



Sexual differences in locomotor performance in *Tropidurus catalanensis* lizards (Squamata: Tropiduridae) – body shape, size and limb musculature explain variation between males and females

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Received 2 September 2015; revised 25 November 2015; accepted for publication 25 November 2015

Sexual dimorphism (SD) is the evolutionary outcome of selection acting differently on males and females. Several studies describe sexual differences in body size, although other morphological traits might be allometric between sexes and imply functional consequences. Here we test whether morphological differences between sexes in size and shape in the lizard *Tropidurus catalanensis* explain variation in performance of four locomotor traits. Our results show that males are larger than females and also exhibit longer limbs, longer muscles and larger muscle cross-sectional areas, while females have longer trunks and more sharpened anterior claws; males outperform females in all locomotor performances measured. Sexual differences in sprinting and climbing is related with body size, and climbing performance is also explained by limb lengths, by differences in lengths and cross-sectional areas of specific muscles, and by interlimb distances. Between-sex differences in exertion are also related to SD, despite associations with sharper posterior claws that are independent of sex. Grasping performance, however, is associated with some muscle and morphological parameters that are not sexually dimorphic. Together our results suggest that morphology might be under sexual selection in *T. catalanensis*, given that better locomotor performance likely favours male lizards in typical activities of this polygenic species, such as territory defence and female acquisition. Moreover, the longer trunks that characterize females may confer more space to accommodate eggs. On the other hand, territory defence by males probably increases their exposure to predators, resulting in a synergistic effect of sexual and natural selection in the evolution of SD in *T. catalanensis*. © 2016 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2016, **00**, 000–000.

KEYWORDS: climbing – exhaustion – functional morphology – grasping – lizard – locomotion – muscle dimensions – natural selection – sexual selection – sprint speed.

INTRODUCTION

Sexual dimorphism (SD) is expressed as phenotypic differences between sexes of a given species, and can be seen as the evolutionary outcome of selection (both natural and sexual) operating differently on the phenotype of males and females. It was Darwin (1871) who first proposed that SD may reflect independent adaptations of each sex to their different

reproductive roles. Since then, processes triggering SD have been under intense debate, but can be summarized as follows (reviewed in Andersson, 1994): (1) intrasexual competition for mates, (2) fecundity selection, and (3) intersexual differences in life habits. The presence of these processes eliciting SD has been investigated in several animal taxa (e.g. Clutton-Brock, 1985; Parker, 1992; Andersson, 1994; Katsikaros & Shine, 1997; Moczek & Emlen, 2000; Butler & Losos, 2002; Bonduriansky & Rowe, 2003), and the lineage Squamata, in special, stands as a particularly good system for addressing the topic

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because all three processes have been hypothesized to occur among lizards. For example, sexual selection appears to favour larger body size in male lizards when both territoriality and male agonistic behaviour result in higher mate acquisition and female choice (Fairbairn, 1997; Cox, Skelly & John-Alder, 2003). In contrast, larger body size in females seems favored when it is positively correlated with offspring number or quality (Fairbairn, 1997; Olsson *et al.*, 2002; Brandt & Navas, 2011). Finally, intersexual resource competition may also trigger variation between sexes (Slatkin, 1984), suggesting that not every dimorphism is purely sexual selected. The effects of sexual and natural selection are, however, difficult to unravel (Hedrick & Temeles, 1989; Shine, 1989), and have been investigated more often in the specific context of SD in body size (e.g. see Fairbairn, 1997; Losos, Butler & Schoener, 2003).

Nevertheless, between-sex phenotypic differences may appear in several characteristics other than overall body size. For example, SD in relative size and shape of some body parts (i.e. relative proportions) may be observed if these traits affect chances of individuals to reproduce by increasing or decreasing fitness (e.g. Emerson, 1994; Butler, Schoene & Losos, 2000). However, selection is actually most likely to act directly on 'higher-level' performance capacities, such as locomotion, than in 'lower-level' traits, such as morphology (Arnold, 1983; Garland & Losos, 1994; Irschick & Garland, 2001). Thus, a complete understanding of morphological variation between males and females requires information of whole-animal performances. Indeed, locomotor performance directly affects some activities related to sexual selection, such as combat, territory defence and mate acquisition, which in turn enhance fitness in males (Huyghe *et al.*, 2005; Husak *et al.*, 2006, 2008; Lailvaux & Irschick, 2006). The performance exhibited during locomotor activities, however, likely evolves also under strong influence of natural selection, as it affects survival by often determining the success of escaping from predators or capturing prey (Jayne & Bennett, 1990; Garland & Losos, 1994; Husak, 2006).

