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A test of Rensch's rule in dwarf chameleons (*Bradypodion* spp.), a group with female-biased sexual size dimorphism

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Abstract Rensch's rule describes a pattern of allometry in sexual size dimorphism (SSD): when males are the larger sex (male-biased SSD), SSD increases with increasing body size, and when females are the larger sex (female-biased SSD), SSD decreases with increasing body size. While this expectation generally holds for taxa with male-biased or mixed SSD, examples of allometry for SSD consistent with Rensch's rule in groups with primarily female-biased SSD are remarkably rare. Here, I show that the majority of dwarf chameleons (*Bradypodion* spp.) have female-biased SSD. In accordance with Rensch's rule, the group exhibits an allometric slope of log(female size) on log(male size) less than one, although statistical significance is dependent on the phylogenetic comparative method used. In this system, this pattern is likely due to natural selection on both male and female body size, combined with fecundity selection on female body size. In addition to quantifying SSD and testing Rensch's rule in dwarf chameleons, I discuss reasons why Rensch's rule may only rarely apply to taxa with female-biased SSD.

Keywords Allometry · Allometric scaling · Body size · Comparative method · Fecundity selection · Natural selection · Phylogenetic · Sexual selection

Rensch ([1960](#)) observed that in many taxa, sexual size dimorphism (SSD) varies with body size. The pattern now known as Rensch's rule describes this allometry of SSD: when males are the larger sex, SSD increases with body size (hyperallometry) but when

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females are the larger sex, SSD decreases with increasing body size (hypoallometry; Fairbairn 1997). This pattern of allometry for SSD, known as Rensch's rule, has received substantial theoretical and empirical attention because both the generality of the pattern itself, and the processes generating it, remain controversial (Fairbairn 1997, 2005; Colwell 2000; Szekely et al. 2004). Using modern phylogenetic comparative methods, Abouheif and Fairbairn (1997) tested Rensch's rule within 40 taxonomically diverse groups and showed that the pattern generally holds for taxa with male-biased SSD. Several studies have also shown that Rensch's rule generally holds for taxa that exhibit mixed SSD (both male-biased and female-biased, Abouheif and Fairbairn 1997; Colwell 2000; Kratochvil and Frynta 2002; Szekely et al. 2004; Young 2005; Raihani et al. 2006). In contrast, most tests of Rensch's rule in taxa with exclusively female-biased SSD have failed to confirm the pattern (Abouheif and Fairbairn 1997; Jannot and Kerans 2003; Tubaro and Bertelli 2003; Blanckenhorn et al. 2007), waterstriders and some flies being notable exceptions (Abouheif and Fairbairn 1997; Blanckenhorn et al. 2007). Thus, there is currently little empirical evidence (based on statistically rigorous phylogenetic comparative methods) of allometry for SSD consistent with Rensch's rule in taxa with female-biased SSD. This is especially true for vertebrates, despite this form of SSD being common among many fish, reptiles, amphibians, and some birds (Fairbairn 1997).

For taxa with male-biased or mixed SSD, Szekely et al. (2004) proposed that sexual selection on male body size in conjunction with weaker correlational selection on females may provide a general explanation for Rensch's rule. However, for taxa with female-biased SSD, no general explanation has been proposed and several types of explanation are plausible. First, sexual selection may favor small male size for increased mobility or agility (Zamudio 1998; Szekely et al. 2004) with weaker correlational selection on female size. The correlated evolution of female size may also be influenced by opposing fecundity selection on females (Shine 1989; Fairbairn 1997). In addition, in sex-role reversed species where females compete for mates, sexual selection may favor larger female size (Fairbairn 1997; Szekely et al. 2004). Thus, under these scenarios, hypoallometry (increasing SSD with decreasing body size) results from directional sexual selection for smaller male size, combined with weaker correlated selection and/or opposing directional fecundity or sexual selection on female size. Natural selection can also act differentially on the two sexes, with consequences for the evolution of SSD (Shine 1989; Fairbairn 1997; Butler et al. 2000). For example, resource availability may influence the body size of one sex to a greater degree than the other when relative energy expenditure on mating and reproduction (including mate searching and territorial defense) is greater for that sex (Colwell 2000; Vitousek et al. 2007). Alternatively, ecological factors may select for small body size in both sexes but female body size may be constrained by fecundity selection. In sum, there are multiple ways in which the interaction between sexual selection, natural selection and fecundity selection may interact to produce allometric scaling in SSD.

