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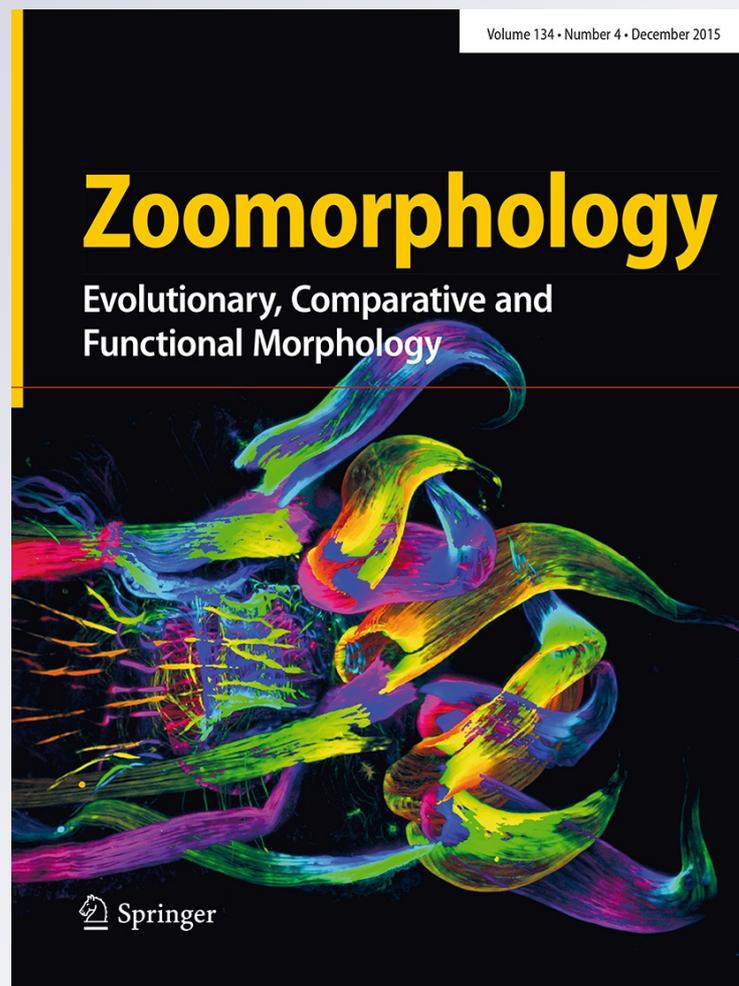
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# Digit ratios in two lacertid lizards: sexual dimorphism and morphological and physiological correlates

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**Abstract** Digit length ratio (primarily 2D:4D) has become increasingly popular as a possible biomarker of intrauterine steroid exposure in the human medical, social and psychological literature. Human males tend to have lower digit ratios than females, and individuals with low ratios tend to excel in physical performance, especially in endurance-related sports. Because early limb development is evolutionarily conservative, it has been speculated that these trends should also be visible in other tetrapod vertebrates. However, studies on non-human vertebrates are scant, and their results suggest that sexual dimorphism in digit ratios and the associations with physical performance are much more intricate and taxon-specific than presumed. In this study, we compared digit ratios of two *Podarcis* lizards among sexes, colour morphs and species. We also tested for associations with three performance characteristics that are of ecological relevance. Both species examined exhibit male-larger sexual dimorphism in digit ratio. 2D:4D, 3D:4D and 2D:3D ratios are tightly correlated within the manus and the pes, but less so between manus and pes. In the colour polymorphic species *P. melisellensis*, the yellow morph exhibits higher dimorphism than the orange and white morphs. Digit ratios did

not correlate with individual performance for sprint speed or endurance, but within males of *P. melisellensis*, individuals with higher digit ratios correlated positively with head size and bite force. We conclude that digit ratios in lizards deserve attention, because they exhibit sexual dimorphism and correlate with ecologically relevant morphological and performance variables. As lizard species differ widely in mating systems, reproductive mode, habitat use and locomotor behaviour, they seem excellent model animals for studying patterns in digit length ratios.

**Keywords** *Podarcis* · Whole-animal performance · Developmental instability · Colour polymorphism

## Introduction

A large body of research indicates that in vertebrates, prenatal exposure to sex hormones affects adult morphology, physiology and behaviour (e.g. Collaer and Hines 1995; Gil 2008; Uller 2008). Studies of digit ratios have played an important role in the development of this idea. Although the sexual dimorphism in the ratio of the length of the second to the fourth finger (2D:4D) in humans had been noted long before that (e.g. Ecker 1875; Baker 1888), investigations into the subject really took off in 1998, when Manning and co-workers suggested that the differentiations of digits and gonads were both affected by intrauterine androgen levels (Manning et al. 1998). This fuelled the idea that digit ratios could be used as a convenient proxy for prenatal exposure to androgens. In subsequent years, digit ratios (and hence putatively prenatal hormone concentrations) have been shown to correlate with a wide variety of physiological, psychological, cognitive and developmental variables in humans (reviewed in Manning

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2002, 2008; McIntyre 2006; Voracek and Loibl 2009; but see Putz et al. 2004).

In recent years, a growing number of studies have explored digit ratios and their correlates in non-human vertebrates, mainly mammals and birds. While female-larger sexual dimorphism in 2D:4D ratio seems to be the rule in mammals (e.g. Brown et al. 2002; McFadden and Bracht 2002; Nelson and Shultz 2010; but see Roney et al. 2004), the trait is less conserved in birds (e.g. Burley and Foster 2002; Navarro et al. 2007; Lombardo et al. 2008). Information available for other taxa is scant. In lizards, the magnitude and the direction of the dimorphism vary among species (Rubolini et al. 2006; Drenzo and Stynoski 2012; Gomes and Kohlsdorf 2012), populations (Chang et al. 2006 versus Lombardo et al. 2008) and even between limb pairs (Drenzo and Stynoski 2012), suggesting that studies of this group could provide valuable information on the evolutionary significance of the phenomenon. Lizard species vary dramatically in mating systems, sexual size dimorphism and androgen levels (Cox et al. 2003; Eikenaar et al. 2012), reproductive mode and physiology (Murphy and Thompson 2011) as well as in habitat use, limb morphology and locomotor behaviour (Garland and Losos 1994). Therefore, the group offers excellent opportunities to study the significance of digit ratios. However, at the moment, taxonomic coverage is insufficient. Here, we investigate digit ratios and their associations with physiological characteristics in two closely related species of lacertid lizards: *Podarcis siculus* Rafinesque 1810 and *P. melisellensis* Braun 1877.

*Podarcis siculus* and *P. melisellensis* resemble one another in many aspects of their morphology, behaviour and ecology. Both are medium-sized diurnal heliothermic lizards that actively search for prey (mostly arthropods). The two species occupy similar semi-open habitats (often stone walls or rocks surrounded by grassy vegetation and maquis) in the Mediterranean. This ecological similitude has been held responsible for the fact that on the smaller islands, almost invariably only one of both species is found (competitive exclusion hypothesis, Nevo et al. 1972). Geographical and experimental evidence suggests that the more 'timid' endemic *P. melisellensis* is expelled from islands on which the more 'assertive' *P. siculus* gets a foothold (Radovanovic 1959; Vervust et al. 2007). The difference in temperament has been confirmed by a behavioural study in which juveniles of the two species were confronted in an experimental arena (Downes and Bauwens 2002). Both species show male-larger sexual size dimorphism, but the difference in snout-vent length between males and females is more pronounced in *P. melisellensis*. A first aim of this study is to compare digit ratios of these lizards between the sexes, among populations and between species. We speculate that digit ratios will differ between

males and females, but the sign of the difference is hard to predict. In about half of the (restricted) number of species of lizards examined in previous studies, males had larger 2D:4D ratios than females; in the second half, the reverse was the case (Lombardo et al. 2008; Drenzo and Stynoski 2012; Gomes and Kohlsdorf 2012). If the difference in 'temperament' between the study species is mediated by testosterone, we expect the 'bolder' *P. siculus* to have a lower digit ratio than more 'shy' *P. melisellensis*. We have no precise hypotheses on the nature of the among-population variation in digit ratios, this topic has not been explored before. However, assessing the hierarchical level at which ratios vary may be important for future comparative studies.

