

Macroevolutionary pattern of sexual size dimorphism in geckos corresponds to intraspecific temperature-induced variation

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Abstract

Many animal lineages exhibit allometry in sexual size dimorphism (SSD), known as 'Rensch's rule'. When applied to the interspecific level, this rule states that males are more evolutionary plastic in body size than females and that male-biased SSD increases with body size. One of the explanations for the occurrence of Rensch's rule is the differential-plasticity hypothesis assuming that higher evolutionary plasticity in males is a consequence of larger sensitivity of male growth to environmental cues. We have confirmed the pattern consistent with Rensch's rule among species of the gecko genus *Paroedura* and followed the ontogeny of SSD at three constant temperatures in a male-larger species (*Paroedura picta*). In this species, males exhibited larger temperature-induced phenotypic plasticity in final body size than females, and body size and SSD correlated across temperatures. This result supports the differential-plasticity hypothesis and points to the role phenotypic plasticity plays in generating of evolutionary novelties.

Introduction

Body size is a fundamental trait determining a suite of physiological and ecological characteristics of organisms. Within a particular animal species, we can often observe most notable variation in body size between males and females. Evolutionary changes in sexual size dimorphism (SSD), i.e. in differences between sexes in overall body size, are common. In many phylogenetic lineages, we can even find mixed SSD, i.e. some closely related species possess male-biased, whereas other female-biased SSD (e.g. Colwell, 2000; Kratochvíl & Frynta, 2002; Székely *et al.*, 2004; Cox *et al.*, 2007). The SSD of a particular species can be attributed to various evolutionary processes such as sexual selection, divergence in reproductive roles or intersexual niche divergence (Darwin, 1871; Andersson, 1994; recently reviewed in Fairbairn *et al.*, 2007). Nevertheless, SSD exhibits one notable empiri-

cally supported macroevolutionary trend. Males seem to be more evolutionary plastic in body size, and male-biased SSD tends to increase with increasing body size among related species. As a consequence, within a taxonomic group displaying mixed SSD, often those species with female-biased SSD are on average smaller than species with male-biased SSD. This broadly, but not universally, found pattern of allometry of SSD is known as Rensch's rule (Abouheif & Fairbairn, 1997; Fairbairn, 1997; Fairbairn *et al.*, 2007 and references therein). On the other hand, Webb & Freckleton (2007) and Stephens & Wiens (2009) have recently demonstrated that patterns inconsistent with Rensch's rule are often found in lineages with female-biased SSD. Even though Rensch's rule is based on interspecific comparison, a similar allometric pattern of SSD is found intraspecifically among populations of insects and vertebrates (Fairbairn & Preziosi, 1994; Fairbairn, 2005; Young, 2005; Pylon *et al.*, 2007; Lengkeek *et al.*, 2008; but see Kraushaar & Blanckenhorn, 2002).

Webb & Freckleton (2007) alerted that Rensch's rule should be understood as the pattern of increasing SSD with body size in male-larger lineages and of decreasing

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SSD with body size in female-larger lineages. According to them, Rensch's rule should not be tested at once in lineages with mixed SSD. Instead, they recommended testing Rensch's rule separately for male-larger and female-larger species/populations within a lineage, because both these groups can overlap in body size distribution (cf. Fig. 1b in Webb & Freckleton, 2007). In such cases, allometric line fitted to pooled data can poorly reflect underlying scaling relationships within any of the groups (for an analogous situation concerning body-size correction see McCoy *et al.*, 2006). Nevertheless, in many lineages with mixed SSD, female-larger species use to be smaller than male-larger species and both groups fit well a single allometric line (e.g. Colwell, 2000; Kratochvíl & Frynta, 2002, 2007; Serrano-Meneses *et al.*, 2008). In lineages with mixed SSD meeting the earlier mentioned criteria (non-overlapping size distribution, common allometric line), using all species in a single analysis is a legitimate test of Rensch's rule.

