Eye orbit geometric shape in *Liolaemus* as an indicator of polygyny or monogamy

Geometría de la órbita ocular en *Liolaemus* como indicador de poliginia o monogamia

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ABSTRACT

Most animal groups have sexual dimorphism in morphological characters, especially body size. In many cases, sexual dimorphism may be a consequence of a hierarchical social organization within populations. However, polygyny or monogamy may evolve independently of sexual dimorphism. Two *Liolaemus* species are known to be good model species to study the relationship between sexual dimorphism and sexual social system: *Liolaemus tenuis* (polygyny) and *Liolaemus copiapensis* (monogamy). In this study, I evaluate the morphological variation in the geometric shape of the orbit between sexes in the two species, comparing their social condition (polygyny, monogamy) and applying a geometric morphometrical methodology. The results show morphological differentiation in orbit shape, suggesting potentially adaptive characters associated with social condition. There are variety of possible causes which could explain these differences (e.g., multiple origins of the social system in *Liolaemus*), which could provide new perspectives; however, the generalized lack of knowledge of social systems in *Liolaemus* species imposes barriers to new studies on the subject.

KEYWORDS: Geometric morphometrics, *Liolaemus copiapensis*, *Liolaemus tenuis*, social behavior.

RESUMEN

La mayoría de los grupos de animales muestran dimorfismo sexual en los caracteres morfológicos, en particular el tamaño del cuerpo. En muchos casos, el dimorfismo sexual puede ser una consecuencia de una organización social jerarquizada dentro de las poblaciones. Sin embargo, la poliginia o la monogamia pueden evolucionar por líneas independientes del dimorfismo sexual. Existen dos especies de *Liolaemus* conocidas por ser buenas especies de estudio, puesto que permiten relacionar el dimorfismo sexual y el sistema social: *Liolaemus tenuis* (poliginica) y *Liolaemus copiapensis* (monógama). En este estudio se evalúa la variación morfológica de la forma de las órbitas entre los sexos de ambas especies, comparando su condición social (poliginia, monogamia) y aplicando la metodología de morfometría geométrica. Los resultados muestran diferencias morfológicas en la forma de la órbita, sugiriendo que corresponden a un carácter potencialmente adaptativo asociado a la condición social. En este sentido, hay una variedad de posibles causas que podrían explicar estas diferencias (e.g., orígenes múltiples del sistema social en *Liolaemus*), las cuales podría llevar a nuevas perspectivas de estudio. Sin embargo, la falta de conocimiento acerca de los sistemas sociales en las especies de *Liolaemus* impone barreras a nuevos estudios.

PALABRAS CLAVES: Morfometría geométrica, *Liolaemus copiapensis*, *Liolaemus tenuis*, conducta social

INTRODUCTION

In most animal groups, sexual differences in morphological characters (sexual dimorphism) are a common phenomenon, particularly in body size. The direction of the difference, i.e., whether males or females are larger, differs between animal groups; in vertebrates males are typically the larger sex (Schoener *et al.* 1982; Shine 1986; Fairbairn 1990, 1997;

Andersson 1994). Several proximate mechanisms have been proposed to explain sexual dimorphism, such as differential mortality of sexes (Stamps 1993) and different growth rates of sexes (Watkins 1996). However, natural or sexual selection remains the ultimate mechanism explaining sexual dimorphism (Shine 1986; Andersson 1994; Watkins 1998). Sexual dimorphism is one consequence of a hierarchical social organization within populations (Verrastro 2004).

However, polygyny or monogamy may be independent of sexual dimorphism (Desjardins *et al.* 2008). Thus, a species may exhibit sexual dimorphism and a male may have a harem of many females and also defend a territory (Luetenegger 1978; Gage 1994; Fairbairn 1997; Balshine *et al.* 2001), but in other species a male may pair with a single female during a season (Cuadrado 2002). Although the mechanisms that determine monogamy or polygyny are known (Bull 2000 and references therein), alternative morphological features related to these social conditions (not related to body size) have been poorly studied.