One of our two study species, *P. melisellensis*, exhibits a striking but little understood colour polymorphism: the vents of both males and females can be white, yellow or orange (Huyghe et al. 2007). Orange males have relatively larger heads and therefore bite harder than both yellow and white males (Huyghe et al. 2007). In Australian painted dragons (*Ctenophorus pictus*), adult colour morphs have been shown to exhibit differences in digit ratios, suggesting that prenatal androgen exposure may be modulating the polymorphism (Tobler et al. 2011). Levels of early sex hormone exposure are also believed to mediate morph-specific adult behaviour in American tree lizards (*Urosaurus ornata*) (Hews et al. 1994; Moore et al. 1998). A second aim of this study is to compare digit ratios among colour morphs of *P. melisellensis*. We predict that orange males will exhibit lower digit ratios than yellow and white males.

An extensive body of the literature testifies that in humans, 2D:4D digit ratio is a strong predictor of athletic prowess (reviewed in Hönekopp and Schuster 2010). In populations varying from female fencers (Voracek et al. 2010) to male sumo wrestlers (Tamiya et al. 2011), individuals with lower digit ratios tend to be more successful. The information on non-human vertebrates is much scarcer and less consistent. In laboratory rats (*Rattus norvegicus*), individuals with higher 2D:4D ratios tend to be more active in open field tests (Talarovicova et al. 2009), but Yan et al. (2009) found no differences in activity among laboratory mice (*Mus musculus*) strains with different digit ratios. In captive-reared zebra finches (*Taeniopygia guttata*), digit ratios correlate negatively with female activity but positively with male song rate (Forstmeier 2005). In contrast, Dreiss et al. (2007) found no relationship between digit ratio and song rate in male barn swallows (*Hirundo rustica*). In the one study that examined digit ratio in relation to physiological performance in a reptile, Tobler et al. (2012) found no effect of digit ratio on the endurance of male painted dragons (*Ctenophorus pictus*). The third aim of this study is to test for relations between digit ratios and

physiological performance (bite force, stamina and sprint speed) in our study species. In line with the human sports literature, we expect that lizards excelling in performance to have relatively low digit ratios.

## Materials and methods

In August and September 2009, we caught a total of 1025 lizards from several islands in the Adriatic Sea. *Podarcis melisellensis* (303 males and 242 females) were sampled from the island of Lastovo and five satellite islands (42°16'N, 16°54'E). *Podarcis siculus* (267 males and 213 females) were obtained from four islands in the Kornati Archipelago (43°48'N, 15°16'E). Individuals were caught by hand or noose and transported in cloth bags to a nearby field station, where measurements were taken within 48 h following capture. Only adult individuals were considered.

## Morphological measurements

In the field station, we measured the snout-vent length, head length, head width and head height of each lizard to the nearest 0.01 mm using electronic callipers (CD-20PP, Mitutuyo Corporation, Japan). We also noted its sex (males exhibit an extended tail base due to the presence of the hemipenis) and vent colour in *P. melisellensis*.

Digit ratios were calculated from digital RX images obtained with a portable X-ray unit (AJEX9020H, Ajex Meditech, Korea). Exposure parameters were set at 40 kV and 0.4 mAs. We took separate images of both fore and hind limbs. Using the ImageJ software (Abramoff et al. 2004), we measured the length of the second, third and fourth digit, from the mid-point of the proximal end of the proximal phalanx bone to the mid-point of the distal end of the distal phalanx bone. The measurements were converted to mm by comparing them to a scale that was photographed along with the animals.

## Performance measurements

We estimated maximal sprint speed, stamina and bite force of each individual lizard. In between measurements, lizards were kept in outside terraria where they could thermoregulate freely. Just prior to a measurement, we measured the lizard's cloacal body temperature using a thermocouple connected to an electronic thermometer (APPA 51, precision 0.1 °C). Only lizards that had body temperatures within their preferred range (34–37 °C; Castilla et al. 1999) were tested.

Sprint speed is considered an ecologically relevant index of organismal performance in lizards (e.g. Huey and Stevenson 1979; Bauwens et al. 1995; Irschick and Le

Galliard 2008). In several species, interindividual variation in sprint speed has been shown to correlate with survival (e.g. Warner and Andrews 2002; Miles 2004; Husak 2006), social dominance (e.g. Garland et al. 1990; Robson and Miles 2000; Perry et al. 2004; but see López and Martín 2002) or reproductive success (Husak et al. 2006a, b). We measured sprint speed by chasing the lizard as fast as possible along a horizontal 2-m racetrack, equipped with a cork substrate, which provides excellent traction. Photocells, positioned at 25-cm intervals along the track, registered the passing of the lizards to a laptop, which calculated the sprint speed over each interval. Every individual was tested three times with at least 1 h between trials. A previous study has shown that lizards do not fatigue over trials (Vervust et al. 2008). The fastest velocity attained over any 25 cm was retained as an estimate of an individual's maximum sprint capacity. Each trial was also characterized as 'good' or 'poor', depending on the continuity of the run (van Berkum 1988; Van Damme et al. 1997). Speed estimates from 'poor' runs were not included in the analysis.

Like sprint speed, stamina has a long tradition as an indicator of physical performance (e.g. Garland and Losos 1994) and has been shown to be under natural (LeGalliard et al. 2004) or sexual selection (Sinervo et al. 2000; Brandt 2003) in lizards. We measured stamina by chasing the lizards along a horizontal torus track (1 m diameter). Lizards were considered 'exhausted' if they no longer responded to ten gentle taps on the dorsum. The time between the start and the end of the run was considered as a measure of stamina. Because this procedure is very demanding for the lizard and the experimenter, each individual was only tested once. Previous measurements showed that the procedure yields very repeatable results (Vervust unpublished).

Bite force is an important determinant of the outcome of male combat in several lizard species (e.g. Lailvaux et al. 2004; Huyghe et al. 2005; Husak et al. 2006a, b). We measured bite force using an isometric Kistler force transducer (type 9203, Kistler Inc), mounted on a purpose-built holder and connected to a Kistler charge amplifier (type 5058 A, Kistler Inc). Individuals were forced to bite on two plates, fixed at a distance of 3.65 mm. A full description of the measuring device can be found in Herrel et al. (2001). The bite force of every individual was measured five times, and the highest bite force was considered as an estimate of the maximal bite capacity.

After completion of the measurements, lizards were released at the exact site of capture, always within 2 days.

## Statistical analyses

Preliminary analyses showed no differences among populations (within species) in digit ratios, physiological

measurements or their interaction. For the sake of simplicity, we therefore pooled data per species.

We used general linear model ANOVAs to examine the effects of sex and species on 2D:4D, 3D:4D and 2D:3D ratios of the four limbs. Island of origin was added as random factor to the model. The tests were performed per limb, averaged over the mani and over the pedes and averaged over all four autopodia. Associations among the 12 digit ratios were examined using partial correlations (adjusting for between-species differences). The effect of digit ratio on physiological performance was examined using general linear model ANOVAs, taking into account effects of sex, species and all interactions. All linear measurements and performance variables were log10-transformed prior to statistical analysis. Differences in digit ratios among colour morphs of *P. melisellensis* were tested in a separate ANOVA. All analyses were performed in R version 2.15.2 (<http://www.R-project.org>).

