

Dorsal polymorphism and perch height use by *Liolaemus bellii* (Squamata: Liolaemidae) in central Chile

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Abstract

Dorsal polymorphism and perch height use by *Liolaemus bellii* (Squamata: Liolaemidae) in central Chile. Dorsal polymorphism is a trait broadly studied in different animal species, and polymorphism within a population is common. It is presumed that individuals with a given color pattern will have an ecological or social advantage over conspecifics without it. In several lizard species, dorsal pattern polymorphism has been related to perch use, which may be determined by a lizard's social status. Here, we studied dorsal polymorphism and perch height use by *Liolaemus bellii*, a high-elevation, diurnal, saxicolous, viviparous lizard in central Chile. Discernable sexual dimorphism is absent in the species. Males and females show two morphs, a patternless one and an irregular, colored dorsal pattern characterized by olive or yellowish-brown color, flecked with yellow, black, and brown, with 8 to 10 blackish crossbars broken backward over the vertebral field (chevrons), forming an open V-like angle. We aimed to determine if lizards with this distinct chevron dorsal pattern perch higher than patternless conspecifics and if so, if conspecific social pressures might be responsible. Also, we measured eight morphological variables and evaluated their effect on perch height as covariables when lizards were grouped by sex, age class, and morph. None of the studied variables significantly influenced the presence of any morph. However, the patternless morph was found significantly more often in older lizards. Naturally broken tails increase in older lizards, although lack of a complete tail is not related to dorsal pattern. Bigger lizards with longer tails perched significantly higher, and therefore size may play a social role in perch use in *L. bellii*. Dorsal polymorphism in *L. bellii* is a conspicuous trait that has been overlooked in scientific literature concerning the species.

Keywords: Behavior, Lizard, Reptile, Saxicolous, Sociality.

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Resumo

Polimorfismo dorsal e uso da altura de poleiro por *Liolaemus bellii* (Squamata: Liolaemidae) no centro do Chile. O polimorfismo dorsal é uma característica amplamente estudada em diferentes espécies animais, e o polimorfismo intrapopulacional é comum. Presume-se que os indivíduos com um determinado padrão de coloração terão uma vantagem ecológica ou social sobre os indivíduos da mesma espécie sem o padrão. Em diversas espécies de lagartos, o polimorfismo do padrão dorsal tem sido relacionado ao uso de poleiros, que pode ser determinado pelo status social do lagarto. Estudamos aqui o polimorfismo dorsal e o uso da altura do poleiro por *Liolaemus bellii*, um lagarto vivíparo, diurno, saxícola e de grandes altitudes do centro do Chile. O dimorfismo sexual discernível está ausente na espécie. Machos e fêmeas apresentam duas formas, uma sem padrão e outra com um padrão dorsal colorido irregular, caracterizado pela cor verde-oliva ou marrom-amarelada, salpicado de amarelo, preto e marrom, com 8 a 10 barras transversais enegrecidas dobradas para trás sobre o campo vertebral (divisas), formando um ângulo aberto em forma de V. Nosso objetivo foi determinar se lagartos com esse padrão dorsal distinto de divisas empoleiraram-se em maiores alturas do que os da mesma espécie sem padrão e, em caso afirmativo, se as pressões sociais coespecíficas podem ser responsáveis. Além disso, medimos oito variáveis morfológicas e avaliamos seu efeito na altura do poleiro como covariáveis quando os lagartos foram agrupados por sexo, classe etária e forma. Nenhuma das variáveis estudadas influenciou significativamente a presença de qualquer forma. No entanto, a forma sem padrão foi encontrada significativamente com mais frequência em lagartos mais velhos. Caudas quebradas naturalmente aumentam em lagartos mais velhos, embora a falta de uma cauda completa não esteja relacionada ao padrão dorsal. Lagartos maiores com caudas mais longas empoleiraram-se em alturas significativamente maiores e, portanto, o tamanho pode desempenhar um papel social no uso de poleiros em *L. bellii*. O polimorfismo dorsal em *L. bellii* é uma característica conspícua que tem sido negligenciada na literatura científica relativa à espécie.