Evolutionary causes of Rensch's rule remain largely unknown. The most prominent explanations are the sexual-selection hypothesis, the differential-plasticity hypothesis and the fecundity-driven hypothesis (Abouheif & Fairbairn, 1997; Fairbairn, 1997, 2005; Székely *et al.*, 2004; Kratochvíl & Frynta, 2007). The sexual-selection hypothesis and the fecundity-driven hypothesis assume that allometry in SSD evolves largely via genetic adaptation of SSD to local selective pressures. In contrast, the differential-plasticity hypothesis links the macroevolutionary trend in SSD to phenotypic plasticity. According to this hypothesis, allometry of SSD consistent with Rensch's rule emerges in situations where males show greater phenotypic plasticity in body size than females (Fairbairn, 2005; Fernández-Montraveta & Moya-Laraño, 2007).

Phenotypically plastic responses in body size with respect to various environmental factors such as rearing temperature have been documented in a wide taxonomic spectrum of animals. Most ectotherms exhibit a negative relationship between rearing temperature and adult body size, a pattern known as the temperature-size rule (e.g. Atkinson, 1994; Atkinson & Sibly, 1997; Angilletta, 2009). The extent to which environmental temperature differentially influences body size of each sex, and hence form the pattern of Rensch's rule, is not well understood (but see e.g. Fischer & Fiedler, 2001; Fairbairn, 2005), largely in vertebrates. Blanckenhorn *et al.* (2006) nicely combined the trend described by Rensch's rule with the latitudinal pattern in body size, which is probably imposed by geographic variation in thermal conditions. In their large-scale comparative study, the authors suggested that 'some factor that varies systematically with latitude is responsible for producing Rensch's rule among populations within species'. The suspicious factor is, of course, an ambient temperature. Nevertheless, their comparative study does not allow to estimate the

importance of thermally induced phenotypic plasticity in the observed pattern.

In the present study, we used the sexually dimorphic, male-larger gecko *Paroedura picta* (Peters, 1854) to investigate whether sex differences in the thermal sensitivity of growth and final adult body size create a pattern consistent with Rensch's rule and the temperature-size rule. As variation in adult body size and SSD develop in ontogeny via differences in duration and rate of growth (e.g. Badyaev, 2002), we carefully followed growth in experimental animals to determine which developmental stage is sensitive to environmental manipulation and potentially responsible for shaping of body size and SSD. Moreover, to explore whether environmentally induced differences are mirrored in macroevolutionary pattern of SSD, we conducted an interspecific analysis of SSD within the genus *Paroedura* Günther, 1879.

Material and methods

Studied organisms

The genus *Paroedura*, endemic to Madagascar and the Comores, is a monophyletic group of geckos from the family Gekkonidae (reviewed in Jackman *et al.*, 2008). It consists of nocturnal geckos with prominent differences in body size occupying various habitats in both mesic and xeric areas (Dixon & Kroll, 1974; Henkel *et al.*, 2000; Nussbaum & Raxworthy, 2000). Although some species became popular among herpetoculturalists, information on ecology and general biology of all species in the field is very scarce. The Madagascar ground gecko (*Paroedura picta*), one of the largest species of the genus, is slowly becoming a popular laboratory lizard model species. Recently, *P. picta* has been used in studies on sexual behaviour (Brillet, 1993), thermoregulation (Blumberg *et al.*, 2002), life history and reproductive physiology (Kratochvíl *et al.*, 2006, 2008; Kubička & Kratochvíl, 2009), and developmental biology (Noro *et al.*, 2009). Females of *P. picta* mature at several months of age. Although they lay only two (rarely just one) hard-shelled eggs per clutch, they have short interclutch intervals and are able to breed in captivity continuously (Kubička & Kratochvíl, 2009).

Thermal experiment

We mated 20 adult virgin females to 20 males, all of which were chosen at random from our large laboratory population. All females were individually placed into glass cages (30 × 30 × 20 cm) with dry substrate (sand mixed with coconut shell chippings) and a thermal gradient of 26–40 °C provided by heating cables. A shelter and *ad libitum* water and calcium powder (Vitalcalcin, Zentiva, Czech Republic, or milled cuttlebone) in small dishes were provided in each cage. Each female was

