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Digit ratio in three species of tropidurid lizards

Kelton Gonçalves Miranda[1], Marcella Junqueira Goulart[1], Conrado Barbosa Galdino[1]

1 *Programa de Pós-Graduação em Biologia de Vertebrados da PUC Minas, Avenida Dom José Gaspar 500, Belo Horizonte, Minas Gerais 30535-610, Brazil*

http://zoobank.org/2A126D15-8DD1-4114-BEEA-F86B5A0F2F3F

Corresponding author: Conrado Barbosa Galdino (galdinoc@gmail.com)

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Abstract

Proportions between pairs of digits are linked to fitness in tetrapods and they can be influenced by sex hormones through individuals' ontogenies. Therefore, in many species, the proportions amongst finger length ratios (referred as digit ratio, i.e. 2D second and 4D fourth digits) can differ between males and females. We investigated whether the three most commonly used forelimb digit ratios are sexually dimorphic in three tropidurid species. In one of the three lizard species, *Eurolophosaurus nanuzae*, males and females differ for only 2D:4D digit ratio. Otherwise, our results on the studied *Tropidurus* species conform to previous studies showing no differences in digit ratios between males and females. Hence, it might be the case of local selective forces shaping interpopulation variation in the expression of sexual dimorphism for digit ratio.

Key Words

digit length ratio, Neotropical, population, sexual dimorphism, Tropiduridae

Introduction

The ratio between the lengths of pairs of fingers (referred to as digit ratio, i.e. 2D second and 4D fourth digits) depends on differential effects of variations in concentrations of prenatal steroids during embryonic stages (Manning et al. 1998, 2003, Manning 2002). It can be related to the fitness of individuals in many tetrapod species. For example, Burley and Foster (2004) showed for the bird species *Taeniopygia guttata castanotis* (Gould, 1837) that the ratio between digits of females is associated with their preferences for a given male phenotype. In addition, for this species, the digit ratio correlates with song rate, a secondary sexual trait of the species (Forstmeier 2005). In lizards, the proportion of digit ratio (3D:4D) in males *Ctenophorus pictus* (Peters, 1866) was associated with the presence of a yellow bib, a trait related to reproductive success (Olsson et al. 2009, Tobler et al. 2011).

Indeed, for some lizard species, the digit proportions were shown to be sexually dimorphic. Males of the lacertid lizard *Podarcis muralis* (Laurenti, 1768) had higher values of digit proportions when compared to females (Rubolini et al. 2006). Sexual dimorphism for the proportion between digit length was also found for *Podarcis siculus* (Rafinesque-Schmaltz, 1810) and *Podarcis melisellensis* (Braun, 1877), with males presenting a higher digit ratio than females (Van Damme et al. 2015). Male-biased digit ratios were also found for *Lacerta agilis* Linnaeus, 1758 (Kaczmarski et al. 2020). Gomes and Kohlsdorf (2011) also show that males of some iguanian lizard species present larger digit ratios 2D:4D than females. In other cases, however, digit ratios of females were larger than those of males, for example, *Anolis humilis* Peters, 1863 – Direnzo and Stinosky (2012) – and *Trachylepis planifron* (Parker, 1942) – Rubolini et al. (2006). There are cases in which no intersexual differences were found; as for *Anolis carolinensis* Voigt, 1832 (Chang et al. 2006). Nevertheless, sexual dimorphism for digit ratio evolved in association with ecological divergence amongst iguanian lizards and it might be attributable to the differential

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use of microhabitat between the sexes (Gomes and Kohlsdorf 2011). In addition, Lofeu et al. (2020) show that sexual dimorphism for digit ratio does not follow a clear evolutionary trend in Tropidurid species, varying with respect to the identity of the dimorphic digit, to the pattern of sexual dimorphism (whether male or female-biased) and according to the limb with sexually-dimorphic digits.

We here provide data on sexual dimorphism in digit ratios of three species of the Neotropical lizard family Tropiduridae – *Eurolophosaurus nanuzae* (Rodrigues, 1981), *Tropidurus montanus* Rodrigues, 1987 and *Tropidurus torquatus* (Wied-Neuwied, 1820). *Eurolophosaurus nanuzae* is a small-sized species and *Tropidurus montanus* is a medium-sized lizard species. Both species are saxicolous (Filogonio et al. 2010) and frequently sympatric, occurring on the rocky outcrop habitats from mountain environments. *Tropidurus torquatus* is a generalist species regarding microhabitat use. This medium-sized species is widespread over open habitats from South America, but it can also be found in anthropomorphised environments, such as in urban areas (Uetz and Hošek 2020). As males of iguanian lizards had larger digit ratios (Gomes and Kohlsdorf 2011), we expect to find the same patterns for the studied species.

