



Does ‘gliding while gravid’ explain Rensch’s rule in flying lizards?

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Among species with sexual size dimorphism (SSD), taxa in which males are the larger sex have increasing SSD with increasing body size, whereas in taxa in which females are the larger sex, SSD decreases with body size: Rensch’s rule. We show in flying lizards, a clade of mostly female-larger species, that SSD increases with body size, a pattern similar to that in clades with male-biased SSD or more evenly mixed SSD. The observed pattern in *Draco* appears due to SSD increasing with evolutionary changes in male body size; specifically divergence in body size among species that are in sympatric congeneric assemblages. We suggest that increasing body size, resulting in decreased gliding performance, reduces the relative gliding cost of gravity in females, and switches sexual selection in males away from a small-male, gliding advantage and toward selection on large size and fighting ability as seen in many other lizards. Thus, selection for large females is likely greater than selection for large males at the smaller end of the body size continuum, whereas this relationship reverses for species at the larger end of the continuum. © 2014 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2014, **113**, 270–282.

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INTRODUCTION

Sexual size dimorphism (SSD) is a widespread phenomenon among animal taxa that has remained of interest to evolutionary biologists since Darwin (1871), despite extensive research on the topic (Andersson, 1994; Fairbairn, Blanckenhorn & Székely, 2007). Even though a multitude of selective forces operating on males and females across diverse clades challenge our ability to explain specific patterns of SSD, there are consistent macroecological patterns of SSD in many higher taxa (Fairbairn *et al.*, 2007). Of particular interest to evolutionary biologists is Rensch’s rule, which leads to both SSD increasing with body size in taxa in which males are the larger sex but decreasing with body size in taxa in which females are the larger sex (Rensch, 1950, 1960; Abouheif & Fairbairn, 1997; Fairbairn, 1997). Sexual

selection on males typically explains the former pattern, whereas a myriad of alternative hypothesized selection pressures may explain the latter, including female fecundity selection, sexual selection for larger females, or sexual selection for small males, among others (Colwell, 2000; Székely, Freckleton & Reynolds, 2004; Dale *et al.*, 2007; Stuart-Fox, 2009; Pincheira-Donoso & Tregenza, 2011). Rensch’s rule has been documented in a wide variety of distantly related taxa, ranging from insects (Blanckenhorn *et al.*, 2007a; Serrano-Meneses *et al.*, 2008) to birds (Székely *et al.*, 2004; Székely, Lislevand & Figuerola, 2007) and mammals (Lindenfors, Gittleman & Jones, 2007; Sibly *et al.*, 2012), and even to plants (Kavanagh *et al.*, 2011), but the ‘rule’ is conspicuously and surprisingly absent in others, including some groups of insects (Blanckenhorn, Meier & Teder, 2007b; Bidau, Martí & Castillo, 2013) and spiders (Foellmer & Moya-Laraño, 2007).

Although sexual selection on males largely explains Rensch’s rule in male-larger species (Dale *et al.*,

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2007), female-larger SSD in some taxa can be, seemingly counter-intuitively, associated with strong sexual selection on males. For example, in some turtles (Berry & Shine, 1980; Ceballos *et al.*, 2013), and birds (Székely *et al.*, 2004), it has been hypothesized that there is sexual selection for small-male size, which may convey a locomotor advantage during periods of long-distance mate searching (Zamudio, 1998; Stark, Fox & Leslie, 2005) or during aerial displays (Székely *et al.*, 2004; Dale *et al.*, 2007, see also Husak & Fox, 2008). Such a locomotor advantage for small males (the 'agility hypothesis', Andersson & Norberg, 1981; Temeles, 1985; Raihani *et al.*, 2006) has also been proposed for lizard taxa that concurrently display a high prevalence of female-biased SSD, male mate-searching behavior, and the lack of male territoriality (e.g., dwarf chameleons, genus *Bradypodion*, Stuart-Fox, 2009; horned lizards, genus *Phrynosoma*, Zamudio, 1998).

In general, lizards exhibit male-biased SSD and support Rensch's rule, though all major lizard families have species in which females are the larger sex (Cox, Butler & John-Alder, 2007). Rensch's rule in lizards is largely attributable to a large body-size advantage for males during male–male interactions for access to females (Cox, Skelly & John-Alder, 2003; Cox *et al.*, 2007). For example, among crotophytid lizards (*Crotaphytus* and *Gambelia*), territorial species have male-larger SSD, whereas non-territorial species have female-larger SSD (McGuire, 1996). Such patterns of non-territorial species displaying female-biased SSD, and the reverse condition for territorial species appear to be a common phenomenon among lizards (Cox *et al.*, 2007). Along with male-biased SSD, the general trend for lizard species is for males to have larger relative head sizes due to intra-sexual selection (Stamps, 1983; Carothers, 1984; Vitt & Cooper, 1985; Kratochvíl & Frynta, 2002; Lappin & Husak, 2005; Lappin, Hamilton & Sullivan, 2006). In those species studied to date, larger heads typically result in greater bite force, which is important during male combat for access to females (Lailvaux *et al.*, 2004; Lappin & Husak, 2005; Husak, Lappin & Van Den Bussche, 2009). Thus, deviations from these near-ubiquitous patterns of SSD have the potential to shed light on the selective forces that influence the evolution of body size and SSD.