Here, I examine the scaling relationship of SSD in dwarf chameleons (*Bradypodion* spp.). Specifically, I tested the allometric relationship predicted by Rensch's rule: that the slope of log(female size) on log(male size) should be less than one (Fairbairn 1997). One species of dwarf chameleon has been shown to have female biased SSD (Burrage 1973; Stuart-Fox et al. 2006) but SSD has not been quantified in other members of the genus. In addition to quantifying SSD and testing Rensch's rule in dwarf chameleons, I discuss reasons why Rensch's rule may only rarely apply to taxa with female-biased SSD.

Materials and methods

Study system

Dwarf chameleons (Genus *Bradypodion sensu stricto*) are small [50–110 mm snout-vent length (SVL)], viviparous lizards, endemic to southern Africa (Branch 1998). Fifteen species are currently recognized, although based on recent phylogenetic work (Tolley et al. 2004, 2006), several others are in the process of being described (C. Tilbury, K. A. Tolley, W. R. Branch, personal communication). Dwarf chameleons occur in a wide range of habitats, including montane and lowland rainforest, grasslands, montane and lowland Mediterranean heath and shrubby thicket (Branch 1998). I collected data for 21 populations (Table 1), which include all currently described species except *B. karooicum*, which is a local variant of *B. ventrale* (Tolley et al. 2004). In addition to described species, the 21 populations include three divergent lineages (*B.* sp. Dhlinza, *B.* sp. Ngome, *B.* sp. Swartberg) identified in Tolley et al. (2004, currently being described), as well as four divergent lineages identified by recent phylogeographic work on the *B. transvaalense* complex (T. Townsend, unpublished data), which previous morphological work also suggested comprises several distinct species (Jacobsen 1989). Due to the taxonomic state of flux in this group, I refer to the 21 populations I studied as 'populations' rather than species or taxa. Changes in taxonomic designation, however, will not influence the outcome of this study as the molecular phylogeny of the 21 populations is robust and well-supported (see Stuart-Fox and Moussalli 2007; Stuart-Fox et al. 2007).

Testing Rensch's rule

I captured as many sexually mature adults as possible (mean ± SD = 14.9 ± 8.3 of each sex, Table 1) by hand from each of 21 populations (represented by a single locality within a radius of 20 km). I measured SVL to the nearest mm and released all individuals at their site of capture. I tested Rensch's rule using the average body size of the largest third of individuals of each sex because most lizards follow asymptotic growth curves (see Butler et al. 2000).

To account for phylogenetic non-independence among the 21 taxa, I used phylogenetic generalized least squares (PGLS, Martins and Hansen 1997) to examine the allometric relationship between male and female body size [regression of log(female SVL) on log(male SVL)]. PGLS estimates a parameter (α) for each correlation or regression that represents a measure of phylogenetic constraint or inertia (Hansen 1997; Martins et al. 2002). When the parameter α is set to 0, PGLS produces results identical to Felsenstein's independent contrasts (FIC, Felsenstein 1985) and when α is large (15.5 +), it is equivalent to a non-phylogenetic or cross-species analysis (TIPS) (Martins et al. 2002, 2004). I chose PGLS, as implemented in Compare 4.06 (Martins 2004), because it has been shown to perform consistently well under different evolutionary assumptions (Martins et al. 2002). Comparative analyses were based on a phylogeny with branch lengths (Fig. 1), derived from Bayesian analysis of mitochondrial 16S and ND2 sequences from Genbank (Tolley et al. 2004, 2006) with four additional ND2 sequences provided by Ted Townsend (unpublished data) for the four populations of *B. transvaalense* (see Stuart-Fox and Moussalli 2007; Stuart-Fox et al. 2007).