allowed to mate with her assigned male every month. We collected four two-egged clutches per female, the cages were inspected for eggs daily. We weighed the eggs to the nearest 0.001 g and distributed them based on a predefined balanced design into one of three rearing chambers with constant temperature (± 0.3 °C) and a 12 : 12 h L : D cycle. The environmental temperatures in chambers were 24, 27 and 30 °C, respectively. All conditions were otherwise the same across chambers. The chosen temperatures are physiologically relevant and were selected according to our previous experience with incubating eggs of *P. picta* at these temperatures (see also Blumberg *et al.*, 2002). Hatchlings not older than 24 h were weighed (to the nearest 0.001 g), and their snout-to-vent lengths (SVL) were measured with a digital caliper to the nearest 0.01 mm. Hatchlings were then placed individually back to their specific chamber in an opaque plastic cage (20 × 20 × 15 cm) with a sand substrate, a shelter and a water dish. Water supplemented with calcium was provided *ad libitum*. Twice per month, water was enriched with vitamin E, A and D₃ (Combinol E and Combinol A + D₃; IVAX Pharmaceuticals, Opava, Czech Republic). Lizards were fed with live crickets (*Gryllus assimilis*) dusted with vitamins and minerals (Roboran H, Univit, Czech Republic) twice each week. We provided a superabundance of crickets during each feeding to ensure that lizards fed to satiety. All unfed crickets were removed the following day. Geckos were weighed before and after each feeding, and SVL was measured every three weeks. When females reached a body mass of 6 g, they were randomly assigned to males from the same temperature. The sire was always a male unrelated to the dam, with body mass larger than 4 g and prominent secondary sexual traits such as enlarged hemipenial sacs and active abdominal scent glands. Females were allowed to mate with their assigned male every month (every 14 days until the first oviposition), which seems sufficient because of long sperm storage (pers. observation). We continuously checked growth curves of all individuals and terminated the experiment and measured final SVL when we observed conspicuous cessation of growth in a majority of individuals at a given temperature. Because growth is dependent on physiological time set by temperature, the duration of experiment in astronomical time differed among temperatures.

Ontogeny of SSD in *P. picta* at different temperatures

Evaluation of body size and SSD among adults in animals with potentially indeterminate growth can be highly biased by age structure of a given sample and their respective position on growth curve or by variation in shape of growth curves in different environments (Stamps & Krishnan, 1997). One solution is to follow growth trajectories up to the cessation or significant deceleration of body size increase and to compare body size in sexes and animals reared at different conditions

after this point (e.g. Kratochvíl & Frynta, 2002, 2007). Therefore, for comparison of body sizes and SSD in *P. picta* at three temperatures, we used values of final SVL reached by animals at the termination of experiment at each temperature. We calculated asymptotic SVL for each individual by fitting the asymptotic growth curve, specifically the logistic-by-length model (Schoener & Schoener, 1978; Powell & Russell, 1985), using Levenberg-Marquart computational algorithm. Measured final SVL was highly correlated with asymptotic SVL.

Next, we compared SVL at the age of the first mating and final SVL among sex-temperature categories using a GLM full-factorial ANOVA model with sex and temperature as factors. We used Tukey HSD test to detect categories with significantly different SVL. Altogether, we followed the growth curves in 103 animals (32, 35 and 36 individuals at 24, 27 and 30 °C, respectively). Eight animals died after maturation and were thus not included in the analyses of final body size.

Interspecific pattern of SSD

Species included in the interspecific comparison of SSD were *P. androyensis* (Grandidier, 1867), *P. ibityensis* Rösler and Krüger, 1998, *P. karstophila* Nussbaum & Raxworthy, 2000, *P. picta*, *P. tanjaka* Nussbaum & Raxworthy, 2000 and *P. vazimba* Nussbaum & Raxworthy, 2000. We measured SVL of adult captive bred individuals in *P. androyensis*, *P. ibityensis* and *P. vazimba* with a digital caliper to the nearest 0.01 mm. For *P. picta*, we used data on final SVL of all the animals from the earlier described experiment. We added literature data from Nussbaum & Raxworthy (2000) for the other two species (*P. tanjaka* and *P. karstophila*) with sample size larger than 5 individuals per sex (Table 1). In these two species, we included only the data taken from adult specimens in a single locality (locality Namoroka). The original article includes limited data on SVL of individuals from other localities as well, but the authors noted differences in body size and even scalation among individuals from different localities. SSD within individual species was tested using one-way GLM ANOVA.