The flying lizards (genus *Draco*) of Southeast Asia, although poorly studied, are a lineage containing many species with female-biased SSD (Shine *et al.*, 1998; McGuire, 2003). Nevertheless, because all species studied to date have been shown to have males that are highly territorial (Alcala, 1967; Mori & Hikida, 1993, 1994; McGuire, personal observation), flying lizards represent an interesting case to study SSD, even though information on female social

organization is lacking. *Draco* also are unique among lizards in that females are generally larger, not only in body size, but also in body dimensions (relative to body size), compared with males in those species studied (Inger, 1983; Shine *et al.*, 1998), though this has only previously been examined in a few species. The body dimensions that are relatively larger in female *Draco* include head size, which, to our knowledge, is unique to *Draco* (Shine *et al.*, 1998). In flying lizards, female-biased dimorphism, where it occurs, may be in response to several potential factors, which can be divided into sexual selection models and locomotor performance models that are not mutually exclusive. Sexual selection hypotheses predict either: (1) large male size and/or large relative heads due to male-male competition; or (2) small-male size due to a locomotor performance advantage to small males gliding while defending territories. The locomotor performance models predict either: (1) small-male size due to a locomotor performance advantage to small males (as in sexual selection prediction 2); or (2) larger female size to decrease costs of reproduction by decreasing relative clutch mass (Myers, 1978; Bell, 1980; Shine *et al.*, 1998). Similarly, in some *Draco* it has been suggested that females have larger heads for their body size than males to counterbalance an increased weight burden that is displaced posteriorly during gravidity (Shine *et al.*, 1998). Any of these selective pressures could be operating in different species, or could be operating in combination on the two sexes, but it is likely that a gliding lifestyle has influenced SSD in *Draco*. Because the surface area of the structure providing lift during gliding (the patagium) scales isometrically with body mass (McGuire, 2003), larger flying lizards are relatively poor gliders compared to smaller species (McGuire & Dudley, 2005). Nonetheless, it remains somewhat ambiguous how the constraints imposed by such a locomotor style affect the evolution of sexual dimorphism among *Draco*. This is largely due to the fact that the direction and prevalence of SSD among *Draco* species remains relatively unknown.

Another factor that has likely affected the evolution of body size and SSD in *Draco* is the phenomenon of morphological divergence of species in sympatric assemblages (Inger, 1983; McGuire, 2003). Of the ~45 species of *Draco* (McGuire & Dudley, 2011), some live in isolation from other *Draco* species, whereas others live in sympatric assemblages ranging from two to at least seven congeners (Inger, 1983; McGuire & Kiew, 2001; McGuire, 2003; McGuire *et al.*, 2007). It appears that only in these sympatric assemblages, in which competition presumably resulted in morphological divergence as in Caribbean *Anolis* lizards (Losos, 2009), have *Draco* species evolved a diversity of body sizes (McGuire, 2003), potentially yielding a

diversity of SSD patterns. In isolation, *Draco* species tend to be uniformly small or moderate in size (Musters, 1983; McGuire & Alcalá, 2000; McGuire & Kiew, 2001; McGuire, 2003), but it is unknown whether there is similar SSD among these species. In Caribbean *Anolis* lizards, where larger males are favored via intra-sexual selection, SSD is male-biased on single-species islands and decreases as the number of congeners increases (Schoener, 1977). This negative relationship is presumably due to morphological differentiation among species becoming greater than intra-specific differentiation during adaptive radiation (Butler, Sawyer & Losos, 2007). Since most tests of Rensch's rule, in lizards and in other taxa, have found that SSD tends to increase with body size (Frýdlová & Frynta, 2010), *Draco* represents a model group to study the effects of increasing body size on patterns of SSD. Large body size has evolved independently in *Draco* at least four times under conditions of congeneric sympatry (McGuire, 2003), thus offering an opportunity to determine if SSD has changed concomitantly. Along with the large variation in body size across *Draco*, there are also male-larger species and female-larger species, suggesting that selection pressures may differ across the distribution of body sizes. For example, as female size increases, relative clutch mass likely decreases, potentially decreasing the negative impact of gravity on gliding (Shine *et al.*, 1998). Because larger *Draco* species have been shown to have reduced gliding capabilities relative to smaller species (McGuire & Dudley, 2005), we hypothesize that the intensity of selection on performance may switch across the *Draco* body-size spectrum, with selection acting more strongly on gliding performance in smaller, more agile species, and with selection favoring fighting and bite-force performance in larger species.