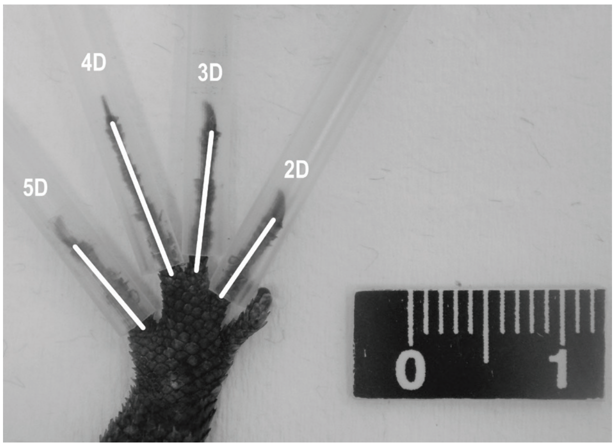

Figure 1. Insertion of the capillary tubes up to the nearest base of each digit. Outlined in white, there is the measuring line of the digits of a male *Tropidurus montanus*. Scale bar nearest: 1 mm. Source: Personal file.

Methods

For each species, all individuals (adults only) were collected, euthanised and preserved for the development of previous ecological studies (Václav et al. 2016: *T. montanus*; Werneck 2017: *T. torquatus*; Melo et al. 2019: *E. nanuzae*). Thus, for a given species, individuals pertain to the same population (from the same single site) and were collected over the same period (*T. torquatus*: January to December 2011; *T. montanus*: September 2013 to April 2014; *E. nanuzae*: November 2014 to August 2015). Therefore, we were able to obtain unbiased samples for 60 individuals of *E. nanuzae* (31 females and 29 males), 64 of *T. montanus* (32 females and 32 males) and 57 of *T. torquatus* (30 females and 27 males). The sex of individuals was determined by inspecting their gonads. We measured snout-to-vent length (SVL) with calipers (nearest 0.05 mm). Exclusively, one of us (KGM) measured the length of the digits 2, 3 and 4 for both forelimbs. For this procedure, following Rubolini et al. (2006), digits of lizards were put into a microhaematocrit capillary glass tube, up to the nearest base limit of each digit (Fig. 1). One of us ensured that the microhaematocrit tubes did not disturb the positioning of the other digits. Therefore, each digit was arranged and aligned as straight as possible to the point of its base (Rubolini et al. 2006). Individuals with damaged fingers were not measured. Limbs were photographed by a standard procedure using a camera mounted on a tripod and a reference scale (Fig. 1). Fingers were measured with ImageJ software, version 1.50i to the nearest 0.001 mm. Claw length was not considered in measurements of digit lengths.

Digit ratios were calculated for the values of digit length for the following pairs of digits: 2D:3D, 2D:4D and 3D:4D. For each studied species, we evaluated the differences in the proportions between the sexes using Generalised Linear Models (GLM) analysis. Following Direnzo and Stynoski (2012), Cohen d effect size were also calculated and reported. Statistical procedures were undertaken in R environment (R Core Team 2018).

Results

Females and males *E. nanuzae* had similar body sizes (female 50.43 mm ± 5.51, male 52.50 mm ± 3.57, $p = 0.15$). For this species, we found intersexual differences only for 2D:4D ratio of the left forelimb ($\beta = 0.105$, $t = 2.29$, $p = 0.025$), with female-biased digit ratio pattern (Table 1).

Table 1. Generalised Linear Models (GLM) test for sexual differences for digit proportions in three lizard species. 2D: digit 2; 3D: digit 3; and 4D: digit 4. Measurements for males and females follow as mean (± one standard deviation); *d* = Cohen d effect size.

Measure	Males (SD)	Females (SD)	β	*t*	*p*	*d*
E. nanuzae						
Right						
2D:3D	0.6644 (0.0658)	0.7041 (0.0821)	0.660	1.51	0.136	0.53
2D:4D	0.6068 (0.0617)	0.6515 (0.0830)	0.097	2.01	0.049*	0.61
3D:4D	0.9140 (0.0445)	0.9262 (0.0653)	0.582	1.75	0.086	0.22
Left						
2D:3D	0.6509 (0.0614)	0.6923 (0.0735)	1.740	1.46	0.149	0.61
2D:4D	0.5853 (0.0619)	0.6273 (0.0627)	0.105	2.29	0.025*	0.67
3D:4D	0.8990 (0.0402)	0.9084 (0.0618)	0.187	0.62	0.537	0.18
T. montanus						
Right						
2D:3D	0.7352 (0.0278)	0.7373 (0.0374)	0.03	0.015	0.797	0.06
2D:4D	0.6654 (0.0309)	0.6599 (0.0278)	-0.01	-0.752	0.455	-0.19
3D:4D	0.9052 (0.0284)	0.8956 (0.0248)	-0.011	-1.43	0.157	-0.36
Left						
2D:3D	0.7325 (0.0278)	0.7316 (0.0329)	0.0008	0.11	0.91	-0.03
2D:4D	0.6801 (0.0292)	0.6689 (0.0307)	-0.026	-1.49	0.141	-0.37
3D:4D	0.9287 (0.0324)	0.9147 (0.0309)	-0.016	-1.77	0.08	-0.44
T. torquatus						
Right						
2D:3D	0.7008 (0.0253)	0.6968 (0.0314)	-0.008	-0.523	0.603	-0.14
2D:4D	0.6532 (0.0254)	0.6512 (0.0328)	-0.004	-0.246	0.807	-0.07
3D:4D	0.9323 (0.0264)	0.9348 (0.0292)	0.002	0.33	0.737	0.09
Left						
2D:3D	0.7068 (0.0248)	0.7123 (0.0250)	-0.005	-0.82	0.416	0.22
2D:4D	0.6613 (0.0187)	0.6650 (0.0269)	0.008	0.592	0.556	0.16
3D:4D	0.9363 (0.0331)	0.9338 (0.0270)	-0.002	-0.319	0.751	-0.08