Many morphological traits seem allometric between sexes, implying functional consequences that might result in sexually dimorphic locomotor performance. Among these traits, body size is by far the most studied trait, as increments in size recurrently enhance performance (see Garland & Losos, 1994), but also trigger differences between sexes in many squamate lineages (Miles, Snell & Snell, 2001; Braña, 2003; Lailvaux, Alexander & Whiting, 2003; Lailvaux & Irschick, 2007). In some species, however, dimorphism in locomotion is not completely explained by variation in body size (e.g. Lailvaux & Irschick, 2007), and therefore may be also attributed

to differences in shape. Although associations between morphology and ecology seem to successfully explain morphological shape variation among populations or species occupying different niches (Biewener, 2003; Kingsolver & Huey, 2003), the consequences of SD for whole-animal performance remains under debate (Bonnet, Ineich & Shine, 2005; Lourdais *et al.*, 2006).

Predictions of functional consequences derived from morphological differences between sexes find support on biomechanical studies. For example, some male lizards exhibit longer limbs and shorter trunks in comparison with females (Butler & Losos, 2002). In these species it would be plausible to expect between-sex differences in locomotor performance because running on horizontal substrates may be enhanced by relatively longer limbs (Losos, 1990; Bonine & Garland, 1999) and shorter trunks (Goodman, Miles & Schwarzkopf, 2008). Longer limbs may allow larger steps, longer floating distances and larger stride lengths (Van Damme *et al.*, 2003). Shorter trunks might also contribute for enhanced sprinting (Goodman *et al.*, 2008) by decreasing energy loss imposed by trunk undulation (Van Damme *et al.*, 2003). Longer limbs and shorter trunks also likely improve other performance traits, as climbing and clinging (Goodman *et al.*, 2008), reinforcing the idea that a given phenotype may perform better in different activities. Equivalent predictions could be proposed connecting locomotor performances with muscle morphology, although information on SD of limb musculature is even scarcer than that available for external morphology. Despite the considerable literature sustaining the associated evolution of form and function in lizards, specially focusing on locomotion (Garland & Losos, 1994; Aerts *et al.*, 2000; Irschick & Garland, 2001), coevolution of morphology and performance in the context of SD remains relegated.

The present study aims to fill the aforementioned gaps by focusing on the predicted interface between SD and the functional morphological relationships of locomotor performance. We use the tropical lizard species *Tropidurus catalanensis* Gudynas & Skuk 1983 to test for associations between body size, body shape, muscle dimensions, and SD in different locomotor activities. To test for such associations, we first verified if the relationships between morphology and locomotor performance that have been previously described in comparative studies with Tropidurinae (Kohlsdorf & Navas, 2012) remain detectable at the intraspecific level. Then we tested for associations between morphology, accessed at two levels (external morphology and muscle dimensions), and performance in the context of SD. In this second step, we predict that (1) *T. catalanensis* exhibit SD not only in size but also in other morphological

variables characterizing their shape; (2) males perform better than females in all four locomotor activities tested – grasping, climbing, sprinting and capacity for exertion; (3) between-sex differences in locomotor performance are probably associated with morphological SD – males should have relatively longer limbs and shorter trunks, and should have also stronger muscles (given by larger cross-sectional areas), besides being larger than females. The tropidurid lizard *T. catalanensis*, formerly known as *T. torquatus* (Kunz & Borges-Martins, 2013), has been described as being dimorphic at least in size (Pinto, Wiederhecker & Colli, 2005; Kohlsdorf, Ribeiro & Navas, 2006; Brandt & Navas, 2013), and is a polygynous and territorial species. Dominant males of this species are constantly involved in aggressive interactions (Pinto *et al.*, 2005; Kohlsdorf *et al.*, 2006), suggesting some degree of sexual selection acting during the evolution of phenotypic traits.

MATERIAL AND METHODS

ANIMALS AND HUSBANDRY

Ten males and 12 females of *Tropidurus catalanensis* lizards were collected during the summer (January 2013) at the locality of São Simão, state of São Paulo, Brazil. Females of this species mature at 65 mm and males at 70 mm of snout–vent length (Wiederhecker, Pinto & Colli, 2002), and we included only animals that were at least 9 mm longer than this limit. Lizards were captured by noose during activity, placed in cloth bags and transported to the laboratory of University of São Paulo at Ribeirão Preto (São Paulo, Brazil). Animals were housed in 160-litre plastic terrariums with a 12 h : 12 h light:dark cycle given by an UVA/UVB lamp (Repti-glo 5.0–30W, Exoterra) and an incandescent lamp (60 W) that also provided a basking area for behavioural thermoregulation. We offered water *ad libitum* and live cockroaches or tenebrionidae larvae three times a week, always after performance trials. At the end of experiments animals were killed by intraperitoneal overdose of tyopental solution, fixed with 10% formalin, and preserved in 70% ethanol at the Coleção Herpetológica de Ribeirão Preto (CHRP-USP) from University of São Paulo. All the procedures, including performance tests, were authorized by IBAMA permits (feb/2012, number: 35624-1) and approved protocols by the Ethics Committee for the Use of Experimental Animals (CEUA, University of São Paulo, protocol number 12.1.156.53.5).

