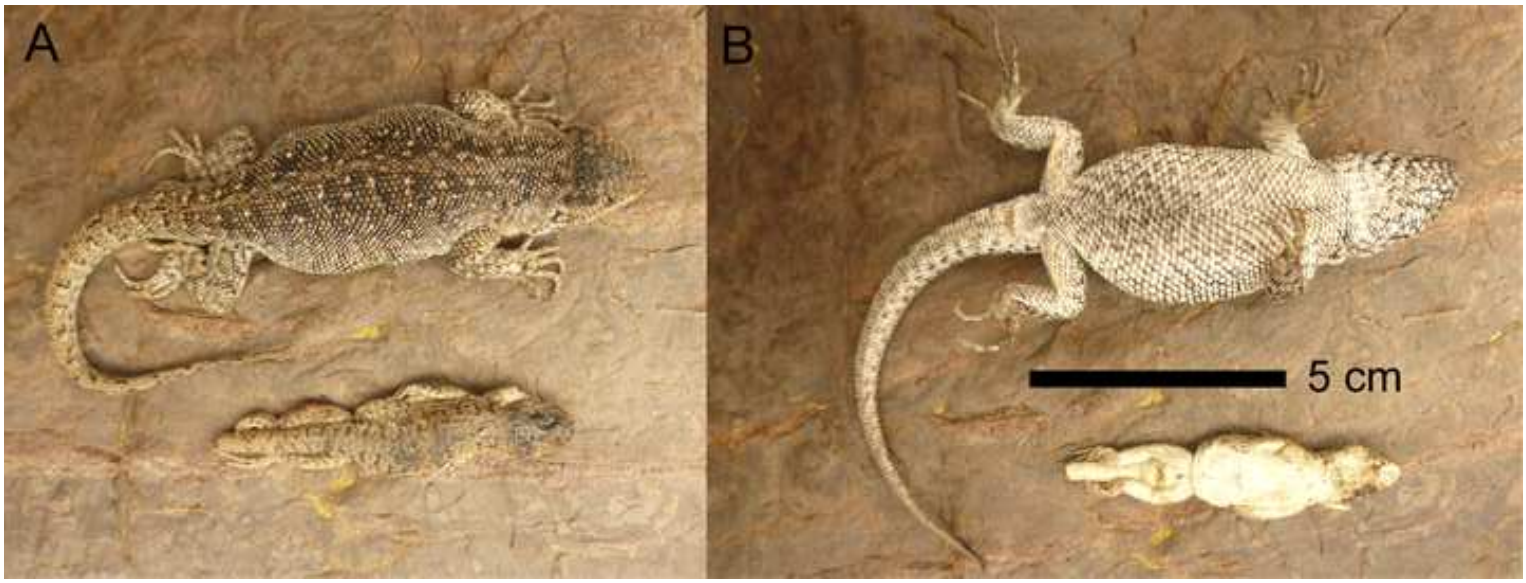

Figure 1. Female *L. orientalis* that regurgitated the juvenile with a partially digested head in Abra de Paredes, Reserva Biológica Cordillera de Sama, Tarija, Bolivia. A) Dorsal and B) ventral view of both specimens.