Palavras-chave: Comportamento, Lagarto, Réptil, Saxícola, Socialidade.

Introduction

Dorsal polymorphism has been studied in many insect, arachnid, bird, crustacean, mammal, and herpetofauna species (Mayr 1963, Oxford and Gillespie 1998, Hoffman and Blouin 2000, Steffen 2010). The polymorphism may be expressed as color or as pattern variation between populations and within individuals of the same population (Eifler and Fogarty 2006, Santos *et al.* 2018, Utsumi *et al.* 2021). Dorsal polymorphism may be sex-restricted, or age-associated, but in both scenarios, the polymorphism may have different ecological functions (Mayr 1963, Eifler and Fogarty 2006, Steffen 2010, Ortega *et al.* 2014). In squamate reptiles, dorsal polymorphism is associated with background matching, antipredator defense and escape, habitat use, resource availability, mating opportunities, sexual selection, social structure, and perch use (Mayr 1963, Zucker 1986, Eifler

and Fogarty 2006, Ortega *et al.* 2014, Medina *et al.* 2017). Thus, it is expected that individuals with a certain dorsal color or pattern will have some sort of advantage over conspecifics without the trait (Farallo and Forstner 2012). These traits may influence perch selection.

Perching is a common behavior in numerous arboreal and saxicolous lizard species (Zucker 1986, Núñez 1996, Smith and Ballinger 2001, Losos 2009). This behavior may be influenced by ecological selective forces (Losos 1990, Baird and Sloan 2003, Radder *et al.* 2006, Ortega *et al.* 2014, Medina *et al.* 2017). Both perch type and location may affect the lizard's thermoregulation, visibility, mating opportunities, and opportunities to escape from predators (Scott 1976, Avery 1991, Eifler and Fogarty 2006, Vicenzi *et al.* 2021). For example, after the reproductive season, female *Crotaphytus collaris* (Say, 1822), a saxicolous diurnal lizard, decreased predation risk primarily by diurnal snakes by perching on high rocks close

to a refuge and distant from vegetation that might conceal a snake (Eifler and Fogarty 2006). In different *Liolaemus* lizard species, tail loss has been correlated with the frequency of observations on elevated perches (Jaksić and Fuentes 1980). Noteworthy, perch height selection by a lizard may vary throughout the year to increase its feeding opportunities while adjusting its diet as shown in *Gonatodes humeralis* (Guichenot, 1855) (Miranda and Andrade 2003).

Perch height occupation may also result from social relations among conspecifics (Zucker 1986, Fox and Shipman 2003, Deodhar and Isvaran 2018). For example, in *Agama*, *Anolis*, *Crotaphytus*, *Psammophilus*, *Sceloporus*, and *Urosaurus* lizards, males and older individuals perch higher than females and younger conspecifics (Pounds and Jackson 1983, Zucker 1986, Anibaldi *et al.* 1998, Ramírez-Bautista and Benabib 2001, Baird and Sloan 2003, Losos 2009). During the breeding season, territorial males of *Psammophilus dorsalis* (Gray, 1831) display from prominent rock perches (Deodhar and Isvaran 2018). Although males use high perches year-round, bigger males perch on higher perches compared to smaller lizards (Radder *et al.* 2006).

Thus, use of higher perches may relate to lizard sociality: higher perches might offer better opportunities for individuals to establish a dominance hierarchy, defend their territory, advertise their presence to conspecifics, and perform courtship displays (especially in polygamous species) (Zucker 1986, Ramírez-Bautista and Benabib 2001, Radder *et al.* 2006). It is expected that saxicolous lizard species will inhabit suitable rocky habitats; however, high perches may not be in abundance and may be considered a limited resource occupied primarily by bigger, older, dominant individuals (Radder *et al.* 2006, Deodhar and Isvaran 2018).