PERFORMANCE TESTS

We measured performance during four different locomotor activities: sprinting (speed), climbing (speed),

grasping (force) and capacity for exertion [distance travelled until exhaustion while running at high speed (Bennett & Huey, 1990)]. All trials of the same type of performance test were carried out by the same investigator. Sprint speed, climbing speed and grasping force were tested in duplicate, at 3 different days, summing up six trials for each individual. The capacity for exertion was tested once a day, at 3 different days. A 1-day interval between exhaustion tests was used to allow animals resting before a new trial. The order of the trials was randomized to avoid sequential repeats of the same performance test, and all individuals were tested on the same activity at a time. The maximal value for each individual in each performance test was retained for statistical analysis. All locomotor performances were measured at $35^{\circ}\text{C} \pm 1.5^{\circ}$ (for details on preferred temperatures of *T. catalanensis* see Kohlsdorf *et al.*, 2006); animals were placed inside an incubator chamber set at the experimental temperature for 1 h before starting each trial. Body temperature of each individual was verified before the tests using a pistol-grip infrared thermometer (Instrutherm LTDA.). Readings were taken at the centre of the trunk region, with the thermometer oriented in line with the animal's body axis and completely covered by their skin, in close range to their belly (Hare, Whitworth & Cree, 2007). Experiments were concluded in 20 days, reducing possible acclimation effects imposed by captivity.

Sprint speed

We used a 2 m racetrack equipped with sets of photocells disposed every 35 cm, which were connected to an electronic interface that recorded speed in each section. Pine clapboard was used as substrate and animals were stimulated to run by hand.

Maximal exertion

Animals were placed in a 2.5 m circular track and stimulated to run by hand until exhaustion, which was determined by the time when the animal stopped responding to stimulation. Exertion trials were recorded by a web camera positioned above the track, and the number of laps was used to calculate the total distance travelled in centimetres by each animal.

Climbing

We stimulated lizards by hand to climb a concrete wall while being recorded by a Canon SX40 HS camera set at 120 fps. Climbing speed was determined by manual digitalization of a point at the scapular girdle every 12 frames, using the video analysis software Tracker (version 4.72, Open Source Physics, USA).

Grasping

Grasping force was measured by placing the lizard on a level concrete block, allowing it to grasp with both hands and feet, and then dragging the individual horizontally at a constant speed until its complete detachment from the block. Animals were connected to a dynamometer (accuracy: 0.1 g – Pesola scale) by a string attached to their pelvic girdle. Every trial was recorded and the maximum grasping force registered by each individual at the dynamometer was confirmed through video analysis.

MORPHOLOGICAL TRAITS

Variation in body size and shape was assessed from all individuals tested for locomotor performance based on six linear external morphological traits, their masses, and two measurements taken on six limb muscles. Snout–vent length (SVL), interlimb length (ILL, distance between fore- and hindlimbs), forelimb (FLL) and hindlimb (HLL) length (from the tip of digit IV to the insertion of the limb on the body), hand width (HW) and foot width (FW) were measured using a digital caliper (Mitutoyo CD-15B; ± 0.01 mm). Body mass was recorded with an electronic scale (Marte ASF13, precision of ± 0.01 g). In addition to external morphology, animals were also dissected to measure the length of muscles involved in movements of the forelimb – flexor carpi ulnaris (wrist flexion), extensor digitorum longus (wrist extension), triceps longus (forearm extension); and the hindlimb – peroneus longus (pedal rotation), superficial femoral gastrocnemius (plantar flexion) and flexor digitorum longus (stabilization of the ankle joint). All muscles consist of fibres packed in parallel. After measuring length of each muscle, we calculated cross-sectional area by transversally cutting across their maximum diameter and photographing in transversal view using a Leica stereoscope. We placed a scale on each image and measured the muscles using ImageJ (Schneider, Rasband & Eliceiri, 2012). This set of morphological variables except for body length and mass is hereafter named ‘body shape’.

We also analyzed the outline shape of the anterior and posterior claws of digit IV. We converted lateral views into (x; y) coordinates and performed Elliptic Fourier Analysis (EFA), a morphometric approach used to describe shape variation in 2D forms lacking clearly defined homologous landmarks (Crampton, 1995). On EFA, the shapes are summarized with a series of harmonic curves, each one describing an ellipse in the xy-plane. The result is a multidimensional matrix of $4n$ Fourier descriptors (2 coefficients for each axis) for each specimen, where ‘n’ is the number of harmonics used. The coefficient of the first

harmonic was used to standardize size, position and orientation (Crampton, 1995), resulting in 44 coefficients to be used as quantitative variables in multivariate statistical analyses. Outline shape analyses were performed with Momocs R package (Bonhomme *et al.*, 2014). Claw shape was calculated using digital photographs taken on a Leica stereomicroscope. Images were processed using ImageJ (Schneider *et al.*, 2012).