The consistence of the macroevolutionary pattern of SSD among species of the genus *Paroedura* with Rensch's rule was tested by departure of the log (male size) against log (female size) relationship from isometry (expected isometric slope = 1; Fairbairn, 1997). The allometric slope was assessed by the Model II regression model – reduced major axis regression (RMA). As the estimation of interspecific relationship can be biased by intraspecific variation in body size, following Webb & Freckleton (2007), we applied also Simulation-Extrapolation approach (SIMEX) estimating slope of a simple regression as implemented in R (Lederer & Küchenhoff, 2006).

Species traits are not independent and can be shared from a common ancestor. Therefore, we carried out the

Table 1 Body size in males and females and the test of sexual size dimorphism within species of the genus *Paroedura*. The data for *P. tanjaka* and *P. karstophila* were taken from Nussbaum & Raxworthy (2000). The data for *P. picta* are calculated as means of final SVL from all three experimental temperatures. Means \pm SE are given.

Species	<i>n</i> (males, females)	Larger sex	Male SVL	Female SVL	F	<i>P</i>
<i>Paroedura androyensis</i>	6, 7	F	37.28 \pm 0.640	40.55 \pm 0.493	16.98	0.002
<i>Paroedura vazimba</i>	24, 10	F	42.66 \pm 0.255	46.56 \pm 0.698	43.03	< 0.00001
<i>Paroedura karstophila</i>	19, 12	–	45.84 \pm 0.548	47.42 \pm 0.484	3.96	0.056
<i>Paroedura ibityensis</i>	6, 22	M	55.38 \pm 0.494	53.11 \pm 0.323	11.39	0.002
<i>Paroedura tanjaka</i>	14, 16	–	76.86 \pm 1.370	76.19 \pm 1.389	0.12	0.735
<i>Paroedura picta</i>	37, 58	M	92.38 \pm 1.286	82.01 \pm 0.587	67.63	< 0.00001

phylogenetically adjusted analysis using the independent contrast method (Felsenstein, 1985) employed in COMPARE vers. 4.6b (Martins, 2004). We used the topology and branch length of the phylogenetic hypothesis of the genus *Paroedura* based on Fig. 1 in Jackman *et al.* (2008). With the exception of the phylogenetically adjusted analysis and SIMEX, all computations were performed in Statistica 6.0 (StatSoft, Inc, 2001).

Results

At each temperature, males and females did not differ in SVL at the age of the earliest female mating, i.e. at the age when the first female reached body mass above 6 g (GLM ANOVA, sex: $F = 0.15$, $P = 0.69$, sex-temperature interaction: $F = 1.87$, $P = 0.16$; $n = 103$). This indicates that SSD develops later in ontogeny. Note that growth trajectories of males and females did not significantly depart from each other for at least nine consecutive weeks after the first mating (Fig. 1). The growth of both sexes of *P. picta* in our experiment was essentially determinate (Fig. 1). The mean difference between final SVL and asymptotic SVL estimated for each individual was only 3.6%. Although males reached larger final SVL than females at all three temperatures, SSD at the end of experiment was highly temperature-dependent (GLM ANOVA, sex-temperature interaction: $F = 3.41$, $P = 0.04$, $n = 95$; Figs 1 and 2). Females from 24 °C were significantly smaller than females from 27 and 30 °C. The largest SSD developed at the temperature 27 °C, where males reached significantly larger final SVL than males at 24 and 30 °C (Tukey HSD test). Such pattern is consistent with Rensch's rule.

Mean SVL values and results of GLM one-way ANOVA comparing male and female size within particular *Paroedura* species are shown in Table 1. The genus contains both male-larger species (*P. picta*, *P. ibityensis*) and female-larger species (*P. vazimba*, *P. androyensis*). In *P. karstophila* and *P. tanjaka*, we did not detect significant SSD. Within the genus, female-larger species are much smaller than male-larger species. Although it is difficult to decide in data set with such a small number of species, it seems that both female-larger and male-larger species of the genus *Paroedura* fit a single relationship between

female and male size (see Fig. 3). Pooling all species into a single analysis testing consistency with Rensch's rule is thus justifiable (cf. Webb & Freckleton, 2007). We found positive allometry between log male and log female mean SVL. The slope of RMA regression was 1.24 ± 0.08 SE, which is significantly different from isometry (slope = 1; Fig. 3). The SIMEX analysis confirmed this result (slope 1.24 ± 0.09 SE). The independent contrasts analysis gave essentially the same result: the slope (1.19 ± 0.09 SE) stayed significantly larger than 1. This positive allometry confirms that the macroevolutionary pattern of SSD within the genus *Paroedura* is consistent with Rensch's rule as well.