We studied patterns of sexual dimorphism in the genus *Draco* to determine whether they exhibit Rensch's rule. Further, we tested whether SSD in the genus is predicted by male or female body size. Finally we tested whether SSD is predicted by a measure of gliding capability (wing loading) or a measure of male intra-sexual selection intensity used in studies of other lizards (head size relative to body size). Since *Draco* as a genus exhibits mixed SSD (male-larger and female-larger SSD), we predicted support for Rensch's rule. Because of decreasing relative gliding performance in larger species, we also predicted to find a positive relationship between SSD and male wing loading. That is, males in species with female-biased SSD should have low wing loadings for their body size (i.e., better gliding performance), whereas males in species with male-biased SSD should have high wing loadings for their body size (i.e., worse gliding performance). Similarly, we pre-

dicted that male-biased SSD would be associated with male-male competition similar to other lizard taxa studied (e.g., Lappin & Husak, 2005; Husak, Lappin & Van Den Bussche, 2009 and references therein), with larger relative head size more advantageous to males than better gliding performance. Thus, males in species with male-biased SSD are predicted to have proportionally larger heads than males in species with female-biased SSD, resulting in a positive relationship between SSD and male head size (relative to body size) across species. We also predict different patterns of SSD in species that are solitary versus those occurring in assemblages of multiple *Draco* species.

MATERIAL AND METHODS

DATA COLLECTION

We studied 39 lineages (in 38 currently recognized species) of *Draco* lizards (Table 1), obtaining average male and female measurement data from preserved museum specimens housed in the California Academy of Sciences (San Francisco, CA, USA), Field Museum of Natural History (Chicago, IL, USA), Museum of Vertebrate Zoology (Berkeley, CA, USA), Texas Natural History Collection (Austin, TX, USA), Louisiana State University Museum of Natural Science, and Western Australia Museum (Perth, WA, Australia). For every individual, we measured to the nearest 0.01 mm using digital calipers (Mitutoyo CD-15DC; Mitutoyo Ltd, Telford, UK) snout-vent length (SVL; measured from tip of snout to cloaca) and head depth (measured as the height just posterior to the orbits). We chose head depth because it is a strong predictor of bite force in many lizard species (Herrel *et al.*, 1999; Herrel, De Grauw & Lemos-Espinal, 2001a; Herrel *et al.*, 2001b; Verwajen, Van Damme & Herrel, 2002), and increased bite-force performance has been shown to be advantageous in male-male competition for a variety of lizard taxa (Lailvaux *et al.*, 2004; Lappin & Husak, 2005; Husak *et al.*, 2006, 2009; Henningsen & Irschick, 2012). Average wing loading values are those presented in McGuire (2003), but with *D. modigliani* ($N = 20$ females, 22 males) and *D. rhytisma* ($N = 25$ females, 36 males) added. Wing loading (p_w in $N\ m^{-2}$) was calculated as $p_w = (Mg)/S$, where M = body mass, g is acceleration due to gravity (a constant), and S = the total surface area of the patagium. Patagial area was obtained with NIH Image, v. 1.55 (developed at the U.S. National Institutes of Health and available on the internet at <http://rsb.info.nih.gov/nih-image/>) from scanned museum specimens (McGuire, 2003). Wing loading data were not available for all species for which we had body-size measurements, so

Table 1. *Draco* species examined in study. Sample sizes (N) represent the total number of individuals measured for snout vent length (SVL). From those we calculated average SVL from the largest third of measured individuals. We also report the maximum SVL for each sex of each species. For two species only one or two individuals were measured, so only a maximum SVL is shown. Species with * did not have data available for wing loading