The majority of previous tests of Rensch's rule have used reduced major axis (RMA) regression of Felsenstein's independent contrasts. As this method may result in differences

Table 1 Sampling localities, sample sizes, greatest one third body size and standard errors (SVL ± SE) for each population and results of one-way ANOVAs testing for a significant difference in body size between the sexes

Population	Locality	Female N	Greatest 1/3 SVL ± SE	Max SVL	Male N	Greatest 1/3 SVL ± SE	Max SVL	F	P
B. sp.	Swartberg Pass, WC	14	78.3 ± 2.3	81.2	27	70 ± 3.1	74.0	31.26	<0.0001
B. caffrum	Port St Johns, EC	12	68 ± 1.0	70.8	15	70 ± 1.2	73.5	1.41	0.27
B. damaranum	George to Knysna, WC	9	72.6 ± 0.7	74	27	78.1 ± 1.0	82.3	9.18	0.01
B. dracomontanum	Royal Natal NP, KZN	19	79.0 ± 1.0	81.5	16	71.4 ± 1.2	76	24.07	0.001
B. gutterale	Anysberg NR, WC	10	80.1 ± 0.8	81	12	83.4 ± 0.7	84.5	10.16	0.02
B. kentanicum	Vicinity of Kentani, EC	11	66.2 ± 0.5	67.3	8	56.8 ± 1.6	59.9	36.21	0.002
B. melanocephalum	Kennethstainbank NR, KZN	17	62.4 ± 1.5	68.3	19	53.0 ± 1.0	57.2	28.77	0.0003
B. nemorale	Nkandla Forest, KZN	5	83.1 ± 4.4	87.5	8	66.7 ± 1.5	68.3	19.94	0.02
B. occidentale	Paternoster, WC	11	91.2 ± 1.7	96.4	20	86.0 ± 2.1	91	3.76	0.09
B. pumilum	Stellenbosch, WC	32	92.3 ± 1.6	103.6	51	85.1 ± 1.4	102.1	10.7	0.003
B. pumilum	Vogelgat NR, WC	5	69.3 ± 0.5	69.9	10	64.9 ± 0.6	66.1	25.12	0.015
B. setaroi	St Lucia, KZN	21	66.0 ± 0.8	70.2	10	60.7 ± 1.1	63.7	17.28	0.0025
B. sp.	Dhlinza Forest, KZN	18	65.9 ± 0.6	67	9	58.5 ± 1.1	60.4	40.25	0.0004
B. sp.	Ngome Forest Reserve, KZN	11	77.1 ± 2.5	83.8	20	72.6 ± 0.5	74.3	5.59	0.04
B. taeniabronchum	Lady's Slipper, EC	16	65.1 ± 1.4	70.7	17	56.7 ± 0.8	59.3	31.63	0.0003
B. thamnobates	Bulwer, KZN	11	89.5 ± 1.1	91.6	11	78.0 ± 0.6	79.0	65.8	0.0002
B. transvaalense	Barberton, MP	15	74.8 ± 1.0	76.7	6	71.1 ± 2.2	73.3	3.2	0.13
B. transvaalense	Tullach Moor NR, MP	9	85.7 ± 0.2	85.9	5	78.0 ± 0.3	78.3	570.9	0.0002
B. transvaalense	Graskop area, MP	15	74.1 ± 0.6	75.9	10	77.7 ± 1.6	80.6	4.69	0.07
B. transvaalense	Woodbush Forest, LP	14	77.6 ± 1.7	82.4	24	73.0 ± 0.6	76.4	9.19	0.01
B. ventrale	Grahamstown area, EC	12	95.2 ± 2.6	102.0	15	81.6 ± 1.3	85.9	26.96	0.001

Abbreviations for provinces: *EC* Eastern Cape, *WC* Western Cape, *MP* Mpumalanga, *LP* Limpopo, *KZN* KwaZulu Natal. *NR* Nature Reserve and *NP* National Park

Fig. 1 Phylogenetic
relationships of the 21 lineages of
dwarf chameleon based on
mitochondrial 16S and ND2
sequences from Genbank (Tolley
et al. 2004, 2006) with four
additional ND2 sequences from
Ted Townsend (unpublished
data) for the four populations of
'*B. transvaalense.*' Divergent
lineages currently being
described are denoted as *B.* sp.
followed by the locality
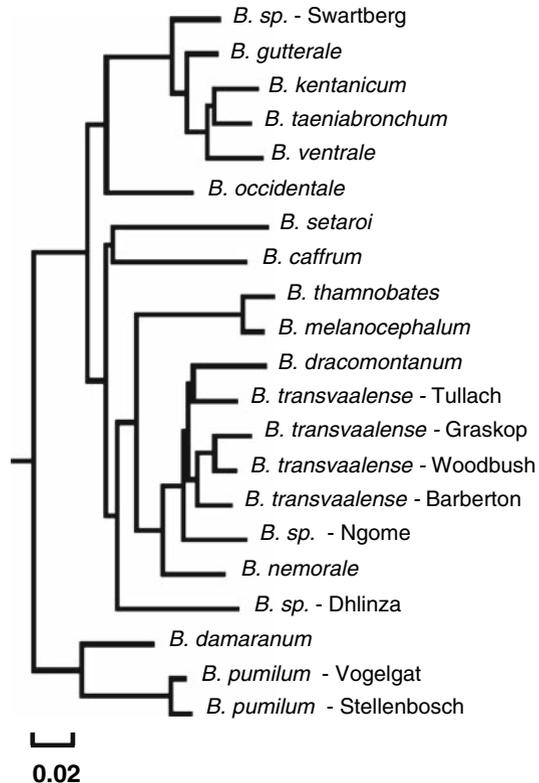
Results