**Results**

While digit ratios in *P. melisellensis* almost invariably exhibited sexual dimorphism with higher ratios in males (Table 1), for *P. siculus* this was only significant in three out of 12 tests (Table 1). There was a statistically significant interaction between sex and species, supporting that at least for some ratios in some mani or pedes, sexual dimorphism was more pronounced in *P. melisellensis* (Table 1; Fig. 1). On average, sexual dimorphism was

higher for 2D:4D, intermediate for 2D:3D and lowest for 3D:4D (Table 1; Fig. 1).

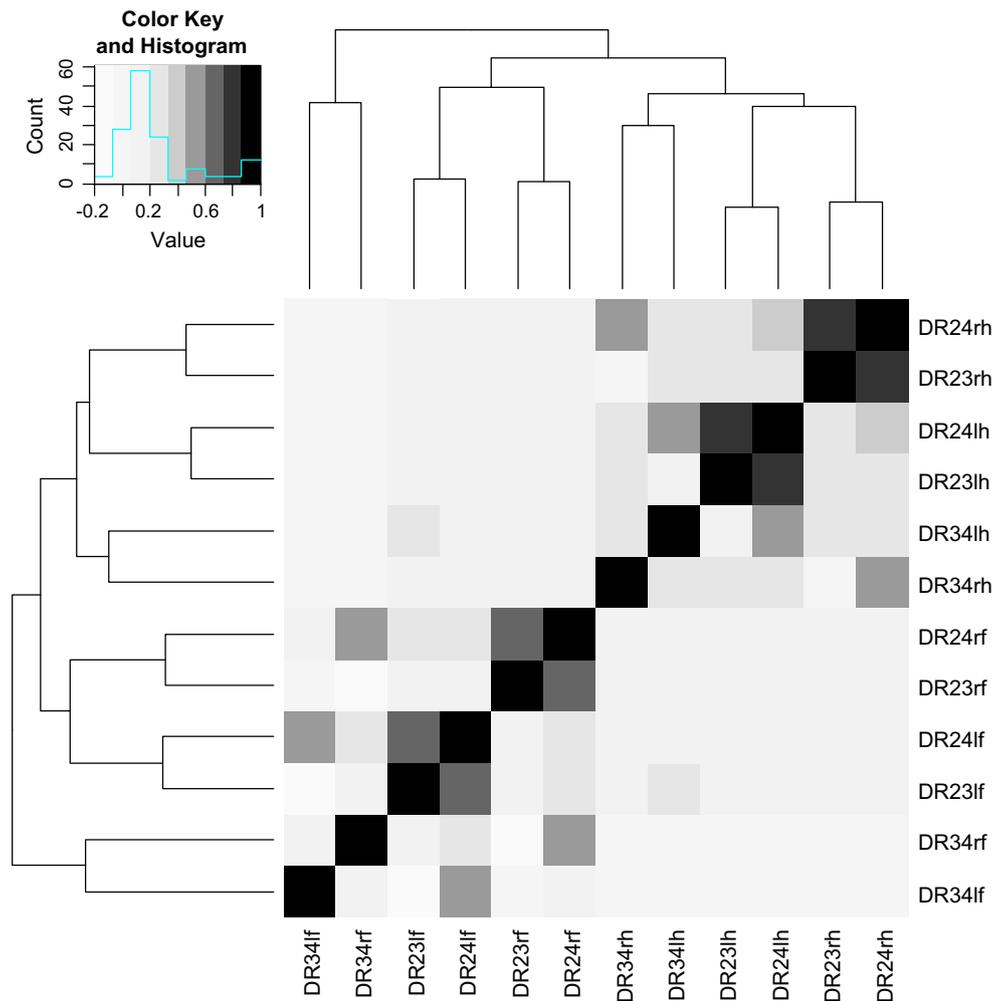
Partial correlation analyses indicated a close association among the three digit ratios of the mani and among the digit ratios of the pedes, but a smaller correlation between mani and pedes. Hence, individuals with high 2D:4D digit ratios on the left manus tend to have high 3D:4D and 2D:3D ratios on both mani, but not necessarily exhibit high ratios on the pedes (Fig. 1). On the basis of this result, we studied associations between ratios and sprint speed, stamina and bite force for average ratios combined over both sides in mani and pedes.

Associations between digit ratio and both sprint speeds and stamina were overall weak and showed no differences between males and females or species (Table 2). For bite force, however, patterns were stronger and showed differences between species. Individuals with high digit ratios in both mani and pedes bit harder than individuals with lower ratios, but the relationship was only significant for *P. melisellensis* (Table 2; Fig. 2). In *P. melisellensis*, but not in *P. siculus*, individuals with high digit ratios had longer snout-vent lengths and larger heads (Fig. 3). Apparently, the association between digit ratio and head size sufficed to explain the variation in bite force as the associations between digit ratios and bite force reported above, remained no longer statistically significant if head size or SVL was added to the linear model (details not shown).

In *P. melisellensis*, sexual dimorphism in digit ratio differed significantly among the three colour morphs for

**Table 1** Significance tests and estimates of sexual dimorphism (SDI = sexual dimorphism index) in digit ratios in *Podarcis melisellensis* and *P. siculus*

	Right/front		Left/front		Right/hind		Left/hind	
2D:4D								
Sex	$F_{1,906} = 12.3^{***}$		$F_{1,904} = 19.2^{***}$		$F_{1,847} = 69.2^{***}$		$F_{1,836} = 56.3^{***}$	
Species	$F_{1,906} = 14.3^{***}$		$F_{1,904} = 48.2^{***}$		$F_{1,847} = 367.0^{***}$		$F_{1,836} = 299^{***}$	
Sex*Species	$F_{1,906} = 4.84^*$		$F_{1,904} = 12.1^{***}$		$F_{1,847} = 14.8^{***}$		$F_{1,836} = 11.9^{***}$	
	<i>P. meli</i>	<i>P. sic</i>	<i>P. meli</i>	<i>P. sic</i>	<i>P. meli</i>	<i>P. sic</i>	<i>P. meli</i>	<i>P. sic</i>
SDI (%)	0.99***	0.20	1.27***	0.11	1.37***	0.47*	1.42***	0.54*
2D:3D								
Sex	$F_{1,901} = 6.8^{**}$		$F_{1,919} = 28.5^{***}$		$F_{1,908} = 20.8^{***}$		$F_{1,910} = 11.6^{***}$	
Species	$F_{1,901} = 41.0^{***}$		$F_{1,919} = 84.9^{***}$		$F_{1,908} = 33.3^{***}$		$F_{1,910} = 35.8^{***}$	
Sex*species	$F_{1,901} = 2.38$		$F_{1,919} = 11.9^{***}$		$F_{1,908} = 11.1^{***}$		$F_{1,910} = 1.47$	
	<i>P. meli</i>	<i>P. sic</i>	<i>P. meli</i>	<i>P. sic</i>	<i>P. meli</i>	<i>P. sic</i>	<i>P. meli</i>	<i>P. sic</i>
SDI (%)	0.60*	0.15	1.31***	0.26	1.02***	0.14	0.63***	0.54*
3D:4D								
Sex	$F_{1,895} = 3.92^*$		$F_{1,905} = 0.01$		$F_{1,851} = 17.7^{***}$		$F_{1,826} = 28.9^{***}$	
Species	$F_{1,895} = 7.28^{**}$		$F_{1,905} = 6.89^{**}$		$F_{1,851} = 190^{***}$		$F_{1,826} = 135^{***}$	
Sex*species	$F_{1,895} = 0.64$		$F_{1,905} = 0.23$		$F_{1,851} = 1.60$		$F_{1,826} = 10.6^{**}$	
	<i>P. meli</i>	<i>P. sic</i>	<i>P. meli</i>	<i>P. sic</i>	<i>P. meli</i>	<i>P. sic</i>	<i>P. meli</i>	<i>P. sic</i>
SDI (%)	0.33	0.13	0.05	-0.07	0.47***	0.24	0.92***	0.23



**Fig. 1** Heat map of the partial correlations between digit ratios of mani and pes. *L* left, *r* right, *h* hand (manus), *f* foot (pes)

pes ( $F_{2,385} = 5.91$ ,  $p = 0.003$ ) but not for mani ( $F_{2,431} = 0.01$ ,  $p = 0.99$ ). The degree of sexual dimorphism in average digit ratio in pes was higher in the yellow morph than in the white and orange morphs (yellow: 1.77 %; orange: 0.45 %; white: 1.06 %). This effect seems to originate from the fact that yellow males have relatively high digit ratio, but also because females have low ratios compared to other morphs (Fig. 4).