With 289 recognized species, *Liolaemus* is the world's second most speciose genus of lizards and the most diverse in South America (Pincheira-Donoso 2012, Stellateli *et al.* 2016, Abdala *et al.* 2020). As with many other lizards around the world (Losos 2009), little is known

about the ecology of most of them (Utsumi *et al.* 2021). Thanks to recent studies, our knowledge of the natural history, sociality, and ecology of various *Liolaemus* species is on the rise (Fox and Shipman 2003, Pincheira-Donoso 2012, Santoyo-Brito *et al.* 2021).

Liolaemus bellii (Gray, 1985) is a high-elevation, diurnal, viviparous lizard. Individuals inhabit open rocky mountainous areas in central Chile (Donoso-Barros 1966, Pincheira-Donoso and Núñez 2005). The species is abundant and conspecific tolerance suggests a social structure of dominance hierarchy (Fox and Shipman 2003). Discernable sexual dimorphism is absent in the species although males have two precloacal pores that females lack (Pincheira-Donoso and Núñez 2005). Adult *L. bellii* are medium-sized and stocky, and both sexes show irregular dorsal patterning, characterized by olive or yellowish-brown color, flecked with yellow, black, and brown (Figure 1A), sometimes with 8–10 blackish crossbars broken backward over the vertebral field (chevrons), forming an open V-like angle (Pincheira-Donoso and Núñez 2005) (Figure 1B), and sometimes without this chevron pattern (Figure 1C).

Although dorsal polymorphism in *L. bellii* is evident (Donoso-Barros 1966, Pincheira-Donoso and Núñez 2005), the influence that dorsal pattern may have on habitat use, social status, and fitness of individuals has not been tested. In this sense, *L. bellii* is an excellent model to address behavior questions and evaluate some variables that may affect perch use by conspecifics of different age classes, sexes, and dorsal pattern morphs.

In this study, we collected data from *L. bellii* in a high-elevation population in central Chile. Our objectives were to determine if lizards with a distinct chevron dorsal pattern perch higher than patternless conspecifics and, if so, if conspecific social pressures might be responsible. At the same time, we measured eight morphological variables and evaluated their effect on perch height as covariables when lizards were grouped by sex, age class, and morph.