	Female N	Greatest 1/3 SVL ± SE	Max SVL	Male N	Greatest 1/3 SVL ± SE	Max SVL
<i>D. species</i> – Alor*	17	94.0 ± 1.5	99.6	16	79.7 ± 0.7	82.6
<i>D. beccarii</i> *	19	72.3 ± 0.5	74.1	52	70.3 ± 0.4	74.1
<i>D. biaro</i> *	6	75.0 ± 1.0	76.1	10	75.6 ± 0.4	76.1
<i>D. bimaculatus</i>	36	65.6 ± 0.4	70.8	54	68.2 ± 0.3	70.6
<i>D. blanfordii</i>	23	107.8 ± 1.4	113.6	40	123.9 ± 0.5	127.1
<i>D. boschmai</i> *	21	83.3 ± 2.5	90.6	22	75.7 ± 0.7	78.1
<i>D. caerhulians</i>	9	78.2 ± 1.4	80.9	11	73.6 ± 0.4	74.5
<i>D. cornutus</i>	23	82.4 ± 0.5	84.8	29	77.4 ± 0.8	82.6
<i>D. cristatellus</i> *	2	–	91.7	2	–	87.7
<i>D. cyanopterus</i>	7	91.2 ± 0.1	91.3	7	88.1 ± 1.1	89.1
<i>D. dussumieri</i> *	9	87.8 ± 1.2	90.0	16	77.1 ± 0.7	79.0
<i>D. fimbriatus</i>	11	115.5 ± 3.3	125.4	17	117.1 ± 3.1	132.1
<i>D. formosus</i>	11	89.3 ± 2.0	95.0	27	103.3 ± 1.0	108.0
<i>D. guentheri</i>	9	90.9 ± 3.7	98.4	22	86.5 ± 1.6	92.4
<i>D. haematopogon</i>	23	85.8 ± 1.8	94.6	54	82.0 ± 0.7	88.3
<i>D. iskandari</i>	10	74.5 ± 0.5	75.4	11	71.4 ± 0.3	72.0
<i>D. lineatus</i>	16	82.9 ± 0.7	85.4	26	79.8 ± 0.6	84.4
<i>D. maculatus</i>	20	77.2 ± 1.0	82.4	50	77.4 ± 0.8	84.7
<i>D. maximus</i>	31	133.4 ± 1.4	143.0	42	138.4 ± 0.9	147.8
<i>D. melanopogon</i>	60	84.5 ± 0.4	90.7	72	81.5 ± 0.4	84.9
<i>D. mindanensis</i>	4	107.3	107.3	6	103.1 ± 2.8	105.9
<i>D. modigliani</i>	14	70.0 ± 1.2	74.2	19	66.0 ± 0.2	66.7
<i>D. obscurus</i>	14	90.4 ± 1.2	93.7	31	89.8 ± 1.7	97.9
<i>D. ornatus</i>	29	84.0 ± 1.0	92.1	21	75.8 ± 0.6	78.0
<i>D. palawanensis</i>	6	74.5 ± 1.5	76.0	8	77.2 ± 0.7	78.7
<i>D. quadrasi</i>	13	86.4 ± 1.2	89.4	21	77.9 ± 1.1	81.5
<i>D. quinquefasciatus</i>	35	102.5 ± 1.1	108.5	33	100.6 ± 0.6	104.1
<i>D. reticulatus</i>	11	86.8 ± 1.4	89.5	28	85.2 ± 0.9	90.6
<i>D. rhytisma</i>	18	79.6 ± 0.7	81.5	22	75.9 ± 0.3	77.0
<i>D. spilonotus</i>	37	71.8 ± 0.5	75.8	55	68.3 ± 0.4	72.2
<i>D. spilopterus</i> – Visayas	53	89.6 ± 0.9	99.3	66	81.7 ± 0.4	88.1
<i>D. spilopterus</i> – Bicol peninsula	1	–	79.2	5	74.3 ± 0.8	75.5
<i>D. spilopterus</i> – Polillo	9	84.9 ± 1.0	86.9	11	73.7 ± 0.5	76.8
<i>D. sumatranus</i>	5	80.2 ± 0.4	80.6	5	78.4 ± 3.9	82.3
<i>D. supriatnai</i> *	10	78.7 ± 0.9	80.5	13	73.6 ± 0.7	75.2
<i>D. taeniopterus</i>	15	75.3 ± 0.8	78.2	40	75.4 ± 0.4	78.7
<i>D. timoriensis</i> *	26	88.0 ± 1.1	92.1	19	76.7 ± 0.7	80.0
<i>D. volans</i>	47	78.6 ± 0.5	83.9	42	76.9 ± 0.7	82.5
<i>D. walkeri</i>	30	78.6 ± 1.7	91.5	61	74.7 ± 0.4	79.4

analyses that included wing loading only included species with all variables. Table 1 indicates species for which wing loading data were unavailable.