## Discussion

### Interspecific variation in digit ratio

In both *Podarcis* species we studied, males exhibit larger 2D:4D digit ratios than females. Our data thus support a pattern seen in humans and several other tetrapods: relative developmental rates of the second and fourth digit vary between the sexes. However, in contrast to what has been documented in humans and most mammals, male

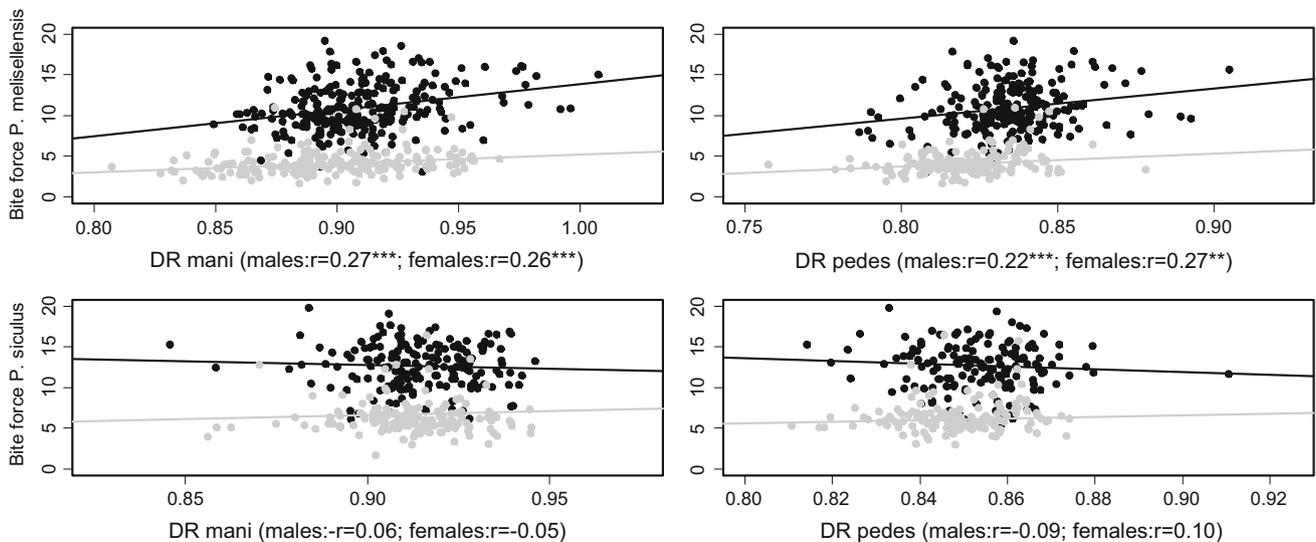
*P. melisellensis* and *P. sicula* tend to have larger 2D:4D ratios than females. Such a ‘reversed’ sexual dimorphism in digit ratio has been noted in another *Podarcis* species (*P. muralis*, Rubolini et al. 2006). Moreover, in 16 of the 32 lizard species examined up to now, males have larger, rather than smaller, 2D:4D digit ratios (Rubolini et al. 2006; Lombardo et al. 2008; Drenzo and Stynoski 2012; Gomes and Kohlsdorf 2012). This, combined with evidence from birds (e.g. Burley and Foster 2002; Navarro et al. 2007; Saino et al. 2007; Dreiss et al. 2008; Leoni et al. 2008) clearly refutes Manning’s (2002) early hypothesis that all tetrapods would exhibit female-biased 2D:4D ratios.

Why tetrapod species vary so much in the size and direction of the dimorphism in 2D:4D ratio remains highly unclear. On a proximate level, species may vary in the effect that steroids have on the secretion of growth hormone, or in the way that such steroids are deposited in eggs that will give rise to male and female offspring (Rubolini et al. 2006; Lombardo et al. 2008). These ideas could be

**Table 2** Results of general linear model ANOVAs, taking into account effects of digit ratio (DR), sex, species and all interactions

	Mani	Pedes
<i>Bite force</i>		
DR	<b><math>F_{1,701} = 303; p &lt; 0.001</math></b>	<b><math>F_{1,787} = 164; p &lt; 0.001</math></b>
Species	<b><math>F_{1,701} = 33.8; p &lt; 0.001</math></b>	<b><math>F_{1,787} = 92.5; p &lt; 0.001</math></b>
Sex	<b><math>F_{1,701} = 1067; p &lt; 0.001</math></b>	<b><math>F_{1,787} = 1395; p &lt; 0.001</math></b>
DR × sex	$F_{1,700} = 0.11; p = 0.74$	$F_{1,786} = 2.51; p = 0.11$
DR × species	<b><math>F_{1,701} = 8.20; p = 0.004</math></b>	<b><math>F_{1,787} = 10.8; p = 0.001</math></b>
Sex × species	$F_{1,699} = 0.00; p = 0.97$	$F_{1,785} = 1.13; p = 0.29$
Sex × species × DR	$F_{1,698} = 3.2; p = 0.07$	$F_{1,784} = 1.39; p = 0.24$
<i>Speed</i>		
DR	$F_{1,767} = 0.10; p = 0.76$	$F_{1,685} = 3.62; p = 0.06$
Species	<b><math>F_{1,767} = 66.7; p &lt; 0.001</math></b>	<b><math>F_{1,685} = 6.71; p = 0.01</math></b>
Sex	<b><math>F_{1,767} = 4.59; p = 0.03</math></b>	$F_{1,684} = 0.36; p = 0.55$
DR × sex	$F_{1,764} = 0.60; p = 0.44$	$F_{1,682} = 0.61; p = 0.43$
DR × species	$F_{1,765} = 0.71; p = 0.40$	<b><math>F_{1,685} = 6.11; p = 0.01</math></b>
Sex × species	$F_{1,766} = 3.38; p = 0.07$	$F_{1,683} = 1.24; p = 0.27$
Sex × species × DR	$F_{1,763} = 1.43; p = 0.23$	$F_{1,681} = 0.11; p = 0.74$
<i>Exertion</i>		
DR	<b><math>F_{1,564} = 4.59; p = 0.03</math></b>	<b><math>F_{1,488} = 5.86; p = 0.02</math></b>
Species	<b><math>F_{1,564} = 60.4; p &lt; 0.001</math></b>	<b><math>F_{1,488} = 31.4; p &lt; 0.001</math></b>
Sex	$F_{1,564} = 3.53; p = 0.07$	<b><math>F_{1,488} = 6.02; p = 0.02</math></b>
DR × sex	$F_{1,561} = 0.00; p = 0.99$	$F_{1,487} = 2.86; p = 0.09$
DR × species	$F_{1,562} = 1.16; p = 0.28$	$F_{1,485} = 0.00; p = 0.99$
Sex × species	$F_{1,563} = 0.95; p = 0.33$	$F_{1,486} = 0.21; p = 0.64$
Sex × species × DR	$F_{1,560} = 0.16; p = 0.69$	$F_{1,484} = 0.65; p = 0.42$