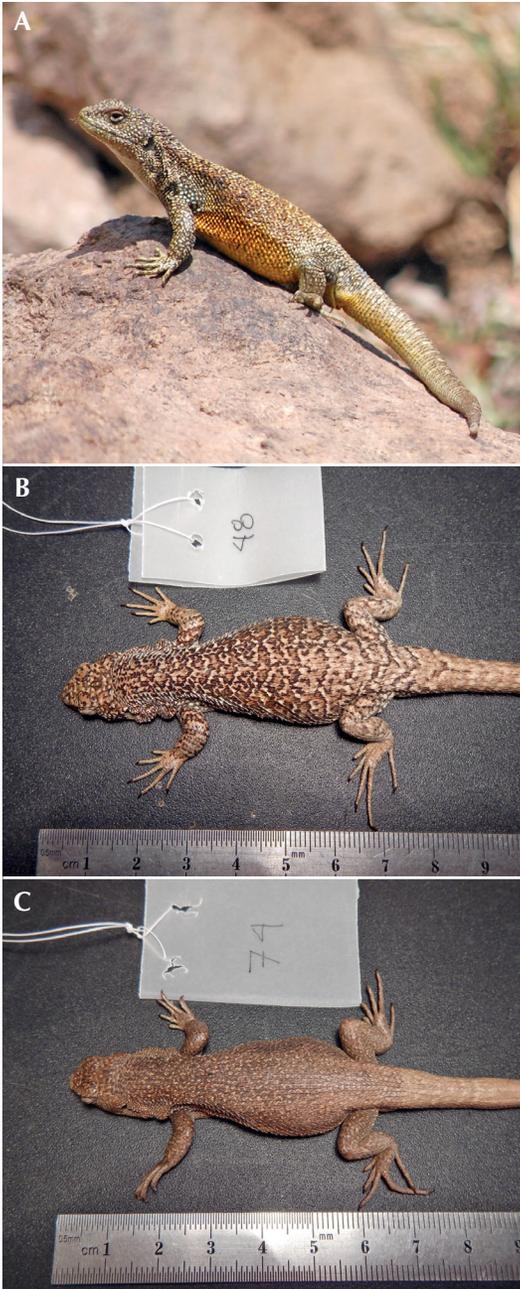


Figure 1. Three adults of *Liolaemus bellii* observed or collected in 2017 at our field site at 2960 m a.s.l. nearby the village of El Colorado, central Chile. The two vouchered adult female specimens (**B** and **C**) show the dorsal pattern polymorphism of the species.

Materials and Methods

We collected 69 *L. bellii* from 23 to 25 February 2017 (austral Summer) at our study site (2960 m a.s.l.; 33°20' S, 70°16' W) near the village of El Colorado, Metropolitan Region, in central Chile. This site is characterized by bare rocks aligned in straight-line formations (Figure 2). The rock lines are likely human-made since our site is located on the slope and open-ground ski lines of a popular ski resort. Vegetation at the site is predominantly spiny and shrub-like (*Berberis empetrifolia* Lam., *Chuquiraga oppositifolia* D. Don, and *Azorella* sp.).

We used binoculars to scan the area and locate lizards from a distance; all specimens were caught by noosing (Ferner 2007, Cooper 2009, Santoyo-Brito *et al.* 2018) from 09:00 to 18:00 h, when lizards are active and displaying normal behavior. The body temperature (BT) readings were obtained via a quick-reading Miller & Webber (0–50°C) cloacal bulb thermometer within 30 seconds of capture. Snout–vent and tail length (SVL and TL, respectively) were measured with a ruler (error: ± 1 mm). Lizards were assigned to one of two age classes as per SVL measurements as modified from Labra *et al.* (2003): juveniles = 4.4–6.7 cm; adults > 6.7 cm. Tail break status was recorded (i.e., intact tail or naturally broken tail [i.e., result of a predation attempt or an agonistic encounter]). Mass was measured with a 30-g Pesola spring scale. Left forearm length (LFAL), front left third digit length (FLDL), left hind leg length (LHLL), and hind left fourth digit length (HLDL) were measured with digital calipers. All variables were measured by one person, ES-B.

Perch height from the ground (PH in cm) was measured with a flexible measuring tape positioned close to the base of the perch type. The categorical dorsal pattern (i.e., chevron vs. patternless; Figure 1 B and C) of each lizard was determined at the point of capture by ES-B and corroborated by HN. No intermediate pattern categories were considered in this study. Data



Figure 2. View of our study site (2960 m a.s.l.) nearby the village of El Colorado, central Chile.

normality was tested using the Kolmogorov-Smirnov test. We used the Pearson Correlation test to estimate the correlation between body-size variables (LFAL, FLDL, LHLL, HLDL, mass, and SVL). We used a Factor Analysis to reduce the dimensionality of highly correlated morphological variables. Statistical differences of PH and BT between age groups (adults vs juveniles), and of PH, BT, BODY, and TL between sex (males vs females), and morph (pattern vs. patternless) were determined by the Student's t-test. We tested for homogeneity of variances using Levene's test. If variances were not homogeneous, we used the Welch's t-test. We first conducted an exploratory analysis, a full General Linear Model (GLM) with PH as the dependent variable and the main factors (age, sex, and morph), all two-way interactions, and the one three-way interaction, plus the covariates BODY and TL as the independent variables. Subsequently, we subsetted the data and conducted separate one-way ANCOVAs to more closely examine the individual effects of explanatory variables age, sex, and morph on PH. Interactions were evaluated in the respective model with BODY and TL as covariables. The

Pearson Chi-Square test estimated the association between age and morph, sex and morph, age and natural tail break, and sex and natural tail break in contingency tables. All statistical analyses were performed using SPSSv21 (IBM 2012).