Many lizard species of the genus *Liolaemus* show sexual dimorphism (Donoso-Barros 1966; Pincheira & Núñez 2005), including polygynous and monogamous species. Two *Liolaemus* species provide a good model to study the relationship between sexual dimorphism and sexual social system: *Liolaemus tenuis* (polygyny) and *Liolaemus copiadoensis* (monogamy). For *L. tenuis*, Müller & Hellmich (1933) reported color sexual dimorphism; males are very colorful with predominance of yellow in the anterior body region and blue-green colors in the posterior body region, in contrast to the melanistic color of females (Müller & Hellmich 1933; Donoso-Barros 1966; Vidal *et al.* 2005; Vidal *et al.* 2007). It has a polygynous social system; males are territorial (Manzur & Fuentes 1979) and use visual displays in their agonistic interactions (Trigoso-Venarío *et al.* 2002). In contrast, *L. copiadoensis* shows sexual size dimorphism (Donoso-Barros 1966, Pincheira & Núñez 2005) however, the dorsal coloration is gray-brownish and the color variation between sexes is not apparent (Donoso-Barros 1966). *Liolaemus copiadoensis* has been reported to be monogamous, since when individuals have been extracted from sand caves in the desert they were always observed in couples (i.e. a single male with a single female) (Ortiz 1981). While there is no other reported data explicitly demonstrating monogamy in this species, the observations of Ortiz (pers. com.) were made during several years while doing his doctoral thesis. Monogamy has not been reported in other species of Chilean *Liolaemus*, thus *L. copiadoensis* was the best candidate for this study. In a previous study, Vidal *et al.* (2005) suggested that geometrically the sexual differentiation in *L. tenuis* is evident in the ocular area; males tend to develop more rounded and extended orbits than the females, with a frontal scale in the posterior position. These authors suggested that the male ocular extension could be related to a greater capacity for territory domination and more efficient vision of the females in the harem. The conjunction of these sexual advantages with the polygynous social system of *L. tenuis* (Manzur & Fuentes 1979, Labra & Niemeyer 1999) may be the most likely mechanism determining and explaining the observed sexual dimorphism (Vidal *et al.* 2005).

The aim of this study is to evaluate the morphological variation in the geometric shape of the orbit between sexes

in *L. tenuis* and *L. copiadoensis*, comparing their social condition (polygyny, monogamy), applying the method of geometric morphometrics. Given that both species show sexual size dimorphism but differ in their social system (polygyny and monogamy), it predicted that orbit shape in *L. tenuis* (polygynous) will be different between sexes, while orbit shape in *L. copiadoensis* (monogamous) will be similar between sexes.

MATERIALS AND METHODS

All materials used in this study belong to the collection of the Museum of Zoology of the Universidad de Concepción (MZUC). A geometric morphometric analysis was used to assess the variation attributed exclusively to shape by analyzing landmarks or outlines of the shape (Kuhl & Guardina 1982; Bookstein 1991). Dorsal views of the heads of 77 adult specimens (Males = 41; Females = 36) of *L. tenuis* and 78 adult specimens (Males = 39; Females = 39) of *L. copiadoensis* were photographed with a Sony-Mavica digital camera. The outlines of the left orbits of each specimen (Fig. 1) were drawn. Using Elliptic Fourier transforms (which express outlines in periodic signals) these signals were then fitted by a sum of trigonometric functions (or harmonics) that have different amplitudes and phases. This method is based on the separate Fourier decompositions of the incremental changes of the x - and y - coordinates as a function of the cumulative length along the outline (Kuhl & Guardina 1982). Any harmonic corresponds to four coefficients: A_n and B_n for x and C_n and D_n for y , defining an ellipse in the xy -plane. The coefficients of the first harmonic, describing the best-fitting ellipse of any outline, are used to standardize the size and orientation of the object. These coefficients therefore correspond to the residuals after standardization, and should not be included in statistical analyses (Crampton 1995; Renaud & Millien 2001; Renaud & Michaux 2003). This method also limits the influence of measurement errors by filtering out the noise that occurs in the details of the outline (Renaud & Millien 2001). Based on the Fourier coefficients, the shape was reconstructed by an inverse method (Crampton 1995) that allows visualization of the changes of the form involved, which are directly developed in the program Morphueus *et al.* (Slice 1998).