We conducted analyses on the average of the largest third of individuals measured (Stuart-Fox, 2009) to estimate maximal size, but also to consider variation present in each species. We took this conservative approach, because our samples are not from well studied populations, but instead from

museum specimens, and we wanted to ensure that we were analysing sexually mature individuals near asymptotic size (e.g., Butler, Schoener & Losos, 2000). The average of the largest third of individuals correlated strongly with the average for all individuals measured (males: $R^2 = 0.99$, slope = 0.90, $P < 0.0001$; females: $R^2 = 0.97$, slope = 0.84, $P < 0.0001$), the largest 50% measured (males: $R^2 = 0.99$, slope = 0.98, $P < 0.0001$; females: $R^2 = 0.99$,

slope = 0.98, $P < 0.0001$) and the maximal value (males: $R^2 = 0.98$, slope = 1.09, $P < 0.0001$; females: $R^2 = 0.96$, slope = 1.09, $P < 0.0001$) for each sex. Thus, we are confident that we have captured reasonable estimates of SSD across species using the largest third of individuals, as has been done in some recent studies of lizard SSD (Stuart-Fox, 2009). In addition to the average of the largest third of individuals, we also present the maximal values for each sex of each species (Table 1). For some species (*D. cristatellus*; *D. spilopterus* from the Bicol peninsula, Philippines) very few individuals were available to measure, so we used the maximal value to better estimate adult size. We calculated dimorphism in body size using two standard methods. First, we subtracted \log_{10} -transformed female SVL from \log_{10} -transformed male SVL, and second, we divided male values by female values (Smith, 1999; Fairbairn, 2007; Serrano-Meneses *et al.*, 2008). Results from analyses of these two measures were virtually identical, so we only present results from the analysis of the first measure of SSD.

PHYLOGENY

Our regression analyses were conducted in the context of a multispecies coalescent phylogenetic estimate for *Draco* (McGuire, in preparation) that includes all described *Draco* species, plus several undescribed species (42 *Draco* species in total, plus seven outgroup agamid species). The data set includes nine loci screened for 134 individual flying lizards, with nearly complete data (missing one locus for *D. dussumieri*), and with at least two representatives for each ingroup species except *D. dussumieri*. The primary phylogenetic findings are in close agreement with those of McGuire & Kiew (2001), as well as with concatenated Bayesian phylogenetic analyses based on a data set composed of six genes (four loci) screened for 762 *Draco* exemplars and 66 outgroup samples (McGuire, in preparation). We then used Mesquite v. 2.72 (Maddison & Maddison, 2009) to prune off species for which we had no morphological data.

STATISTICAL ANALYSIS

We used the PDAP:PD TREE module (Phenotypic Diversity Analysis Programs; Garland, Midford & Ives, 1999; Midford, Garland & Maddison, 2005) in Mesquite v. 2.72 (Maddison & Maddison, 2009) to calculate standardized phylogenetically independent contrasts (Felsenstein, 1985) of species and sex averages of \log_{10} -transformed SVL. Neither of the variables showed significant correlations between the absolute value of the contrast and the standard deviation of the contrast (male SVL, 2-tailed $P = 0.86$; female SVL,

2-tailed $P = 0.93$), so contrast analyses should perform equally well to alternative methods of analysis (Garland, Harvey & Ives, 1992; Revell, 2010). To test Rensch's rule, we fit reduced major axis regressions (RMA) between male (dependent variable) and female (independent variable) SVL for all species, forcing the regression through the origin (Garland *et al.*, 1992). We report values obtained using RMA v. 1.17 (Bohonak, 2002). We present the slope of this regression, as well as the 95% confidence intervals calculated by bootstrapping the contrasts. We performed our test of Rensch's rule with the above methods to conform to those done in other studies, making our estimates comparable with others. However, we note that slope estimates obtained from this software were identical to slope estimates obtained with the PDAP module of Mesquite and 'phyl.RMA' in the 'phytools' package (Revell, 2012) of R (R Development Core Team, 2011). To examine the effect of being a solitary species versus a species that occurs in sympatry with other *Draco* species we used phylogenetic generalized least squares (PGLS; Martins & Hansen, 1997) analyses with an interaction term included in the model (factor = isolated or sympatric). A significant SVL*isolation state interaction term would indicate that isolated and sympatric species have different slopes between male and female SVL. Alternatively, a non-significant slope but significant factor would indicate significantly different intercepts between the two groups of species. We performed PGLS using both a Brownian motion model and an Ornstein-Uhlenbeck model (Martins & Hansen, 1997), and we present parameter estimates from both.

We used PGLS to determine, separately, whether each of the following variables predicted SSD: male SVL, female SVL, residual female wing loading, residual male wing loading, residual female head depth, and residual male head depth. Residuals were obtained by regressing each variable of interest on SVL (e.g. Frýdlová & Frynta, 2010) using PGLS with 'phyl.resid' (Revell, 2009) in the 'phytools' package of R.

RESULTS

Draco exhibit both male- and female-biased SSD (Table 1, Fig. 1), but the majority of species exhibited female-biased SSD. The median for SSD was significantly different from zero (median = -0.019; Wilcoxon one-sample test, $P < 0.001$).