Results

The One-Sample Kolmogorov-Smirnov Test indicated that all variables were normally distributed. The Pearson correlation matrix indicated a high correlation between LFAL, FLDL, LHLL, HLDL, mass, and SVL. Because correlation values among all six body-size indicators were highly significant, we used Factor Analysis to reduce the dimensionality (Johnson and Wichern 1998) of body variables into a new variable, BODY, in which larger values indicated a larger overall body and appendage size.

Results of the full GLM with PH as the dependent variable showed a significant ($F_{9,59} = 2.320$; $p = 0.026$) full model explaining PH (but explaining only 26% of its variation) and no explanatory variable was significant except for BODY ($F_{1,59} = 8.22$; $p = 0.006$). In

other words, the interaction age*sex, age*morph, sex*morph, and age*sex*morph played no significant role in the determination of PH.

Statistical Analyses by Age Class

The independent sample t-test and Welch's t-test indicated no statistical difference in PH or BT between adults (47) and juveniles (22) (both $p > 0.05$; descriptive statistics in Table 1).

Table 1. Perch height and body temperature [mean \pm SD (range)] statistics of 69 *Liolaemus bellii* collected at 2960 m a.s.l. nearby the village of El Colorado, central Chile. Lizards are grouped by age. Abbreviations: N = number of individuals, PH = perch height, and BT = body temperature.

Age	PH (cm)	BT ($^{\circ}$ C)
Adults ($N = 47$)	23.21 \pm 12.97 (0–62.00)	31.7 \pm 2.68 (24.00–36.20)
Juveniles ($N = 22$)	18.00 \pm 16.60 (0–50.00)	31.61 \pm 1.66 (29.90–36.00)

Setting Age as the independent variable, BODY as the covariate, and PH as the dependent variable, the one-way ANCOVA showed a statistical difference in perch height use in relation to BODY ($F_{1,65} = 10.02$; $p = 0.002$), but not Age. The interaction Age*BODY was not significant. In a second analysis setting Age as the independent variable, TL as the covariate, and PH as the dependent variable, the one-way ANCOVA showed a statistical difference in perch height use in relation to TL ($F_{1,65} = 6.30$; $p = 0.015$), but not Age. The interaction Age*TL also was not significant. Larger lizards (i.e., bigger BODY) and those with longer tails occupied significantly higher perches. The lack of interactions indicates that the effect of BODY and TL was the same for juveniles and adults.

Statistical Analyses by Sex

The independent sample t-test indicated no statistical difference in PH, BT, BODY, or TL between males (32) and females (37) (all $p > 0.05$; descriptive statistics in Table 2).

Setting sex as the independent variable, BODY as the covariate, and PH as the dependent variable, the one-way ANCOVA showed a statistical difference in perch height use in relation to BODY ($F_{1,65} = 10.98$; $p = 0.002$), but not sex. The interaction sex*BODY also was not significant. In a second analysis setting sex as the independent variable, TL as the covariate, and PH as the dependent variable, the one-way ANCOVA showed a statistical difference in perch height use in relation to TL ($F_{1,65} = 6.98$; $p = 0.010$), but not sex. The interaction between sex*TL was not significant. Larger lizards (i.e., bigger BODY) and those with longer tails occupied significantly higher perches. The lack of interactions indicates that the effect of BODY and TL was the same for males and females.

Statistical Analyses by Morph

The independent sample t-test indicated no statistical difference in PH, BT, BODY, or TL between patternless (19) and chevron patterned morphs (50) (all $p > 0.05$; descriptive statistics in Table 3).