For each outline, thirty-two variables considering eight harmonics were obtained. Since the first harmonics showed no variation, only 29 coefficients or variables were considered. A characteristic of the Fourier harmonics is that the higher the rank of the harmonic, the more details of the outline are described. This property can be used to filter out measurement noise, which increases with harmonic rank (Renaud 1999). These variables were then used in multivariate statistical analyses. A two-way multivariate

analysis of variance (MANOVA) (contrasting by sexes and species) were performed on these variables in order to evaluate the shape differences. Additionally, the orbit shape of all specimens was compared using a one-way analysis of variance (ANOVA), with sexes and species as a factor separately.

RESULTS AND DISCUSSION

Liolaemus tenuis and *L. copiadoensis* showed morphological differentiation in orbit shape. MANOVA indicated in all cases a morphological differentiation of the orbit shape between species (MANOVA, Wilks Lambda = 0.558; $p = 0.0001$) and sexes (Wilks Lambda = 0.697; $p = 0.0119$), but the interaction between the factors was not significant (Wilks Lambda = 0.760; $p = 0.1389$). Differentiation among *Liolaemus* species has been frequently evaluated from the morphological and genetic perspective (Donoso-Barros 1966; Cei 1986, 1993; Young 1998; Pincheira & Núñez 2005). Specifically, the variation between *L. tenuis* and *L. copiadoensis* has been evaluated only in taxonomic terms, suggesting morphological differentiation because they belong to distinct lineages (Schulte *et al.* 2000; Lobo 2001), although Pincheira & Núñez (2005) synonymized the species *L. copiadoensis* with *L. bisignatus*. On the other hand, from a phylogenetic point of view the polygynous social system

present in *Phymaturus palluma* is interesting (Habit & Ortiz 1996), since it is an ancestral species of the genus *Liolaemus* (Schulte *et al.* 2000; Lobo 2001). This allows speculation that the disappearance of this type of social system as in *L. copiadoensis* may have had multiple causes, which could be approached from a higher perspective (e.g., multiple origins of the social system in *Liolaemus*), which could lead to new research on the subject. However, the widespread lack of knowledge of the social systems in *Liolaemus* imposes a barrier to new studies.

Significant differences were found between sexes for *L. tenuis* (Wilks Lambda = 0.458; $p = 0.019$; Fig. 2a); males had a more rounded and extended orbit shape than females. Although Vidal *et al.* (2005) suggested that *L. tenuis* differentiates its orbit shape according to social condition, there is currently no evidence to indicate that this type of differentiation is related to mating systems, except for the present study. Many other characters have been proposed to explain sexual dimorphism and the existence of a polygynous social system in reptiles, e.g., larger body size in males, occipital crest development, gular folds in males and other traits (Andersson 1994; Fairbairn 1997). Similarly, this new character (orbit shape) may also be related to this kind of differentiation. The results obtained in *L. copiadoensis* (monogamous) appear to corroborate these results since it did not have significant differences in orbit shape between sexes (Wilks Lambda = 0.578; $p = 0.278$; Fig. 2b).

FIGURE 1 Eye orbit considered in shape analysis.

FIGURA 1. Órbita del ojo considerada en el análisis de forma.

There were no significant differences between the orbit shape of *L. tenuis* females and both sexes of *L. copiapoensis* (Wilks Lambda = 0.647, $p = 0.586$) which indicates that differences are given mainly by the orbit shape of males from the polygynous species. While the differences found in this study are interesting, it is important to note that microhabitats used by the two *Liolaemus* species are different, affecting orbit shape. In fact, Schulte *et al.* (2004) reported that *L.*

tenuis is an arboreal species that uses high perches, while *L. copiapoensis* is a desert species whose activity is mainly in the sand (although there are rocks available as perches). However, differences in orbit shape in *L. tenuis* could be explained because a male increases the height of his perch to increase his number of females (Manzur & Fuentes 1979), favoring morphological changes (shape of the orbit), which could have an adaptive value.

FIGURE 2. Eye orbit shape of males and females of a) *Liolaemus tenuis* and b) *Liolaemus copiapoensis*.

FIGURA 2. Forma de la órbita de machos y hembras de a) *Liolaemus tenuis* y b) *Liolaemus copiapoensis*.

FIGURE 3. Principal component showing shape variation. F: females; M: males; *Liolaemus copiapoensis* (Lcop); *Liolaemus tenuis* (Lten).