Discussion

Reptiles as well as fish, amphibians and many invertebrates exhibit indeterminate growth, i.e. they grow continuously after maturation, although their growth slows down with age (e.g. Kozłowski, 1996; Stamps & Krishnan, 1997; Charnov *et al.*, 2001). Our results show that *P. picta* grows intensively after maturation, however, in contrast to some other indeterminate growers (e.g. many fish, West *et al.*, 2001), this species reached final SVL closely approaching the asymptotic SVL at a relatively young age. Therefore, the final SVL of *P. picta* obtained in our experiment is a good measure of body size and is appropriate for comparisons of the thermal dependence of body size and SSD. We confirmed that final SVL is influenced by environmental temperature. However, the pattern does not conform to the temperature-size rule (cf. Atkinson & Sibly, 1997; Angilletta, 2009). In contrast to the unidirectional relationship between body size and temperature expected under this rule, our experimental animals (especially males) reached the largest SVL at the intermediate temperature of 27 °C, which is probably the optimal temperature for this species. Both lower and higher temperatures affected final SVL negatively.

Male-biased SSD developed at all three temperatures only later in ontogeny because of a decrease in growth rate of females compared to males. We detected SSD neither at the time of the first mating nor for at least several weeks after the first mating, after females had

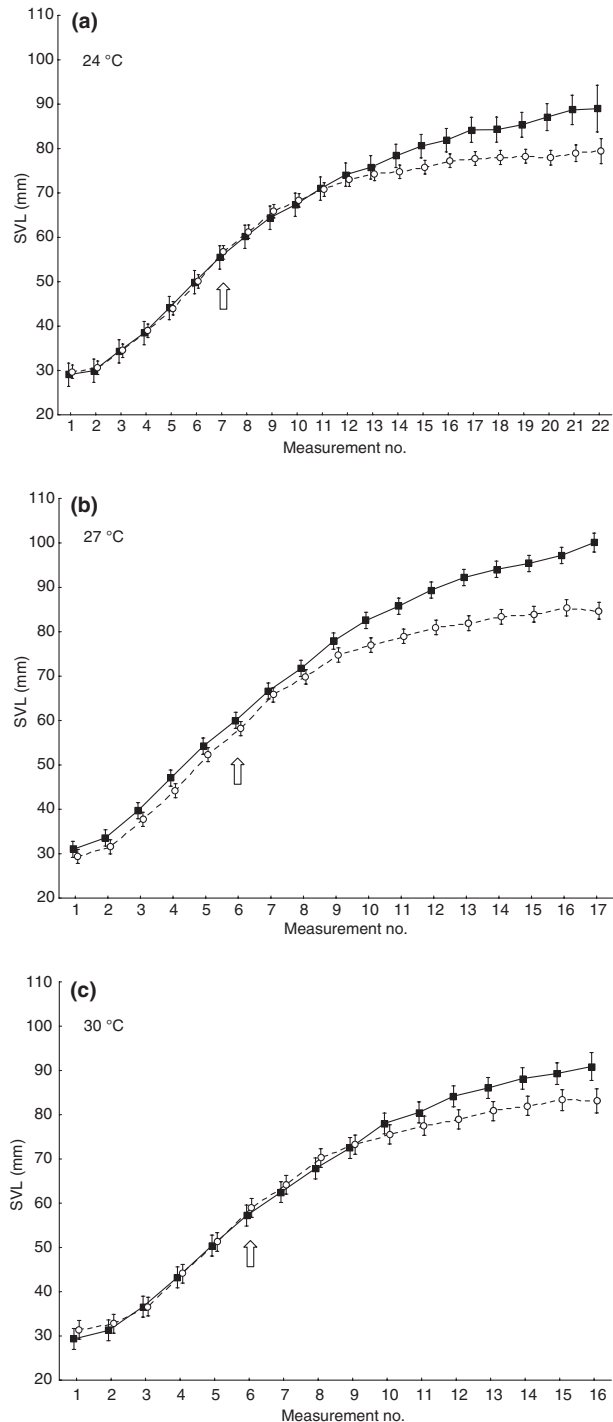


Fig. 1 Growth trajectories of males (squares) and females (circles) of *Paroedura picta* at 24 (a), 27 (b) and 30 °C (c). Means and 95% confidence intervals of SVL for each age cohort is plotted, the intervals between two subsequent measurements are three weeks. Arrows indicate the earliest female mating, i.e. the age of reaching body mass above 6 g by the first female. Growth was followed in eight males and 24 females at 24 °C, 15 males and 20 females at 27 °C and 16 males and 20 females at 30 °C.