Setting morph as the independent variable, BODY as the covariate, and PH as the dependent variable, the one-way ANCOVA showed a statistical difference in perch height use in relation to BODY ($F_{1,65} = 9.45$; $p = 0.003$), but not morph. The interaction morph*BODY also was not significant. In a second analysis setting morph as the independent variable, TL as the covariate, and PH as the dependent variable, the one-way ANCOVA showed a statistical difference in perch height use in relation to TL ($F_{1,65} = 6.12$; $p = 0.016$), but not morph. The interaction between morph*TL was not significant. Larger lizards (i.e., bigger BODY) and those with longer tails occupied significantly

Table 2. Descriptive morphometrics, body temperature, and perch height [mean \pm SD (range)] statistics of 69 *Liolaemus bellii* collected at 2960 m a.s.l. nearby the village of El Colorado, central Chile. Lizards are grouped by sex. Abbreviations: *N* = number of individuals, PH = perch height, BT = body temperature, BODY = reduced dimensionality of body variables, and TL = tail length.

Sex	PH (cm)	BT (°C)	BODY (no unit)	TL (mm)
Males (<i>N</i> = 32)	20.71 \pm 13.43 (0–50.00)	31.54 \pm 2.20 (26.00–36.20)	0.11 \pm 1.06 (-2.10–1.93)	97.28 \pm 20.24 (55.00–132.00)
Females (<i>N</i> = 37)	22.27 \pm 15.19 (0–62.00)	31.78 \pm 2.56 (24.00–35.20)	-0.10 \pm 0.94 (-2.58–1.25)	94.83 \pm 18.95 (67.00–139.00)

Table 3. Descriptive morphometrics, body temperature and perch height [mean \pm SD (range)] statistics of 69 specimens of *Liolaemus bellii* collected at 2960 m a.s.l. nearby the village of El Colorado, central Chile. Lizards are grouped by morph. Abbreviations: *N* = number of individuals, PH = perch height, BT = body temperature, BODY = reduced dimensionality of body variables, and TL = tail length.

Morph	PH (cm)	BT (°C)	BODY (no unit)	TL (mm)
Patternless (<i>N</i> = 19)	21.36 \pm 12.28 (0–42.00)	31.20 \pm 2.22 (26.00–35.30)	0.27 \pm 0.79 (-1.95–1.44)	96.23 \pm 21.40 (64.00–139.00)
Chevron (<i>N</i> = 50)	21.62 \pm 15.13 (0–62.00)	31.85 \pm 2.45 (24.00–36.20)	-0.10 \pm 1.05 (-2.58–1.93)	95.86 \pm 18.89 (55.00–134.00)

higher perches. The lack of interactions indicates that the effect of BODY and TL was the same for patternless and lizards with pattern.

Pearson Chi-square results indicated there was a significant relationship between age and morph. The patternless morph becomes more prevalent as lizards age (Pearson Chi-square = 5.51, *df* = 1, *p* = 0.019) (Table 4). The dorsal pattern does not appear to be a sexual dimorphism. Sex did not significantly relate to morph in individuals of *L. bellii* (Pearson Chi-square = 0.42, *df* = 1, *p* = 0.521).

Interestingly, 40 of the 69 lizards had a naturally broken tail (Table 4). Of those, 7 were juveniles and 33 were adults, 20 were males and 20 were females, and 13 were patternless and 27 had chevron patterns. Natural tail break was statistically different only between age classes (Pearson Chi-square = 9.07, *df* = 1, *p* = 0.003), with adults having proportionately more broken tails than juveniles (Table 5).