FIGURA 3. Componente principal que muestra la variación de la forma. F: hembras; M: machos; *Liolaemus copiapoensis* (Lcop); *Liolaemus tenuis* (Lten)

FIGURE 4. Mean orbit shape configuration of females of *Liolaemus tenuis*, and males and females of *Liolaemus copiapoensis*.

FIGURA 4. Configuración de la forma promedio de la órbita de hembras de *Liolaemus tenuis* y machos y hembras de *Liolaemus copiapoensis*.

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BIBLIOGRAPHY

- ANDERSSON, M. 1994. Sexual selection. Princeton University Press, Princeton, New Jersey.
- BALSHINE, S., LEACH, B., NEAT, F., REID, H., TABORSKY, M. & WERNER, N. 2001. Correlates of group size in a cooperatively breeding cichlid fish (*Neolamprologus pulcher*). Behavioral Ecology and Sociobiology 50: 134-140.
- BOOKSTEIN, F.L. 1991. Morphometrics tools for landmark data: geometry and biology. New York. Cambridge University Press.
- BULL, C.M. 2000. Monogamy in lizards. Behavioural Processes 51: 7-20.
- CEI, J.M. 1986. Reptiles del centro, centro-oeste y sur de la Argentina. Herpetofauna de las zonas áridas y semiáridas. Museo Regionale di Scienze Naturali Torino (Italy) 4: 1-527.
- CEI, J.M. 1993. Reptiles de noroeste, nordeste y este de la Argentina. Herpetofauna de las selvas subtropicales, Puna y Pampas. Museo Regionale di Scienze Naturali (Italy) 14: 1-949.
- CRAMPTON, J.S. 1995. Elliptic Fourier shape analysis of fossil bivalves: some practical considerations. Lethaia 28: 179-186.
- CUADRADO, M. 2002. Sistemas de apareamiento en reptiles: una revisión. Revista Española de Herpetología 2002: 61-69.
- DESJARDINS, J.K., FITZPATRICK, J.L., STIVER, K.A., VAN DER KRAAL, G.J. & BALSHINE, S. 2008. Costs and benefits of polygyny in the cichlid *Neolamprologus pulcher*. Animal Behaviour 75: 1771-1779.
- DONOSO-BARROS, R. 1966. Los reptiles de Chile. Ediciones de la Universidad de Chile, Santiago, Chile.
- FAIRBAIN, D. 1990. Factors influencing sexual size dimorphism in temperate waterstriders. American Naturalist 136: 61-86.
- FAIRNAIRN, D. 1997. Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. Annual Review of Ecology, Evolution, and Systematics 28: 659-687.
- GAGE, M.J.G. 1994. Associations between body size, mating pattern, testes size and sperm lengths across butterflies. Proceedings of the Royal Society London-Series B. 258: 247-254.
- HABIT, E. & ORTIZ J.C. 1996. Patrones de comportamiento y organización social de *Phymaturus flagellifer* (Reptilia, Tropiduridae). In: Herpetología Neotropical (Ed. J.E. Péfaur) Mérida, Universidad de Los Andes, Consejo de publicaciones. pp. 141-154.
- KUHL, F.P. & GIARDINA, C.R. 1982. Elliptic Fourier features of a closed contour. Computer Graphics and Image Processing 18: 236-258.
- LABRA, A. & NIEMEYER, H.M. 1999. Intraspecific chemical recognition in the lizard *Liolaemus tenuis*. Journal of