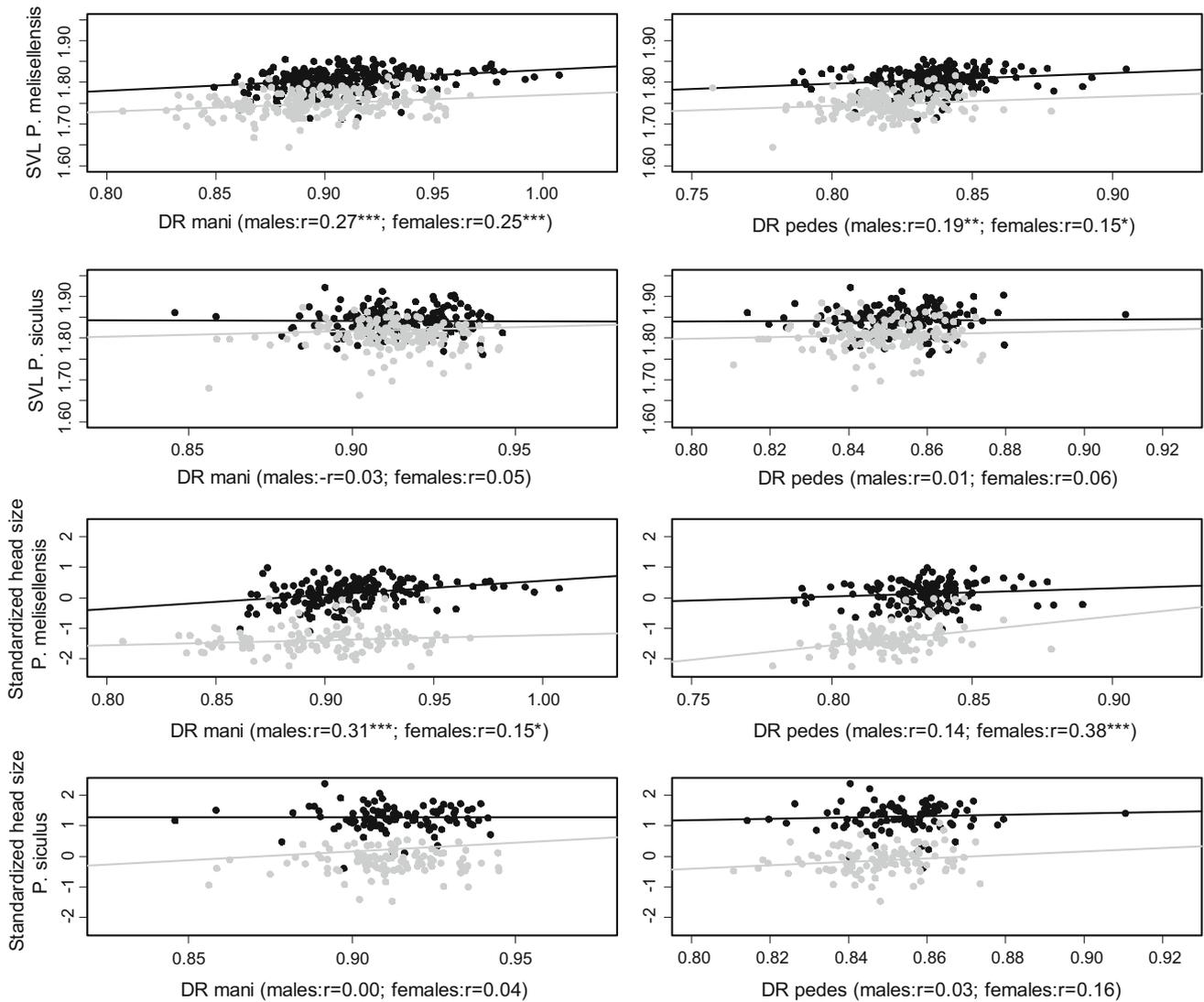
Significant results are shown in bold



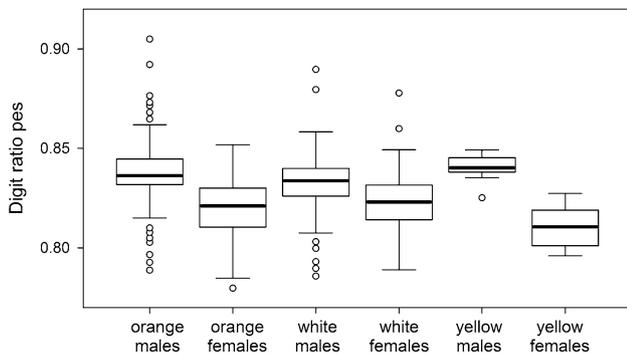
**Fig. 2** Relationships between whole-animal performance (y axis) and digit ratios (x axis) for mani and pedes. Males are shown in *black*, and females in *grey*

tested by manipulating prenatal steroid hormone concentrations at different stages of development in a number of species (e.g. Romano et al. 2005; Talarovicova et al. 2009;

Tobler et al. 2011). It has also been suggested that sexual dimorphism in digit ratio may echo (or rather anticipate) adult body size dimorphism across species (Direnzo and



**Fig. 3** Relationships between morphological traits (y axis) and digit ratios (x axis) for mani and pedes. Males are shown in *black*, and females in *grey*



**Fig. 4** Degree of sexual dimorphism in average digit ratios (pedes) among colour morphs of *Podarcis melisellensis*

Stynoski 2012). Our results lend some support to this hypothesis: of the two species studied, the one that exhibits the larger intersexual difference in adult SVL (*P. melisellensis*) also shows the higher 2D:4D dimorphism. But of course, a thorough test of this hypothesis will require a phylogenetically informed analysis of digit ratios, using data on many more species. As they vary greatly in the extent and direction of their adult size dimorphism (Abouheif and Fairbairn 1997; Cox et al. 2003), lizards may constitute an excellent group to perform such a test. Dizenzo and Stynoski (2012) have suggested a possible role of the chromosomal sex determination system: digit ratios may be smaller in the heterogametic sex (males in mam-

mals, females in birds). In both species studied here, and in most *Podarcis*, females are the heterogametic sex, so our results also corroborate this idea. Again, given the extraordinary variability in sex determination systems within this group (Viets et al. 1994; Olmo and Signorino 2005), lizards seem an interesting group to further explore this suggestion. Yet another line of thought is that selection acting directly on the 2D:4D digit ratio may cause deviations from the ancestral developmental programme in some species more than in others. In a recent comparative study on Iguania, Gomes and Kohlsdorf (2012) found that females of arboreal species tend to have small digit ratios in the fore limbs, which translated in a greater ratio dimorphism in this group. Apparently, ecological selection pressures may override the developmental programme in some squamate groups. It seems unlikely, however, that ecological divergence is responsible for the differences in digit ratio observed in our study species, because *Podarcis siculus* and *P. melisellensis* resemble each other in almost every aspect of their ecology, including microhabitat use (Radovanovic 1959; Nevo et al. 1972; Arnold 1987). Phylogenetic studies comparing large sets of species differing in sex determination, developmental mode and ecology will be required to test these hypotheses.