STATISTICAL ANALYSES

All variables were log-transformed prior to analyses and we first estimated how body length and mass relate to each other. We then estimated how morphological variables scale against body length with standard major axis (SMA: Warton *et al.*, 2006), using the package smatr 3 (Warton *et al.*, 2012). We use SMA as an alternative to linear regression as it is more appropriate for estimating scaling effects (Warton *et al.*, 2006). We then size-corrected the morphological variables that scaled with body size (interlimb, hindlimb and forelimb length; hand and foot width; flexor carpi ulnaris length and cross-sectional area; triceps length and cross-sectional area; extensor digitorum longus length and cross-sectional area; extensor digitorum longus length and cross-sectional area; peroneus longus length and cross-sectional area; extensor digitorum longus length and cross-sectional area; superficial femoral gastrocnemius length and cross-sectional area) by calculating the residuals of the line fit procedure.

In the next step, we implemented linear models to test if morphology (body size, body shape and/or claw shape) predicted variation in performance. First we reduced the number of variables by performing principal component (PC) analyses with varimax rotation on the size-corrected body shape and summarized the information contained in the resultant coefficients of the EFA describing claw shape (Rohlf & Archie, 1984) in two separate analyses (for anterior and posterior claws shape). The number of principal components retained was determined from scree plots of the eigenvalues (Jackson, 1993). We used these retained components and size to test for between-sex differences in morphology, by fitting one-way ANOVAs using each morphological component as dependent variables and sex as factor. We further tested if locomotor performance was sexually dimorphic and which body or claw shape retained components were related to such variation, always controlling for the effect of size. We followed the method of Purvis *et al.* (2000) and Stuart-Fox & Ord (2004) and sequentially removed variables explaining the least variation on each model tested. We always started by fitting a model that included the

interaction between sex and size and, if these had no significant interaction effects, then these characterized our first removal (Engqvist, 2005). We report results together with Akaike Information Criterion (AIC), a heuristic indicator of model support. We followed Burnham & Anderson (2002) and considered that the best-fit model is the one with the lowest AIC. As a rule of thumb, models with AIC within 2 units of the best-fit model were considered to have substantial support. All variables included in the best-fitting models had a significance level of $P < 0.1$ via partial-F tests. All analyses were implemented on R (version 3.1.2) using RStudio (version 0.98.1103).

RESULTS

The main goal of this study was to address morphological associations of locomotor performance in the context of SD in *Tropidurus catalanensis* lizards. To do that, we first reduced our morphological data by performing two PC analyses – one performed on the body shape dataset and the other one on the claw shape dataset – and then tested for SD and associations between locomotor performance and sexual differences in morphology. The analysis performed on body shape (morphological variables as well as muscle lengths and cross-sectional areas) resulted in two main rotated components explaining 52% of total variation, hereafter referred to as body shape components (BSc). The first BSc (BSc1) was mainly influenced by hindlimb length, forelimb length, extensor digitorum length and cross-sectional area, peroneus longus cross-sectional area, flexor digitorum longus cross-sectional area (high positive loadings) and interlimb length (high negative loading, see Table 1), while the second one (BSc2) was influenced by hand width, triceps length and cross-sectional area, and flexor digitorum longus (high positive loadings, see Table 1). Regarding the claw shape data, PC analyses resulted in one main component for the anterior claw explaining 88.6% of variation (ACc1), and two posterior claw components explaining 65% (PCc1) and 21.7% (PCc2) of variation (Fig. 1).

Sexual dimorphism was identified in several morphological traits. Males were heavier and longer than females (mass: $F_{1,20} = 20.23$, $P < 0.001$; SVL: $F_{1,20} = 6.21$, $P = 0.022$) with relatively longer fore and hindlimbs, longer extensor digitorum longus, as well as stronger muscles (inferred by larger cross-sectional areas) regarding the extensor digitorum longus, the peroneus longus and the flexor digitorum longus in comparison with females (BSc1: $F_{1,19} = 5.27$, $P = 0.033$). In contrast, males had shorter trunks than females (BSc1: $F_{1,19} = 5.27$,

Table 1. Loadings of a principal component analysis performed on size-free body shape variables (residuals of standard major axis regressions versus SVL)

Variable	Component	
	1	2
ILL	-0.683	
HLL	0.863	0.275
FLL	0.709	0.412
HW	0.184	0.809
FW	0.511	0.478
PLL	0.479	0.574
GL	0.109	0.546
FDLL	0.160	0.787
TLL	-0.148	0.840
EDLL	0.636	
FCUL	0.161	
EDLA	0.821	
GA	0.385	0.510
FCUA	0.384	0.334
FDLA	0.657	0.243
PLA	0.777	0.355
TLA	0.287	0.684
<i>Eigenvalue</i>	4.755 (28)	4.12 (23.2)
(% variation explained)		

ILL, interlimb length, HLL, hindlimb length, FLL, forelimb length, HW, hand width, FW, foot width, FCUL, flexor carpi ulnaris length, FCUA, flexor carpi ulnaris cross-sectional area, TLL, triceps longus length, TLA, triceps longus cross-sectional area, EDL, extensor digitorum longus length, EDA, extensor digitorum longus cross-sectional area, PLL, peroneus longus length, PLA, peroneus longus cross-sectional area, FDLL, flexor digitorum longus length, FDLA, flexor digitorum longus cross-sectional area, GL, superficial femoral gastrocnemius length, GA, superficial femoral gastrocnemius cross-sectional area.