Draco species exhibit Rensch's rule, as indicated by the RMA slope between male and female body size ($\beta = 1.13$, SE = 0.09; Fig. 2A) that is marginally significantly greater than one (lower 95% CI - upper 95% CI: 0.96, 1.30). In the PGLS analysis of male and female body size with isolation (isolated or sympatric with other *Draco* species) as a factor, the

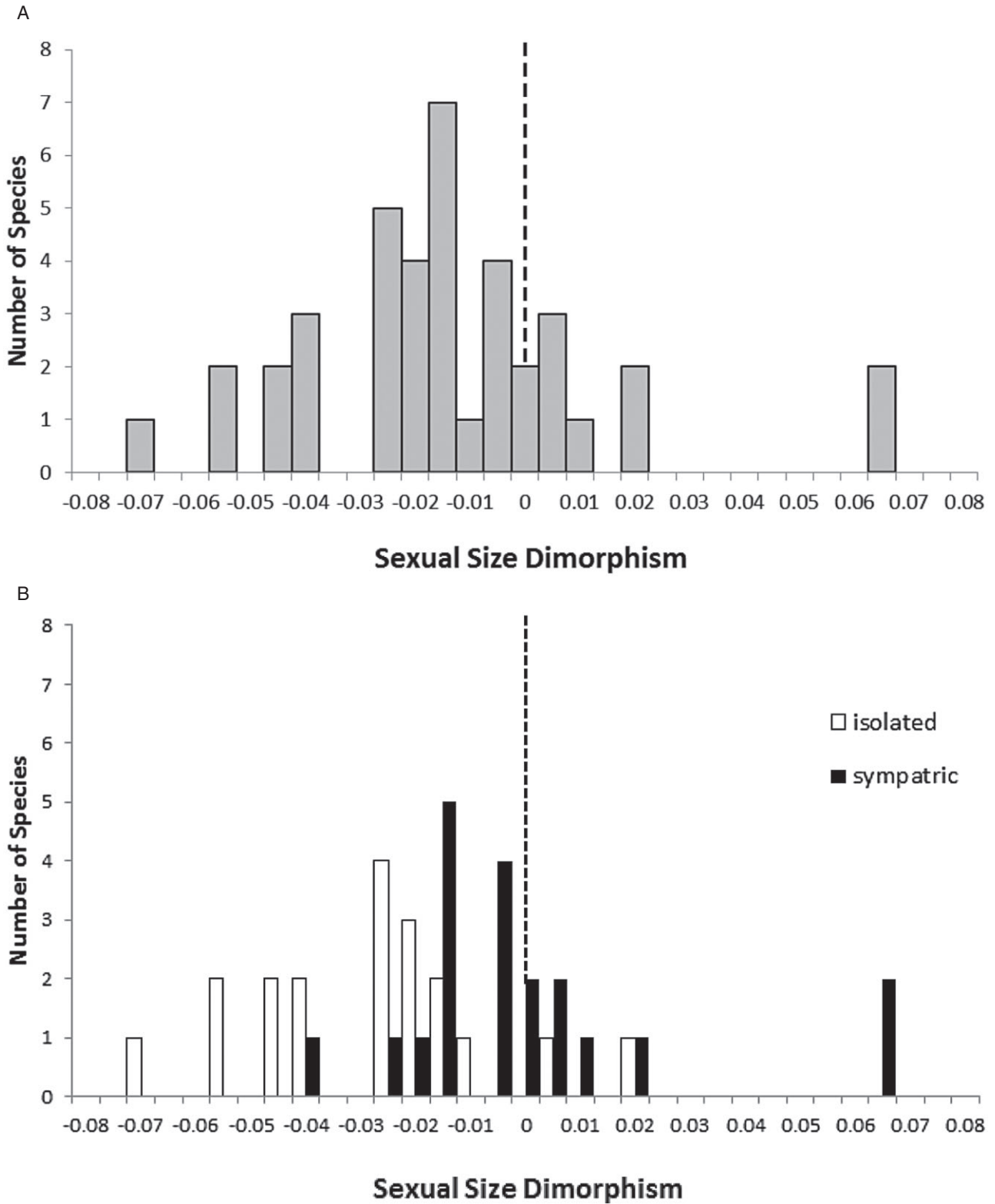


Figure 1. Distribution of sexual size dimorphism in *Draco* lizards for (A) all species together and (B) species separated by whether they are part of a sympatric assemblage of *Draco* species (solid bars) or live in isolation from other *Draco* species (open bars). Positive sexual size dimorphism (SSD) values indicate male-larger species, whereas negative SSD values indicate female-larger species. The dotted line represents monomorphism, and axes are scaled the same on A and B for comparative purposes.