In the prospect of such comparative studies, standard procedures for measuring and analysing digit ratios seem highly desirable. Currently, the kinds of digit ratios reported differ among studies and little is known on whether such information is exchangeable, or whether a particular type of ratio outperforms others. Most studies on humans have focused on 2D:4D-ratios, although other digit ratios (3D:4D and 2D:3D) have proved superior in a number of cases (McFadden et al. 2005; Burton et al. 2005; McIntyre et al. 2006; but see Voracek 2009). Our analyses show a close relationship between alternative digit ratios, at least within one pair of limbs (forelimbs or hind limbs). We therefore advocate the continued use of 2D:4D ratios in future studies. Although other digit ratios may largely reflect similar prenatal conditions, the consistent use of one digit ratio will greatly facilitate future meta-analyses. In sharp contrast with the wealth of information available on digit ratios of the human hand, almost nothing is known on human toe ratios (Harrison 2010), partly because of the difficulty of adequately measuring toe length (McFadden and Shubel 2002). Although we are unaware of explicit tests in this respect, the squamate digit ratio literature suggests that the effects of prenatal steroid exposure on digit ratios may differ between the manus and the pes. Compared to females, male *Anolis humilis* have smaller 2D:4D in the forelimbs but larger 2D:4D in the hindlimbs (Direnzo and Stynoski 2012). Similarly, Chang et al. (2006) report male smaller 2D:4D ratios in the forelimb, but female smaller 2D:4D ratios in the hindlimbs of *Anolis*

*carolinensis*. Although not as extreme as in the *Anolis* species studied, our correlation analyses show that between-limb pair associations are weaker than within-pair associations of alternative digit ratios. In other words, lizards with high finger digit ratios not necessarily also have high toe digit ratios. This suggests that the developmental programmes of fingers and toes are less developmentally integrated. Such a decoupling could arise from heterochrony; if anterior and posterior digits develop at different times, they may experience different hormonal milieus. The relative timing of forelimb versus hindlimb development has been shown to vary considerably among the major vertebrate clades, but there is little evidence for such variation at lower taxonomic levels (e.g. within squamates, Bininda-Emonds et al. 2007). It would be interesting to compare the relative timing of anterior versus posterior limb pairs between lizards with contrasting digit ratio patterns. Alternatively, androgen and oestrogen receptor density, receptivity or activity may differ between developing limb pairs.

### Digit ratios and colour morphs

Studies on other lizard species have shown that differences in early organizational or activational effects of sex steroid hormones may result in alternative behavioural morphs within sexes. In tree lizards (*Urosaurus ornatus*), testosterone implants given to juveniles 1–30 days posthatching increase the frequency of ‘orange-blue’ males, an aggressive and territorial morph characterized by a blue patch in the centre of its orange dewlap (Hews et al. 1994). The time window for this effect is narrow: no effects are evident in juveniles implanted at 60 days posthatching (Hews and Moore 1996). In side-blotched lizards (*Uta stansburiana*), maternal oestradiol levels are implicated in the production of alternative dorsal patterns that relate to reproductive strategies (Lancaster et al. 2007). A third study, on painted dragons (*Ctenophorus pictus*), found no significant effect of intrauterine steroid regime on offspring colour morph frequency, but the authors recognize that this result could be due to the relatively small sample size (Tobler et al. 2011). One of our study species, *P. melisellensis*, also expresses three adult colour morphs. Although the ecological and evolutionary significance of this colour polymorphism remains unclear, several observations suggest that male morphs may differ in reproductive strategies: males with orange throats and vents have larger heads and bite harder than yellow or white males (Huyghe et al. 2007, 2009), which would likely give them an edge in territorial disputes. Interestingly, adult plasma testosterone levels do not differ among male morphs (Huyghe et al. 2009). The colour morph  $\times$  sex interaction effect on 2D:4D ratios in our results suggests that the prenatal steroid environment

may differentially influence morphs in *P. melisellensis*, but the effect is subtle and less straightforward than in *U. ornatus*. First, the significance of the effect is primarily due to lightly deviant digit ratios in the yellow morph, while (based upon differences in performance and morphology) we expected to see differences between orange males, and between white and yellow males. Second, neither male nor female colour morphs differ much in digit ratios—it is the combination of low ratios in females and high ratios in males that causes the significant interaction effect. Additional studies, e.g. using experimentally administered steroids, are required to explain these puzzling results.

### Digit ratio and physiological performance

In humans, performance in a wide range of sports is negatively correlated with 2D:4D digit ratios (reviewed in Hönekopp and Schuster 2010). Because the predictive power of the digit ratio is higher in fields like distance running (Manning et al. 2003, 2007) and soccer (Manning et al. 2003) than in sprinting (Manning and Hill 2009) and gymnastics (Hönekopp et al. 2006), it has been suggested that it is a marker of traits underlying endurance, rather than strength or speed (Manning and Hill 2009; Hönekopp and Schuster 2010). However, exactly which components of physical fitness are responsible for the relationship between digit ratios and athletic prowess remains largely unknown (Hönekopp and Schuster 2010). Interestingly, recent evidence suggests that increased prenatal levels of testosterone may even contribute to athletic performance through its effect on mental toughness, optimism and goal orientation (Golby and Meggs 2011).

As far as we know, only two previous studies have examined the association between digit ratios and locomotor performance in animals. Yan et al. (2008) showed that laboratory mice selected for high wheel running activity also evolved higher 2D:4D ratios. However, Tobler et al. (2012) failed to find any significant correlation between locomotor endurance and digit ratio in painted dragons. Our results are in line with the latter study: neither of the two locomotor performance indices we measured showed significant association with digit ratio. Interestingly, we did find that lizards with high digit ratios had superior bite forces—although the correlation was statistically significant for male *P. melisellensis* only. Our analyses indicate that the link between bite force and digit ratio may be simply mediated by head size, thus providing a rare insight into the mechanism of prenatal steroid programming. The observed effect on head size and bite force cannot be considered trivial, because these traits have repeatedly been shown to correlate with behavioural dominance in lizards (e.g. Lailvaux et al. 2004; Husak et al. 2006a, b), including lacertids (Huyghe et al. 2005). If

confirmed, our results would thus provide another example of how the adult life of an organism can be influenced by the ephemeral conditions of the intrauterine environment.

In conclusion, our study confirms that sexual dimorphism in digit ratios is taxonomically widely distributed. Digit ratios correlate with morphological and performance traits that are ecologically relevant. At the same time, our results seem at odds with several observations on human populations: in the lizard species we studied, males have higher 2D:4D ratios than females (humans: lower), males with higher digit ratios have increased performance ability (humans: lower), and digit ratios correlate more with physical strength than with endurance (opposite in humans). We believe that a comparative analysis of the causes and correlates of variation in this biomarker constitutes a fruitful avenue for further studies into the importance of the prenatal environment on the development of organisms. Because their ecology, behaviour, reproductive biology and development are so diverse, we think that lizards (Lacertilia) provide an excellent group to study these issues.