$P = 0.033$). Females showed anterior claws that are more sharp than males (ACc1: $F_{1,20} = 10.17$, $P = 0.004$, Fig. 1). The remaining body shape (BSc2: $F_{1,19} = 0.001$, $P = 0.977$) and claw components (PCc1: $F_{1,20} = 3.03$, $P = 0.097$; PCc2: $F_{1,20} = 0.00$, $P = 0.997$) did not differ between sexes.

Locomotor performance also presented between-sex differences in *Tropidurus catalanensis* lizards (Fig. 2). Males always performed better than females in grasping ($F_{1,19} = 31.300$, $P < 0.001$), sprinting ($F_{1,20} = 7.871$, $P = 0.011$), climbing ($F_{1,20} = 6.484$, $P = 0.019$), and exhaustion running ($F_{1,20} = 4.620$, $P = 0.044$). Results for better-fit models showed that sexual differences in locomotor performance relates to morphological variation (Table 2). Better grasping performance was associated with relatively longer triceps longus, longer and stronger flexor digitorum

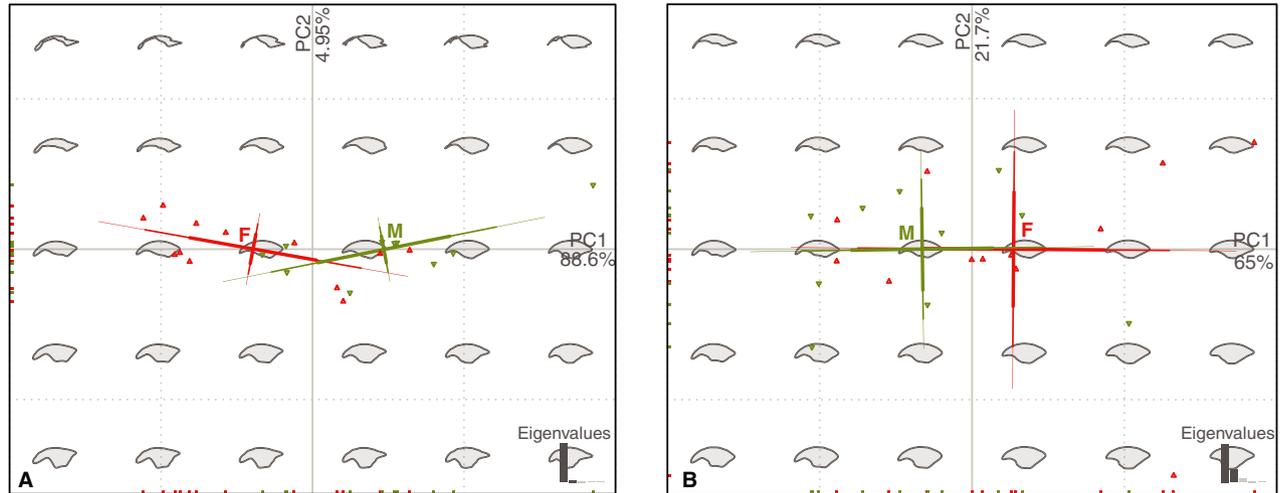


Figure 1. Biplots of principal component analysis (PCA) performed on the coefficients resulting from an Elliptic Fourier Analysis of anterior (A) and posterior (B) claw outlines. Red = females, green = males.