Discussion

Dorsal polymorphism in *L. bellii* is evident (Donoso-Barros 1966, Pincheira-Donoso and Núñez 2005). In our preliminary full model GLM analysis, contrary to our expectations, dorsal pattern morph did not relate to perch height (PH), but BODY did. Interestingly, the interaction age*sex, age*morph, sex*morph, and age*sex*morph played no significant role in the determination of PH. However, when the data were subsetted and analyzed by age, sex, or morph, we found that both BODY and TL significantly influenced PH. Thus, regardless of their age, sex, and morph, lizards with a bigger BODY and longer tail occupied higher perches, suggesting that the combination of both variables may play a social role in *L. bellii*.

How TL influences PH is not clear. Tail loss (i.e., decreased regenerated tail length) has been negatively associated with dominance in side-

Table 4. Tail status (i.e., intact, and naturally broken tail) of 69 specimens of *Liolaemus bellii*, grouped by age, sex, and morph collected at 2960 m a.s.l. nearby the village of El Colorado, central Chile. *N* = number of individuals.

Age	Sex	Morph	N	Intact tail	%	Naturally broken tail	%
Adult	Male	Patternless	9	2	22.2	7	77.8
		Chevron	10	1	10.0	9	90.0
	Female	Patternless	8	3	37.5	5	62.5
		Chevron	20	8	40.0	12	60.0
Juvenile	Male	Patternless	1	0	0.0	1	100.0
		Chevron	12	9	75.0	3	25.0
	Female	Patternless	1	1	100.0	0	0.0
		Chevron	8	5	62.5	3	37.5

Table 5. Observed vs expected counts of 69 *Liolaemus bellii* collected at 2960 masl nearby the village of El Colorado, central Chile. Pearson Chi-square = 9.07, *df* = 1, *p* = 0.003.

		Intact tail	Naturally broken tail	Total
Adult	Observed	14.0	33.0	47.0
	Expected	19.8	27.2	47.0
Juvenile	Observed	15.0	7.0	22.0
	Expected	9.2	12.8	22.0

blotched lizards (Fox *et al.* 1990). According to Fox and Shipman (2003) *L. bellii* is not territorial. Although the specific social organization of the population we studied has not yet been determined, its high density suggests hierarchical dominance. Nevertheless, during visits to our field site and surrounding areas, we never observed aggression between sexes or between individuals of the same or a different age class. From our field observations and results, one can infer that bigger *L. bellii* (controlling for age or sex) with longer tails (controlling for age or sex) may be dominant individuals occupying the less abundant taller rocks, which offer higher perches.

Our results indicate that the patternless morph is significantly more prevalent in older

individuals, indicating an ontogenetic loss of dorsal pattern in *L. bellii*. Even though a rather high frequency of tail breaks occurred in the population, there was no suggestion that dorsal pattern was related to tail loss. Not surprisingly, adults suffered significantly more tail losses than juveniles. Tail loss in different *Liolaemus* species has been interpreted as the result of failed predation events (Jaksić and Fuentes 1980, Medel *et al.* 1988, Utsumi *et al.* 2021). It seems reasonable that adults who have lived longer would have more evidence of tail breaks than juveniles (Tinkle and Ballinger 1972, Núñez and Yáñez 1984, Bateman and Fleming 2009). At the high elevation of our study site, visually oriented bird predators that prey on lizards are two

abundant species of shrike-tyrants, *Agriornis montanus* (d'Orbigny and Lafresnaye, 1837) and *Agriornis lividus* (Kittlitz, 1835); the less abundant American Kestrel, *Falco sparverius* Linnaeus, 1758 (Ridgely and Tudor 1994), and the very common Rufous-banded Miner, *Geositta rufipennis* (Burmeister, 1860) (Santoyo-Brito *et al.* 2014). During March–April, *A. montanus*, *A. lividus*, and *G. rufipennis* are abundant in the area. This abundance of visual predators might explain the high frequency of natural tail loss in our population.

In conclusion, morph is not sex-related nor related to perch height, but still might be involved in social relations among individuals since bigger lizards with longer tails perched significantly higher, and the patternless morph was found significantly more often in older lizards. Morph was related to age but not to the frequency of broken tails.

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