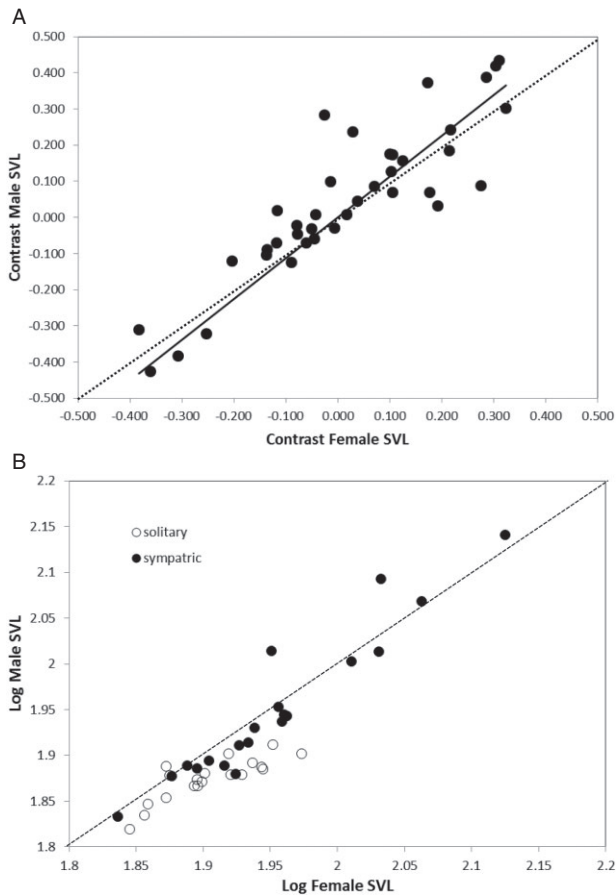


Figure 2. (A) Phylogenetic independent contrasts of \log_{10} (male size) versus \log_{10} (female size) in *Draco* lizards. The solid line represents the fitted relationship using reduced major axis regression through zero ($\beta = 1.13$). The dotted line represents an isometric relationship. (B) Male size versus female size (both \log_{10} transformed) in *Draco* lizards, separated by whether they are part of a sympatric assemblage of *Draco* species (solid circles) or live in isolation from other *Draco* species (open circles). The values shown are species averages and are non-phylogenetically corrected. The dotted line represents an isometric relationship.

Ornstein-Uhlenbeck model (AIC = -161.2) performed slightly better than the Brownian motion model (AIC = -154.3). In both models, there was a significant female SVL*isolation state interaction (OU: $P = 0.002$; BM: $P = 0.01$), but slope estimates were similar between the models for both allopatric and sympatric species (Table 2). Thus, Rensch's rule in *Draco* appears to be driven primarily by species that occur in sympatric assemblages ($\beta > 1$, Table 2), which display a wide range of SSD values (Fig. 2B). Species living in isolation from other *Draco* species, in contrast, largely exhibit female-biased SSD (Fig. 2B) and exhibit a slope less than one ($\beta \leq 0.65$, Table 2).

The only significant predictors of SSD were male SVL, residual male head depth, and residual female head depth (Table 3, Fig. 3). Female SVL and residual male and female wing loadings were not significant predictors of SSD (Table 3).

DISCUSSION

Flying lizards in the genus *Draco* exhibit both male-biased and female-biased SSD, though females tend to be the larger sex in most species. The genus supports Rensch's rule, though not as might be expected. Even though most *Draco* species have female-larger SSD (Fig. 1A), the slope of \log_{10} (male size) versus \log_{10} (female size), we found a slope greater than one, meaning that SSD increases with body size. This is apparently due to SSD increasing with male body size (but not with female body size; Table 3). Thus, the pattern of SSD in *Draco* is most similar to that in clades with male-biased SSD or more evenly mixed SSD. SSD was unrelated to residual wing loadings of either sex, despite the fact that wing loading is positively correlated with body size in *Draco* (McGuire & Dudley, 2005). Further, SSD was negatively related to residual head size of both males and females, meaning that as species become more male-biased in SSD, the residual head size of both sexes decreases. Much of the variation in SSD among *Draco* species is likely explained by divergence in morphology among species that are in sympatric congeneric assemblages, as these are the species that exhibit the greatest diversity in body size (Fig. 1B). We explore each of these components in more detail below.