Regarding *T. montanus*, males had larger body sizes than females (female 84.44 mm ± 6.04, male 102.04 mm ± 7.95, $p < 0.001$) and no intersexual differences for digit ratios (Table 1). Similarly, males of *T. torquatus* had larger body sizes than females (female 87.91 mm ± 10.24, male 105.55 mm ± 18.98, $p < 0.0002$), but we found no intersexual dimorphism for any digit ratio (Table 1). Overall, *E. nanuzae* has medium effect sizes ($0.5 < d < 0.8$), while for *T. montanus* and *T. torquatus* effect sizes were small ($0.2 < d < 0.5$) (Table 1). Digit measurements data are available for download in https://github.com/NeoLiBE/mirandaetaldigitratio.

Discussion

Contrary to our prediction, we found sexual dimorphism for the proportion of digit ratios (2D:4D) of the forelimb of *E. nanuzae* with a female-biased pattern, while both *T. torquatus* and *T. montanus* presented no sexual dimorphism for digit ratios. In an evolutionary context, the digit ratio can be associated with microhabitat usage amongst species and variation in the digit ratio (2D:4D) was negatively correlated to the use of perches in iguanian lizards (Gomes and Kohlsdorf 2011). However, *E. nanuzae* is a saxicolous species and thus males and females use predominantly rocky substrate to perform their activities (Filogonio et al. 2010) and only males were usually seen perched on vegetation (SPR Ventura pers. comm.). Thereby, sexual dimorphism for the digit ratio found for the species cannot be explained in light of perch use of males and females. Still, in an evolutionary context, sexual dimorphism of digit length might be independent in relation to the hind-limb and forelimb within a species and identity of the dimorphic digit. Moreover, it was shown to be labile even amongst closely-related species (see Lofeu et al. 2020). This would explain our findings of sexual monomorphism for the digit ratio of *T. montanus* and *T. torquatus* and the dimorphism in *E. nanuzae*.

Nonetheless, the expression of sexual dimorphism for digit ratios can be population dependent as suggested by Sion et al. (2020). For example, *E. nanuzae* have no sexual dimorphism for digit length and thus no sexual dimorphism for digit proportions might be expected for the species (Lofeu et al. 2020, but also see Kazimirski et al. 2019). On the other hand, Lofeu et al. (2020) found female-biased sexual dimorphism for forelimb digits for *T. montanus* that might suggest a sexual dimorphism for digit ratios for the species. Additionally, in a previous study, *T. montanus* and also *T. torquatus* exhibited sexual dimorphism for the 2D:4D digit ratio (see Gomes and Kohlsdorf 2011). Therefore, there are inconsistencies amongst the results of previous studies and those we are presenting herein. Contrasting results on intersexual dimorphism for digit ratios can be found in literature, as an example for *Anolis carolinensis* (Chang et al. 2006; Lombardo and Thorpe 2008). Those inconsistencies amongst studies are suggestive of within-species (interpopulation) variation in sexual dimorphism for digit ratio.

The magnitude of sexual dimorphism for digit ratio can be plastic, varying amongst populations within a species. As an example, Kaczmarski et al. (2020), studying the association between digit ratio and caudal autotomy, stressed the necessity to understand digit ratio patterns amongst populations of the lizard *Lacerta agilis*. There are divergences in relation to the occurrence or lack of sexual dimorphism for digit ratios amongst the results we presented for three species of tropidurid lizards and those found for them in other studies. This can evidence interpopulation variation in the expression of digit ratio sexual dimorphism. There might be the case of local (proximal) factors, such as environmental stability and predator pressure (see Sion et al. 2020) and also fine-grained microhabitat attributes that affect the spatial structure of individuals lizards within a population and can play a role in shaping intersexual expressions of digit proportions amongst populations.

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