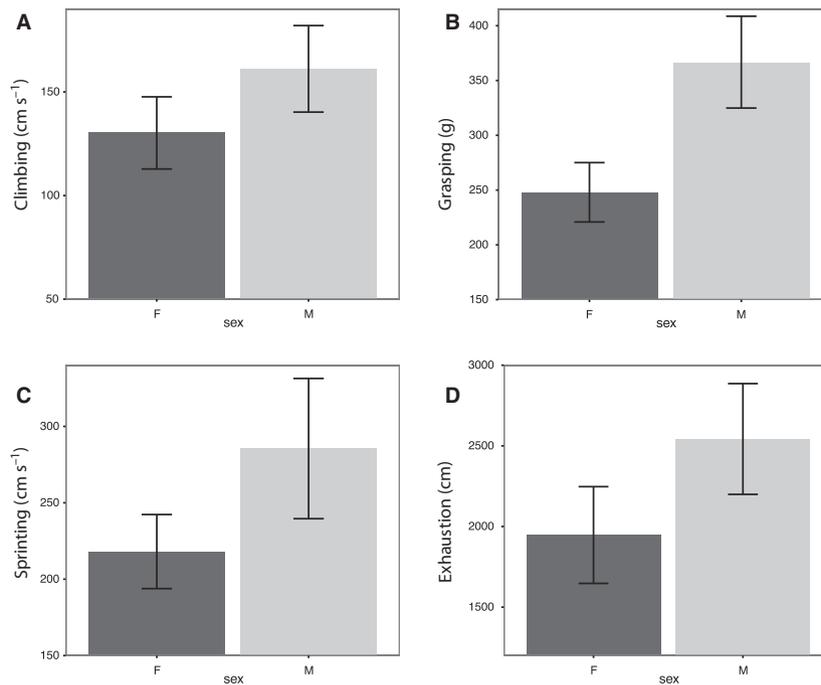


Figure 2. Comparison of performance exhibited by females (dark bars) and males (light bars) in four locomotor activities: Climbing (A: $F_{1,20} = 6.5492$, $P = 0.019$), Grasping (B: $F_{1,19} = 29.781$, $P < 0.001$), Sprinting (C: $F_{1,20} = 9.3461$, $P = 0.006$) and Exhaustion (D: $F_{1,20} = 5.6564$, $P = 0.027$). Males outperformed females in all performance tests. Vertical bars denote 95% confidence intervals.

longus and wider hands (BSc2, Table 2), but these were not sexually dimorphic. Dimorphism in grasping was partially explained by differences in size, but additional traits not accessed here probably explain sex effects on this performance (Table 2). Sexual dimorphism in sprinting and climbing was

identified as function of size (Table 2), but in climbing it was still explained by larger BSc1 (relatively larger forelimb, hindlimb and extensor digitorum longus length, as well as stronger extensor digitorum longus, peroneus longus and flexor digitorum longus, but shorter interlimb). Between-sex differences in

Table 2. Results for best-fit models testing if sexual dimorphism in locomotor performance is related to morphological variation. See supporting information for fully complex models and step-by-step statistical results

Dependent variable	Parameter	Slope	<i>F</i>	d.f.	<i>P</i>	AICc
Grasping force	PCc2	0.50	36.23	4,15	0.070	-37.8
	BSc2	0.06	9.49		0.007	
	SIZE	1.84	65.30		< 0.001	
	SEX		27.86		< 0.001	
Sprint speed	SIZE	1.82	17.78	1,20	< 0.001	-3.8
Climbing	BSc1	0.11	5.33	2,18	0.030	-3.4
	SIZE	1.17	5.85		0.020	
Maximal exertion	PCc1	-0.95	5.16	2,18	0.030	1.2
	BSc1	0.13	7.86		0.010	

exertion were also related to SD in BSc1, despite the associations with sharper posterior claws independent of sex (Fig. 1). Interestingly, the only performance in which SD was explained only by size differences was sprinting. Together these results corroborate that SD in locomotor performance of *Tropidurus catalanensis* is explained by variation both in body size and body shape (external and muscle), including claw shape.

DISCUSSION

Sexual dimorphism (SD) in body size has been widely reported among squamate lineages (Cox, Butler & John-Alder, 2007). Interestingly, in *T. catalanensis* SD is detectable not only in size, as previously expected (Brandt & Navas, 2013), but also in shape. Our study suggests that the classic association between morphology and locomotor performance (Garland & Losos, 1994) detected in *T. catalanensis* has an additional component, SD. Specifically, males outperform females in all four different locomotor performances measured here, but between-sex differences are only partially explained by SD in body size. Size influences grasping and climbing, and explains all sexual variation in sprinting. However, SD in grasping performance remains present after accounting for size effects, and sexual dimorphism in exertion capacity is also independent of size, being influenced by differences in the relative sizes of fore and hindlimbs, in the interlimb distance, as well as in the length and cross-sectional areas of specific limb muscles (extensor digitorum longus, peroneus longus and flexor digitorum longus). Some of the variation in climbing is also related to this body shape component. Finally, we have also identified other associations between morphology and locomotor performance that do not relate with SD: relatively longer flexor digitorum longus, longer and

wider triceps longus and wider hands are observed in lizards that grasp better, regardless of the sex.

The pattern of SD characterized by larger males, which in *T. catalanensis* involves also males having relatively shorter trunks, longer limbs and bigger muscles, seems common among lizards (e.g. Braña, 1996; Olsson *et al.*, 2002; Brecko *et al.*, 2008). Despite the large amount of references reporting morphological SD in lizards, with special attention to body size (Biewener, 2003; Cox *et al.*, 2007), investigations of whether such differences translate into variation in performance remained so far neglected (Cullum, 1998; Lailvaux *et al.*, 2003; Brecko *et al.*, 2008; Kaliontzopoulou, Bandeira & Carretero, 2013). Classical studies ignoring SD had already suggested a frequent correlation between body size and locomotor performance (Garland & Losos, 1994), so it was plausible to propose that the between-sex differences in size reported for *T. catalanensis* (Miles *et al.*, 2001; Braña, 2003; Pianka & Vitt, 2003; Lailvaux & Irschick, 2007) likely contribute to sexual differences in locomotor performance. The present study corroborates this hypothesis, as males of *T. catalanensis* are larger and also in general better performers than females.