- Chemical Ecology 25: 1799-1811.
- LOBO, F. 2001. A phylogenetic analysis of lizards of the *Liolaemus chiliensis* group (Iguania: Tropicuridae). *Herpetological Journal* 11: 137-150.
- LUETENEGGER, W. 1978. Scaling of sexual dimorphism in body size and breeding system in primates. *Nature* 272: 610-611.
- MANZUR, M.I. & FUENTES, E.R. 1979. Polygyny and agonistic behavior in the tree-dwelling lizard *Liolaemus tenuis* (Iguanidae). *Behavioral Ecology and Sociobiology* 6: 23-28.
- MÜLLER, L. & HELLMICH W. 1933. Beiträge zur Kenntnis der Herpetofauna Chiles. VIII. Bemerkungen über *Liolaemus tenuis* (Duméril et Bibron). *Zoologische Anzeiger* 104: 305-310.
- ORTIZ, J.C. 1981. Révision taxonomique et biologie des *Liolaemus* du groupe nigromaculatus (Squamata, Iguanidae). Thèse de Doctorat d'État Sciences Naturelles, Université Paris VII.
- PINCHEIRA, D. & NÚÑEZ, H. 2005. Las especies chilenas del género *Liolaemus* Wiegmann 1834 (Iguania: Tropicuridae: Liolaeminae) Taxonomía, sistemática y evolución. *Museo Nacional de Historia Natural (Chile)* 59: 1-486.
- RENAUD, S. 1999. Size and shape variability in relation to species differences and climatic gradients in the African rodent *Oenomys*. *Journal of Biogeography* 26: 857-865.
- RENAUD, S. & MICHAUX, J.R. 2003. Adaptive latitudinal trends in the mandible shape of *Apodemus* wood mice. *Journal of Biogeography* 30: 1617-1628.
- RENAUD, S. & MILLIEN, V. 2001. Intra- and interspecific morphological variation in the field mouse species *Apodemus argenteus* and *A. speciosus* in the Japanese archipelago: the role of insular isolation and biogeographic gradients. *Biological Journal of the Linnean Society* 74: 557-569.
- SCHOENER, T., SLADE J. & STINSON, C. 1982. Diet and sexual dimorphism in the very catholic lizard genus, *Leiocephalus*, of the Bahamas. *Oecologia* 53: 160-169.
- SCHULTE II, J.A., MACEY, R.J., ESPINOZA, R.E. & LARSON, A. 2000. Phylogenetic relationships in the iguanid lizard genus *Liolaemus*: multiple origins of viviparous reproduction and evidence for recurring Andean vicariance and dispersal. *Biological Journal of the Linnean Society* 69: 75-102.
- SCHULTE II, J.A., LOSOS, J.B., CRUZ, F.B. & NÚÑEZ, H. 2004. The relationship between morphology, escape behaviour and microhabitat occupation in the lizard clade *Liolaemus* (Iguanidae: Tropicurinae: Liolaemini). *Journal of Evolutionary Biology* 17: 408-420.
- SHINE, R. 1986. Sexual differences in morphology and niche utilization in an aquatic snake, *Acrochordus arafurae*. *Oecologia* 69: 260-267.
- SLICE, D.E. 1998. *Morpheus et al.*: software for morphometric research. Stony Brook, NY: Department of Ecology and Evolution, State Univ. of New York.
- STAMPS, J.A. 1993. Sexual size dimorphism in species with asymptotic growth after maturity. *Biological Journal of the Linnean Society* 50: 123-145.
- TRIGOSSO-VENARIO, R., LABRA, A. & NIEMEYER, H.M. 2002. Interactions between males of the lizard *Liolaemus tenuis*: Roles of familiarity and memory. *Ethology* 108: 1-8.
- VERRASTRO, L. 2004. Sexual dimorphism in *Liolaemus occipitalis* (Iguania, Tropicuridae). *Iheringia* 94: 45-48.
- VIDAL, M.A., ORTIZ, J.C. & LABRA, A. 2007. Sexual and geographic variation of color patterns in *Liolaemus tenuis* (Squamata, Liolaeminae). *Gayana* 71: 27-33.
- VIDAL, M.A., ORTIZ, J.C., RAMÍREZ, C.C. & LAMBOROT, M. 2005. Intraspecific variation in morphology and sexual dimorphism in *Liolaemus tenuis* (Tropicuridae). *Amphibia-Reptilia* 26: 343-351.
- WATKINS, G.G. 1996. Proximate causes of sexual size dimorphism in the iguanian lizard *Microlophus occipitalis*. *Ecology* 77: 1473-1482.
- WATKINS, G.G. 1998. Function of a secondary sexual ornament: the crest in the South American iguanian lizard *Microlophus occipitalis* (Peters, Tropicuridae). *Herpetologica* 54: 161-169.
- YOUNG-DOWNEY, A.R. 1998. Phylogenetic studies on *Liolaemus* (Sauria: Tropicuridae): an interpretation based on molecular data and a biochemical test of a biogeographic hypothesis. Tesis Doctoral, University of Miami. 84 pp.

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