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### References

- Abouheif E, Fairbairn DJ (1997) A comparative analysis of allometry for sexual size dimorphism: assessing Rensch's rule. *Am Nat* 149:540–562
- Abramoff MD, Magalhaes PJ, Ram SJ (2004) Image processing with image. *J Bioph Int* 11:36–42
- Arnold EN (1987) Resource partition among lacertid lizards in southern Europe. *J Zool* 1:739–782
- Baker F (1888) Anthropological notes on the human hand. *Am Anthropol* 1:51–76
- Bauwens D, Garland T Jr, Castilla AM, Van Damme R (1995) Evolution of sprint speed in lacertid lizards: morphological, physiological, and behavioral covariation. *Evolution* 49:848–863
- Bininda-Emonds OR, Jeffery JE, Sánchez-Villagra MR, Hanken J, Colbert M, Pieau C, Selwood L, Ten Cate C, Raynaud A, Osabutey CK, Richardson MK (2007) Forelimb-hindlimb developmental timing changes across tetrapod phylogeny. *BMC Evol Biol* 7:182
- Brandt Y (2003) Lizard threat display handicaps endurance. *Proc R Soc Lond B* 270:1061–1068
- Brown WM, Finn CJ, Breedlove SM (2002) Sexual dimorphism in digit-length ratios of laboratory mice. *Anat Rec* 267:231–234
- Burley NT, Foster VS (2002) Digit ratio varies with sex, egg order and strength of mate preference in zebra finches. *Proc R Soc Lond B* 271:239–244
- Burton LA, Henninger D, Hafetz J (2005) Gender differences in relations of mental rotation, verbal fluency, and SAT scores to finger-length ratios as hormonal indexes. *Developm Neuropsychol* 28:93–505
- Castilla AM, Van Damme R, Bauwens D (1999) Field body temperatures, mechanisms of thermoregulation and evolution

- of thermal characteristics in lacertid lizards. *Natura Croatica* 8:275–286
- Chang JL, Doughty S, Wade J, Lovern MB (2006) Sexual dimorphism in the second-to-fourth digit length ratio in green anoles, *Anolis carolinensis* (Squamata: polychrotidae), from the southeastern United States. *Can J Zool* 84:1489–1494
- Collaer ML, Hines M (1995) Human behavioral sex-differences: a role for gonadal hormones during early development. *Psychol Bull* 118:55–107
- Cox RM, Skelly SL, John-Alder HB (2003) A comparative test of adaptive hypotheses for sexual size dimorphism in lizards. *Evolution* 57:1653–1669
- Direnzo GV, Stynoski JL (2012) Patterns of second-to-fourth digit length ratios (2D:4D) in two species of frogs and two species of lizards at La Selva, Costa Rica. *Anat Rec* 295:597–603
- Downes S, Bauwens D (2002) An experimental demonstration of direct behavioural interference in two Mediterranean lacertid lizard species. *Anim Behav* 63:1037–1046
- Dreiss AN, Navarro C, De Lope F, Moller AP (2007) Digit ratios, secondary sexual characters and condition in barn swallows *Hirundo rustica*. *Behav Ecol* 19:16–21
- Ecker A (1875) Einige Bemerkungen über einen Schwankengen Charakter in der Hand des Menschen. *Arch Anthropol* 8:67–75
- Eikenaar C, Husak J, Escallon C, Moore IT (2012) Variation in testosterone and corticosterone in amphibians and reptiles: relationships with latitude, elevation, and breeding season length. *Am Nat* 180:642–654
- Forstmeier W (2005) Quantitative genetics and behavioural correlates of digit ratio in the zebra finch. *Proc R Soc Lond B* 272:2641–2649
- Garland T Jr, Losos JB (1994) Ecological morphology of locomotor performance in squamate reptiles. In: Wainwright PC, Reilly SM (eds) *Ecological morphology: integrative organismal biology*. University of Chicago Press, Chicago, pp 240–302
- Garland T Jr, Hankins T, Huey RB (1990) Locomotor capacity and social dominance in male lizards. *Funct Ecol* 4:243–250
- Gil D (2008) Hormones in avian eggs: physiology, ecology and behaviour. *Adv Stud Behav* 38:37–398
- Golby J, Meggs J (2011) Exploring the organizational effect of prenatal testosterone upon the sporting brain. *J Sport Sci Med* 10:445–451
- Gomes CM, Kohlsdorf T (2012) Evolution of sexual dimorphism in the digit ratio 2D:4D-relationships with body size and microhabitat use in iguanian lizards. *PLoS ONE* 6:e28465
- Harrison MA (2010) An exploratory study of the relationship between second toe length and androgen linked behaviours. *J Soc Evol Cult Psychol* 4:241–253
- Herrel A, Van Damme R, Vanhooydonck B, De Vree F (2001) The implications of bite performance for diet in two species of lacertid lizards. *Can J Zool* 79:662–670
- Hews DK, Moore MC (1996) A critical period for the organization of alternative male phenotypes of tree lizards by exogenous testosterone? *Physiol Behav* 60:425–429
- Hews DK, Knapp R, Moore MC (1994) Early exposure to androgens affects adult expression of alternative male types in tree lizards. *Horm Behav* 28:1–21
- Hönekopp J, Schuster M (2010) A meta-analysis on 2D:4D and athletic prowess: substantial relationships but neither hand out-predicts the other. *Pers Individ Diff* 48:4–10
- Hönekopp J, Manning JT, Müller C (2006) Digit ratio (2D:4D) and physical fitness in males and females: evidence for effects of prenatal androgens on sexually selected traits. *Horm Behav* 49:545–549
- Huey RB, Stevenson RD (1979) Integrating thermal physiology and ecology of ectotherms: discussion of approaches. *Am Zool* 19:357–366
- Husak JF (2006) Does speed help you survive? A test with collared Lizards of different ages. *Funct Ecol* 20:174–179
- Husak JF, Fox SF, Lovern MB, Van Den Bussche RA (2006a) Faster lizards sire more offspring: sexual selection on whole-animal performance. *Evolution* 60:2122–2130
- Husak JF, Lappin AK, Fox SF, Lemos-Espinal JA (2006b) Bite-force performance predicts dominance in male venerable collared lizards (*Crotaphytus antiquus*). *Copeia* 2006:301–306
- Huyghe K, Vanhooydonck B, Scheers H, Molina-Borja M, Van Damme R (2005) Morphology, performance and fighting capacity in male lizards, *Gallotia galloti*. *Funct Ecol* 19:800–807
- Huyghe K, Vanhooydonck B, Herrel A, Tadic Z, Van Damme R (2007) Morphology, performance, behaviour and ecology of three colour morphs in males of the lizard *Podarcis melisellen-sis*. *Integr Comp Biol* 47:211–220
- Huyghe K, Husak JF, Herrel A, Tadic Z, Moore IT, Van Damme R, Vanhooydonck B (2009) Relationships between hormones, physiological performance and immunocompetence in a color-polymorphic lizard species, *Podarcis melisellen-sis*. *Horm Behav* 55:488–494
- Irschick DJ, Le Galliard JF (2008) Studying the evolution of whole-organism performance capacity: sex selection, and haiku—an introduction. *Evol Ecol Res* 10:155–156
- Lailvaux SP, Herrel A, Vanhooydonck B, Meyers JJ, Irschick DJ (2004) Performance capacity, fighting tactics, and the evolution of life-stage morphs in the green anole lizard (*Anolis carolinensis*). *Proc R Soc Lond B* 271:2501–2508
- Lancaster LT, McAdam AG, Wingfield JC, Sinervo BR (2007) Adaptive social and maternal induction of antipredator dorsal patterns in a lizard with alternative social strategies. *Ecol Lett* 10:798–808
- LeGalliard JF, Clobert J, Ferrière R (2004) Physical performance and Darwinian fitness in lizards. *Nature* 432:502–505
- Leoni B, Rubolini D, Romano M, di Giancamillo M, Saino N (2008) Avian hind-limb digit length ratios measured from radiographs are sexually dimorphic. *J Anat* 213:425–430
- Lombardo MP, Thorpe PA, Brown BM, Sian K (2008) Digit ratios in birds. *Anat Rec* 291:1611–1618
- López P, Martín J (2002) Locomotor capacity and dominance in male lizards *Lacerta monticola*: a trade-off between survival and reproductive success? *Biol J Linn Soc* 77:201–209
- Manning JT (2002) Digit ratio: a pointer to fertility, behavior, and health. Rutgers University Press, New Brunswick
- Manning JT (2008) *The finger ratio*. Faber and Faber, London
- Manning JT, Hill MR (2009) Digit ratio (2D:4D) and sprinting speed in boys. *Am J Human Biol* 21:210–213
- Manning JT, Scutt D, Wilson J, Lewis-Jones DI (1998) The ratio of 2nd to 4th digit length: a predictor of sperm numbers and concentrations of testosterone, luteinizing hormone and oestrogen. *Hum Reprod* 13:3000–3004
- Manning JT, Bundred PE, Taylor R (2003) The ratio of 2nd and 4th digit length: a prenatal correlate of ability in sport. In: Reilly T, Marfell-Jones M (eds) *Kinanthropometry vol. VIII*. Routledge, London, pp 165–174
- Manning JT, Morris L, Caswell N (2007) Endurance running and digit ratio (2D:4D): implications for fetal testosterone effects on running speed and vascular health. *Am J Hum Biol* 19:416–421
- McFadden D, Bracht MS (2002) The relative lengths and weights of metacarpals and metatarsals in baboons (*Papio hamadryas*). *Horm Behav* 43:347–355
- McFadden D, Shubel E (2002) Relative lengths of fingers and toes in human males and females. *Horm Behav* 42:492–500
- McFadden D, Westhafer JG, Pasanen EG, Carlson CL, Tucker DM (2005) Physiological evidence of hypermasculinization in boys with the inattentive type of attention-deficit hyperactivity disorder (ADHD). *Clin Neurosci Res* 5:233–246