Males were significantly larger than females in two populations (*B. damaranum* and *B. gutterale*). The sexes did not differ significantly in mean body size for four of the 21 populations (Table 1). In three of these four populations (*B. caffrum*, *B. transvaalense* from Barberton and *B. occidentale*), however, maximum body size was greater for females (Table 1). For the remaining fifteen populations, females were significantly larger than males and attained a greater maximum body size ($P < 0.05$). Thus, dwarf chameleons show female-biased or no SSD for the great majority of species.

Dwarf chameleons exhibited some evidence for hypoallometry, as predicted by Rensch's rule for species with female-biased SSD. The slope of the phylogenetic generalized least squares regression of log(female size) on log(male size) was significantly less than one ($r^2 = 72.6$, slope = 0.76, 95% CI = 0.54 - 0.97), but this difference was not statistically significant for analyses using FIC RMA regression ($r^2 = 83.5$, slope = 0.93, 95% CI = 0.73 - 1.13). The maximum likelihood estimate of α using PGLS was the maximum value of 15.5, indicating little phylogenetic constraint on the evolution of SSD. Because α

Fig. 2 Relationship between log male size and log female size (greatest one third SVL, raw data) showing the slope <1 (*solid line*), as expected under Rensch's rule. *Dashed line* indicates no SSD and a slope of one. Most points fall above the *dashed line*, indicating female-biased SSD
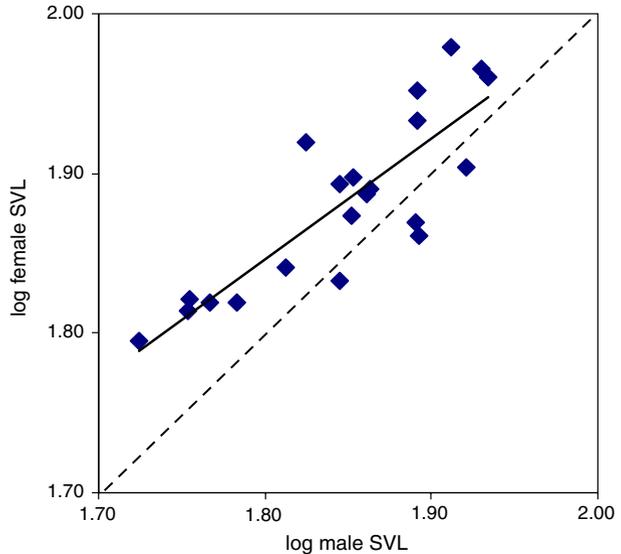
was large, the allometric slope was also significantly less than one under TIPS (non-phylogenetic analysis; $r^2 = 72.0$, slope $= 0.75$, 95%, CI $= 0.53 - 0.97$; Fig. 2).

Discussion

Results of this study show that dwarf chameleons are a taxon with predominantly female-biased SSD; however, evidence supporting Rensch's rule is mixed. The slope of log(female size) on log(male size) was significantly less than one under PGLS and TIPS, but not FIC RMA. Simulation studies have shown that when the evolutionary assumptions of FIC are violated (as when α is large), FIC performs poorly, biasing estimates in the direction of variance-generating Brownian motion forces, thereby leading to inflated type I error rates (Diaz-Uriarte and Garland 1996; Martins et al. 2002). In other words, FIC may be excessively conservative. In contrast, PGLS performs consistently well under different evolutionary assumptions (Martins et al. 2002). Overall, results are suggestive of weak allometry for SSD consistent with Rensch's rule. Rigorous tests of causes for allometry for SSD exist for few taxa (but see Blanckenhorn et al. 2007), but most available evidence supports the view that sexual selection on male body size is an important contributing factor (Szekely et al. 2004; but see Fairbairn 2005). This is unlikely to be the case for dwarf chameleons. In most lizards, the primary mechanism of sexual selection is male-male competition (Olsson and Madsen 1995). However, a previous study found no evidence of intra-sexual selection on male body size in one dwarf chameleon species, *B. pumilum* (Stuart-Fox et al. 2006). In contrast, females use aggressive rejection displays to discourage persistent, courting males (Stuart-Fox and Whiting 2005), and are also aggressive towards other females. This suggests that sexual selection may act directly on female body size, although this hypothesis requires experimental verification.