However, the differences in performance observed between males and females of *T. catalanensis* are not solely explained by body size, suggesting that additional components (for example related to body shape) are likely involved. Sexual dimorphism in leg length is far less commonly reported than between-sex differences in body size, but in some sexually dimorphic lizard species variation in body shape resides on males having longer limbs (e.g. Malhotra & Thorpe, 1997; Butler & Losos, 2002; Schwarzkopf, 2005; Kaliontzopoulou *et al.*, 2013). In some of these species, the relatively longer hindlimbs of males apparently enhance their sprint speeds (Snell *et al.*, 1988; Kaliontzopoulou *et al.*, 2013). Elements from the hindlimb, as femur and tibia, play a major role

during the final propulsion phase of a stride (Reilly & Delancey, 1997; Fieler & Jayne, 1998), often increasing total stride length (Garland & Losos, 1994), so these are considered primary drivers of variation in lizard locomotion (Spezzano & Jayne, 2004). Interestingly, we did not detect an equivalent relationship in *T. catalanensis*, although the longer hindlimbs, together with longer forelimbs and shorter trunks that characterize males, seem to explain variation in two other locomotor activities: climbing and exertion capacity. We recognize that many additional behavioural (e.g. aggressiveness) and design traits not considered here (e.g. muscle biochemistry and metabolic rates) might influence sexual differences in locomotor performance (see Aerts *et al.*, 2000; Kohlsdorf & Navas, 2012), but it is worthy emphasizing that our results already point to a clear association between SD in morphology and locomotor performance, suggesting coevolution between these phenotypic traits.

The expected ecological relevance of SD in locomotor performance of *T. catalanensis* is not restricted to steady sprint speeds, as in nature these animals are observed moving vertically along concrete walls (RB & TK, pers. obs.), a situation where climbing and grasping performances seem crucial. Frequent use of vertical or near-vertical surfaces, as concrete walls, requires extra force and work in order to surpass gravity effects (Van Damme *et al.*, 2003). Accordingly, gravity poses a functional challenge for relatively larger animals, which might be overcome by a powerful autopodium that potentially improves grasping (Van Damme *et al.*, 2003). To achieve a vertical position, animals pull the forefeet towards the substrate, while their hindfeet push on the substrate, a skill that requires maintenance of the lizards centre-of-mass in line with their support (Cartmill, 1985). In *Tropidurus catalanensis*, muscle anatomy seems to contribute for between-sex differences in grasping, as males have longer and stronger extensor digitorum longus, peroneus longus and flexor digitorum longus than females. The ability to climb a substrate requires not only having longer and stronger muscles in the fore and hindlimbs, but also having an efficient grasping. The claws used to penetrate into the surface of the substrate are released or pushed against the substrate with the force exerted on the digits by the limb muscles (Abdala *et al.*, 2009; Sustaita *et al.*, 2013). *Tropidurus* males, however, exhibit longer legs, which likely elevate their centre of gravity (see Cartmill, 1985) and might reduce speed in vertical planes by increasing instability, although longer hindlimbs may also enhance climbing capacity in some species (for examples with lacertids see Vanhooydonck & Van Damme, 2001). Consequently, despite morphological

characteristics of male *T. catalanensis* that would apparently restrict climbing activity (e.g. larger body size and relatively longer hindlimbs), their grasping forces surpass those of females, probably contributing to their better climbing performance. This relationship suggests that some performance measurements may reflect interactions between different locomotor abilities.

Although at this point our data do not allow a formal test of selective regimes acting during the evolution of SD in locomotor performance of *Tropidurus* lizards, it is possible to speculate that locomotor performance is under stronger selection in males than in females. This idea seems particularly likely for sprint speeds and distance travelled until exhaustion (e.g. Robson & Miles, 2000; Perry *et al.*, 2004) because males actively defend their territories in polygynous and territorial species such as *T. catalanensis*. Dominant males apparently rely on speed and stamina while patrolling their territory, chasing intruders or engaging in combats (Husak *et al.*, 2006), but they may be more exposed to predators when patrolling their territories as well as protecting and courting females associated to the harem (Castilla & Labra, 1998; Cooper, 1999; Cooper & Vitt, 2002). In contrast, females probably rely more on crypsis to avoid predation (Schwarzkopf & Shine, 1992). In fact, we actually observe that the distance one can approach a *T. catalanensis* lizard before it flees is greater in females (RB & TK, pers. obs.), which might reflect weak selection for high sprint speeds in females but not males. In the polygynous lizard *Crotaphytus collaris*, faster males have larger territory areas and sire more offspring (Husak *et al.*, 2006; Peterson & Husak, 2006), an association also suggested for a variety of other vertebrate taxa (see Andersson, 1994). Together with sprint speeds, evolution of maximal aerobic capacity and locomotor endurance has also been proposed to be related with territory defence and courtship behaviour via sexual selection (Bennett & Ruben, 1979; Bennett, 1991; Robson & Miles, 2000; Sinervo *et al.*, 2000; Miles *et al.*, 2001), and it is possible that an equivalent process is involved in the evolution of higher endurance in males of *T. catalanensis*, a hypothesis that formally remains untested. Thus, there is a chance that both natural and sexual selection favour enlarged body size and other morphological traits that improve locomotor performance in males of *T. catalanensis*, being future studies necessary to elucidate if better performers actually sire more offspring.