already laid clutches. The long-time lag between the onset of female reproduction and the emergence of SSD suggests that high investment into clutches in females is not the only factor responsible for ontogeny of SSD. Similarly, experimental inhibition of female reproduction alone can explain only about one-third of sexual differences in body size in another lizard, *Sceloporus jarrovi* (Cox, 2006). These observations indicate that protracted growth in adult lizard female cannot be fully attributed to energy allocation to reproduction but that it is controlled by another mechanism as well. In addition, females in *P. picta* on low and high food supply showed equal investment into structural growth but highly different allocation to reproduction and fat reserves (Kubička & Kratochvíl, 2009), further supporting relatively low plasticity in female growth.

Sexually dimorphic reaction norms for final SVL indicate the existence of different proximate mechanisms controlling body size in males vs. females. Consequently, SSD in *P. picta* is temperature-dependent. At the coldest environment, the animals were smallest with males being only slightly larger than females. The largest intersexual size variation was observed at the intermediate temperature, where males were largest and females reached the same size as at the highest temperature. Females tend to be more canalized in final SVL across different environmental conditions than males (see also e.g. Fischer & Fiedler, 2001). The intraspecific pattern in SSD induced by thermal variation hence corresponds to Rensch's rule, although the body size pattern itself does not follow temperature-size rule (Figs 2 and 3).

Male to female ratios in SVL among species of the genus *Paroedura* and among groups of *P. picta* from three different temperatures range from 0.92 to 1.15. In total,

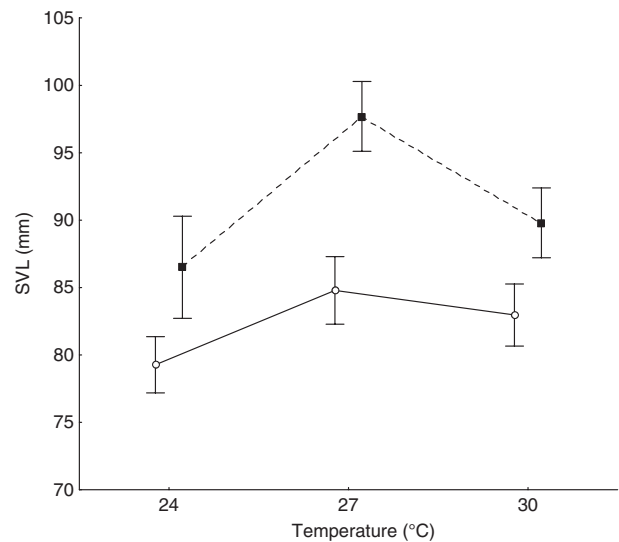


Fig. 2 Means and 95% confidence intervals of final SVL of males (squares) and females (circles) of *Paroedura picta* at three experimental temperatures.