Sexual selection on female body size alone, however, is unlikely to explain allometry for SSD consistent with Rench's rule in dwarf chameleons. For taxa with female-biased SSD, hypoallometry occurs because of greater variance in male than female body size,

suggesting that variation in SSD has occurred primarily through changes in male size (see Zamudio 1998). If sexual selection on female size (in conjunction with correlated evolution of body size between the sexes) cannot explain Rensch's rule, this suggests that fecundity and/or natural selection are likely to play a role. In dwarf chameleons, as in many other taxa, larger females have more offspring (Burrage 1973) but beyond this, too little is known about reproduction in dwarf chameleons to test the inter-specific relationship between fecundity and body size or SSD. However, there is evidence that natural selection acts directly on body size in dwarf chameleons. Body size of both sexes is significantly related to habitat structure (Stuart-Fox and Moussalli 2007). Both sexes are smaller in habitats with higher density of perches such as grasslands and Mediterranean heaths characterized by short, dense shrubs and the slope of this relationship is similar in the two sexes (Stuart-Fox and Moussalli 2007). However, only males are relatively larger in more forested habitats than more open habitats, resulting in a positive relationship between SSD and habitat openness (Stuart-Fox and Moussalli 2007). Thus, in this system, male size may be driven primarily by ecological factors but the correlated evolution of female body size is likely to also be influenced by fecundity selection and/or sexual selection, resulting in hypoallometry for SSD consistent with Rensch's rule.

Although results of this study are suggestive of allometry for SSD, confidence intervals were large and statistical significance was dependent on the phylogenetic comparative method used. In dwarf chameleons, a genus with relatively few species in comparison to other genera of chameleons (Nečas 2001), females are only slightly larger than males and several species do not appear to be sexually size dimorphic. This may explain why the pattern of allometry for SSD was relatively weak in this group. Furthermore, patterns of allometry are dependent on scale (Fairbairn 1997). Some genera of chameleons show female biased SSD (e.g., *Bradypodion*, *Rhampholeon* and *Brookesia*; Nečas 2001), while others show strong male-biased SSD (e.g., *Chameleo* and *Furcifer*; Nečas 2001). Thus, at a broader scale, chameleons show mixed SSD and at this scale, may show stronger patterns of allometry for SSD.

Regardless of scale, however, patterns of allometry for SSD consistent with Rensch's rule are scarce in taxa with female-biased SSD. Why might this be the case? For taxa with male-biased or mixed SSD, sexual selection on male body size in conjunction with weaker correlational selection on females has been proposed as a general explanation for Rensch's rule (Szekely et al. 2004). However, for taxa with female-biased SSD, the processes contributing to the evolution of SSD may be more diverse. For example many birds with female-biased SSD exhibit sex role reversal (discussed in Tubaro and Bertelli 2003), with competition among females for access to mates, whereas most non-avian reptiles with female-biased SSD do not show sex role reversal because there is no parental care. In other systems, female biased SSD may be the result of sexual selection on males rather than females if smaller males have an advantage in agility or scramble competition (Zamudio 1998; Szekely et al. 2004). Natural selection on body size and its influence on the evolution of SSD may also be highly system-specific. For instance, allometry for SSD in hummingbirds and flower mites appears to be influenced by the resource (nectar) productivity of flowers used by both taxa, in conjunction with the relative reproductive costs for males and females (Colwell 2000). Thus, while the evolution of male-biased SSD may be driven primarily by sexual selection, the evolution of female-biased SSD appears to be driven by a more diverse and complex range of selective processes. This may explain why consistent patterns of allometry for SSD may be the exception rather than the rule when females are the larger sex.

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