Among the main factors explaining the evolution of SD at different levels is niche divergence (Darwin, 1871; Slatkin, 1984), a hypothesis that remains controversial (see Fairbairn, 1997) and not necessarily applicable as a rule to different taxa. Niche diver-

gence predicts that natural selection contributes for evolution of distinct morphologies between sexes, minimizing intersexual competition for resources (e.g. Butler & Losos, 2002). Data for between-sex ecological variation in *T. catalanensis* remain scarce, but it is possible that niche divergence between males and females of *Tropidurus* lizards is one of the drivers of sexual differences both in performance and associated morphological traits. Such explanation is particularly favoured by the relevance of locomotor performance in habitat use and the distinct morphological patterns that emerge from this association among squamates (see Garland & Losos, 1994; Van Damme *et al.*, 2003). For example, a recent study on SD of digit ratio of iguanians (tropurines among them) recalls between-sex divergence in microhabitat use as a possible explanation for variation in autopodial morphology between males and females (Gomes & Kohlsdorf, 2011). It is important to note, however, that variation between sexes might also reflect side effects of other selective forces acting on morphology, and thus can be product rather than the cause of morphological SD (e.g. Shine, 1989). For example, one of the most consistently dimorphic traits described in lizards is interlimb length (Olsson *et al.*, 2002), usually attributed to fecundity selection for increased space to hold eggs (see Andersson, 1994). Accordingly, in *T. catalanensis* there is also an association between sexual differences in locomotor performance and relative interlimb length; although still speculative, an alternative scenario would be that such association reflects the side effect of other selective forces acting on morphology, particularly fecundity selection.

The main outcome of the present study resides on the evidence for a correlated evolution between form and function that is coupled with sex differentiation in *T. catalanensis* lizards. As hypothesized earlier, both sexual and natural selection may be acting synergistically in shaping SD between males and females of this species. There is a possibility of intrasexual selection favouring larger body size in males that defend territories and hence conquest access to females (see Kohlsdorf *et al.*, 2006). Given that some traits (body shape or performance, for example) allow males to outcompete other males (e.g. Husak *et al.*, 2006), those traits would also be favored by sexual selection and result on SD, a hypothesis that remains to be formally tested in *T. catalanensis*. Female mate choice might be an additional factor selecting for shape (or locomotor) dimorphism, specifically in a scenario where females prefer males exhibiting particular phenotypes (e.g. Huyghe *et al.*, 2012; Swierk, Ridgway & Langkilde, 2012). Finally, selection may still differ between sexes because of reproductive roles, for example

when males displaying or defending territories become more exposed to predation than females; in this case, natural selection may favour faster males, which in turn are probably those exhibiting longer limbs and stronger limb muscles. The discussion raised from our results not only provides evidence for coevolution of (muscle and external) morphology and performance in the context of SD in *Tropidurus* lizards, but also endorses further investigation seeking for the evolutionary basis of these relationships and the generality of the detected patterns.

ACKNOWLEDGEMENTS

The authors acknowledge colleagues that helped during fieldwork (R. Albuquerque) and design of performance experiments (A. Rodrigues and V.A.S. Cunha). We also thank two anonymous reviewers for their helpful comments. RB was funded by a CAPES post-doctoral fellowship and is funded by a FAPESP fellowship 2013/14125-0, FB is funded by a FAPESP PhD fellowship (2011/24171-3), CN was funded by a FAPESP PhD fellowship (2011/01801-1). This study was funded by a FAPESP grant awarded to TK (2011/18868-1) and an international collaboration grant between CONICET (1035/2013) and FAPESP (2012/51012-6).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Table S1. Results of tests of multiple linear model with 'Grasping force' as dependent variable and components of size, shape and categorical sex as independent variables.

Table S2. Results of tests of multiple linear model with 'Sprint speed' as dependent variable and components of size, shape and categorical sex as independent variables.

Table S3. Results of tests of multiple linear model with 'Climbing' as dependent variable and components of size, shape and categorical sex as independent variables.

Table S4. Results of tests of multiple linear model with 'Maximal exertion' as dependent variable and components of size, shape and categorical sex as independent variables.

Table S5. Mean \pm standard deviation of all morphological variables studied in males and females of *Tropidurus catalanensis* lizards. Lengths are expressed in mm and areas in mm².