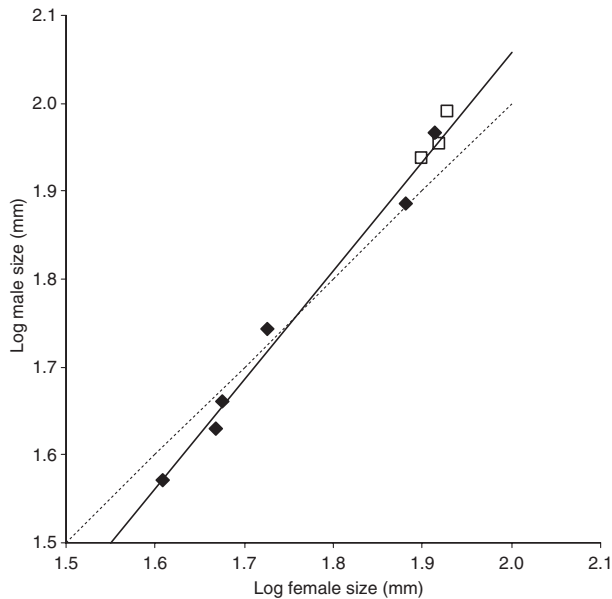


Fig. 3 Mean male size (SVL in mm) plotted against mean female size for the geckos of the genus *Paroedura* (solid squares). The solid line is the reduced major axis fitted to these data. Its slope is significantly greater than 1 which shows the consistency with Rensch's rule. For the sake of illustration, mean final SVL of *P. picta* from three experimental temperatures are plotted as well (open squares). The dashed line represents 1 : 1 relationship.

29% of this variability is covered by the differences in SSD induced by experimental temperatures in a studied species. The differential-plasticity hypothesis (Fairbairn, 2005) proposes that macroevolutionary trends in SSD conforming to Rensch's rule can be an extension of greater phenotypic plasticity in males in comparison to females. The similarity of the intraspecific pattern in SSD induced by thermal variation in *P. picta* and the interspecific pattern in the genus *Paroedura* (Figs 2 and 3) strongly supports this hypothesis. Therefore, we conclude that the interspecific changes in SSD can follow the same trend as those induced by environmental variation. Phenotypic plasticity thus might be an important component of evolutionary shaping of SSD in a process generally known as the Baldwin effect (cf. e.g. Hall, 2001; West-Eberhard, 2003).

On the other hand, we cannot conclude unambiguously that the macroevolutionary trend largely extends the pattern induced by environmental conditions. The causality is not clear and could be opposite to that expected under the Baldwin effect. The substantial increase in body size in male-larger *P. picta* is an evolutionary novelty of this species, as the closely related species are much smaller (Jackman *et al.*, 2008). The sister species *P. androyensis* is even the smallest species of the genus, and it possesses female-biased SSD. The pattern in body size and connected changes in SSD in *P. picta* reared in different environment hence could

reflect coupled macroevolutionary changes in these traits during evolutionary history of the lineage. The phylogenetic comparison of phenotypic plasticity in body size and SSD across species of the genus would be necessary to reconstruct the sequence of evolutionary changes and to evaluate these two alternative scenarios.

In any case, it is notable that we can often observe the same direction of variation attributed to phenotypic plasticity and to evolutionary, most likely genetically controlled, changes among populations or species (West-Eberhard, 2003; Crispo, 2007). In addition to Rensch's rule (Fernández-Montraveta & Moya-Laraño, 2007; this study), we can find the same situation in other biogeographic or macroevolutionary 'rules' and ecomorphological patterns as well. Biogeographic trend in body size known as Bergmann's rule (larger body size in populations from higher latitudes or altitudes facing lower environmental temperatures) is mirrored by phenotypic plasticity induced by thermal variation (Van Voorhies, 1996; Angilletta, 2009). Similarly, variation in vertebrae number induced by rearing temperatures in medaka killifish agrees with the geographical tendency for fish from higher latitudes to have more vertebrae (so called Jordan's rule; Yamahira & Nishida, 2009). As another example, phenotypically plastic response in limb dimensions to substrate width in *Anolis* lizards parallels evolution of ecomorphs resulting from niche partitioning and the adaptation to various branch diameters (Losos *et al.*, 1997, 2000). Likewise, the thermal influence on developmental rate and accompanied changes in body shape in spadefoot toads mirror coupled interspecific changes in both these traits (Gomez-Mestre & Buchholz, 2006). In the future, it will be fascinating to know how general is this pattern, and whether and in which way the conformation of macroevolutionary trends and environmentally induced differences among individuals reflects architecture of living organisms.

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