- McIntyre MH (2006) The use of digit ratios as markers for prenatal androgen action. *Reprod Biol Endocrinol* 4:10
- McIntyre MH, Cohn BA, Ellison PT (2006) Sex dimorphism in digital formulae of children. *Am J Phys Anthropol* 129:143–150
- Miles DB (2004) The race goes to the swift: fitness consequences of variation in sprint performance in juvenile lizards. *Evol Ecol Res* 6:63–75
- Moore MC, Hews DK, Knapp R (1998) Hormonal control and evolution of alternative male phenotypes: generalisations of models for sexual differentiation. *Am Zool* 38:133–151
- Murphy BF, Thompson MB (2011) A review of the evolution of viviparity in squamate reptiles: the past, present and future role of molecular biology and genomics. *J Comp Physiol B* 181:575–594
- Navarro C, de Lope F, Moller AP (2007) Digit ratios (2D:4D), secondary sexual characters and cell-mediated immunity in house sparrows *Passer domesticus*. *Behav Ecol Sociobiol* 61:1161–1168
- Nelson E, Shultz S (2010) Finger length ratios (2D:4D) in anthropoids implicate reduced prenatal androgens in social bonding. *Am J Phys Anthropol* 141:395–405
- Nevo E, Gorman GC, Soulé M, Yang SY, Clover R, Jovanović V (1972) Competitive exclusion between insular *Lacerta* species (Sauria: lacertidae) notes on experimental introductions. *Oecologia* 10:183–190
- Olmo E, Signorino G (2005) Chromorep: a reptile chromosomes database. Internet references: <http://193.206.118.100/professori/chromorep.pdf>
- Perry G, Levering K, Girard I, Garland T Jr (2004) Locomotor performance and social dominance in male *Anolis cristatellus*. *Anim Behav* 67:37–47
- Putz DA, Gaulin SJC, Sporter RJ, McBurney DH (2004) Sex hormones and finger length: what does 2D:4D indicate? *Evol Hum Behav* 25:182–199
- Radovanovic M (1959) Zum Problem der Speziation bei Inseleidechsen. *Zool Jahrb Abt Syst Geogr Biol Jena* 86:395–436
- Robson MA, Miles DB (2000) Locomotor performance and dominance in male tree lizards, *Urosaurus dorsalis*. *Funct Ecol* 14:338–344
- Romano M, Rubolini D, Martinelli R, Alquati AB, Saino N (2005) Experimental manipulation of yolk testosterone affects digit length ratios in the ring-necked pheasant (*Phasianus colchicus*). *Horm Behav* 48:342–346
- Roney JR, Whitham JC, Leoni M, Bellem A, Wielebnowski N, Maestripieria D (2004) Relative digit lengths and testosterone levels in Guinea baboons. *Horm Behav* 45:285–290
- Rubolini D, Pupin F, Sacchi R, Gentilli A, Zuffi MAL, Galeotti P, Saino N (2006) Sexual dimorphism in digit length ratios in two lizard species. *Anat Rec* 288A:491–497
- Saino N, Rubolini D, Romano M, Boncoraglio G (2007) Increased egg estradiol concentration feminizes digit ratios of male pheasants (*Phasianus colchicus*). *Naturwissenschaften* 94:207–212
- Sinervo B, Miles DB, Frankino WA, Klukowski M, DeNardo DF (2000) Testosterone, endurance, and Darwinian fitness: natural and sexual selection on the physiological bases of alternative male behaviors in side-blotched lizards. *Horm Behav* 38:222–223
- Talarovicova A, Krsková L, Blazeková J (2009) Testosterone enhancement during pregnancy influences the 2D:4D ratio and open field motor activity of rat siblings in adulthood. *Horm Behav* 55:235–239
- Tamiya R, Lee SY, Ohtake F (2011) Second to fourth digit ratio and the sporting success of sumo wrestlers. *Evol Human Behav* 33:130–136
- Tobler M, Healey M, Olsson M (2011) Digit ratio, color polymorphism and egg testosterone in the Australian painted dragon. *PLoS ONE* 6:e16225
- Tobler M, Healey M, Olsson M (2012) Digit ratio, polychromatism and associations with endurance and antipredator behaviour in male painted dragon lizard. *Anim Behav* 84:1261–1269
- Uller T (2008) Developmental plasticity and the evolution of parental effects. *Trends Ecol Evol* 23:432–438
- Van Berkum FH (1988) Latitudinal patterns of the thermal sensitivity of sprint speed in lizards. *Am Nat* 132:327–343
- Van Damme R, Aerts P, Vanhooydonck B (1997) No trade-off between sprinting and climbing in two populations of the lizard *Podarcis hispanica* (Reptilia: Lacertidae). *Biol J Linn Soc* 60:493–503
- Vervust B, Grbac I, Van Damme R (2007) Differences in morphology, performance and behaviour between recently diverged populations of *Podarcis sicula* mirror differences in predation pressure. *Oikos* 116:1343–1352
- Vervust B, Lailvaux S, Grbac I, Van Damme R (2008) Do morphological condition indices predict locomotor performance in the lizard *Podarcis sicula*? *Acta Oecol* 34:244–251
- Viets BE, Ewert MA, Talent LG, Nelson CE (1994) Sex-determining mechanisms in squamate reptiles. *J Exp Zool* 270:45–56
- Voracek M (2009) Comparative study of digit ratios (2d:4d and other) and novel measures of relative finger length: testing magnitude and consistency of sex differences across samples. *Percept Motor Skills* 108:83–93
- Voracek M, Loibl L (2009) Scientometric analysis and bibliography of digit ratio (2D:4D) research, 1998–2008. *Psychol Rep* 104:922–956
- Voracek M, Reimer B, Dressler SG (2010) Digit ratio (2D:4D) predicts sporting success among female fencers independent from physical, experience, and personality factors. *Scand J Med Sci Sports* 20:853–860
- Warner DA, Andrews RM (2002) Laboratory and field experiments identify sources of variation in phenotypes and survival of hatchling lizards. *Biol J Linn Soc* 76:105–124
- Yan RHY, Malisch JL, Hannon RM, Hurd PL, Garland T Jr (2008) Selective breeding for a behavioral trait changes digit ratio. *PLoS ONE* 3:e3216
- Yan RHY, Bunning M, Wahlsten D, Hurd PL (2009) Digit ratio (2D:4D) differences between 20 strains of inbred mice. *PLoS ONE* 4:e5801