Wing loading is a good predictor of gliding ability, and species with high wing loadings have less flexibility in their glide angles and in the height from which they begin a glide (McGuire & Dudley, 2005). Thus, we predicted that species with male-biased SSD (which tend to be larger species) would also be species with high residual wing loadings. We found that this is indeed the case. Although PGLS revealed only a slight trend for this relationship in males ($P = 0.15$), but not females ($P = 0.40$), phylogenetic analysis of variance (ANOVA) revealed that species with male-biased SSD have significantly higher wing loading than species with female-biased SSD (males, $F_{1,30} = 8.62$, $P = 0.006$, phylogenetic $P = 0.01$; females, $F_{1,29} = 2.57$, $P = 0.12$, phylogenetic $P = 0.31$). This association is unsurprising because both SSD (see Results section) and wing loading (PGLS: males, $P < 0.001$; females, $P = 0.0003$) are positively correlated with body size. However, we were also interested in exploring the possibility that species with greater SSD would exhibit a more complex relationship with wing loading than would be predicted from size alone. For example, species with female-biased

Table 2. The effects of being an isolated species or a species sympatric with other *Draco* species on Rensch’s rule in *Draco*. Slopes (standard errors) are from phylogenetic generalized least-squares regressions of log10-transformed male body size (SVL) on log10-transformed female body size (SVL) with isolation (isolated versus sympatric) as a factor

	Isolated species Slope (SE)	Sympatric species Slope (SE)	Intercept
Brownian motion model	0.65 (0.15)	1.13 (0.32)	0.63 (0.28)
Ornstein–Uhlenbeck model	0.57 (0.15)	1.12 (0.31)	0.80 (0.28)

Table 3. Sexual size dimorphism in *Draco* species (dependent variable) in relation to body size, wing loading, and head size variables using phylogenetic generalized least squares. Significant predictors are shown in bold

Independent variable	Regression coefficient ± SE	<i>t</i>	<i>P</i>
Male SVL	0.26 ± 0.07	3.90	< 0.001
Female SVL	0.09 ± 0.09	1.04	0.31
Residual male wing loading	-0.02 ± 0.05	-0.42	0.68
Residual female wing loading	0.02 ± 0.04	0.36	0.72
Residual male head depth	-0.32 ± 0.13	-2.38	0.02
Residual female head depth	-0.30 ± 0.15	-2.08	0.04

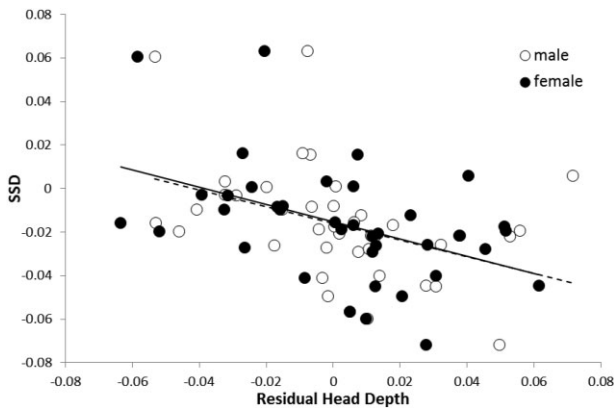


Figure 3. Sexual size dimorphism (SSD) (male–female value) in *Draco* lizards in relation to residual head depth for males (open circles, dashed line) and females (closed circles, solid line).

SSD could be more likely to require improved gliding performance than comparable-sized species with more male-biased SSD if the former are under more intense sexual selection for agility, thereby resulting in reduced wing loadings in these species. Alternatively, species with male-biased SSD could be under more intense sexual selection for fighting/biting performance than species with more female-biased SSD, requiring larger heads and perhaps body proportions and thus higher wing loadings. To test these hypotheses, we regressed SSD on residual wing loadings, which are size-independent. We found no support for either hypothesis. Rather, the tight relationship

between wing loading and SVL is likely to be a design constraint (McGuire, 2003) and may preclude additional correlations between wing loading and other axes of phenotypic variation.

In contrast, we were quite surprised by the finding that increased SSD is associated with decreased residual head depth. This suggests that species with male-biased dimorphism, which also happen to be larger on average, have relatively small heads for their body size. Head depth is a strong predictor of bite-force capacity (Herrel *et al.*, 1999; 2001b; Herrel, De Grauw & Lemos-Espinal, 2001a; Verwajen, Van Damme & Herrel, 2002), and we expected this measure to show the predicted pattern for sexual selection as seen in other lizard taxa. Nevertheless, our results clearly go counter to the hypothesis that selection for larger male size will necessarily result in concomitant increases in residual head size, as is typical for lizards. Instead, a gliding lifestyle likely imposes strong constraints on the evolution of residual head size, especially in males. Previous work on *Draco melanopogon* suggests that females may have relatively larger heads than males to offset the gliding costs of increased weight during gravidity in females (Shine *et al.*, 1998), though actual gliding performance data are needed to empirically confirm this. This relationship is true across *Draco* species as well if we consider head depth: as body size increases, so does head depth, with females having larger relative heads than males (analysis of covariance: sex*SVL interaction, *P* = 0.29; sex, *P* = 0.02; Fig. 4). Whereas females of all species have a relatively large head than males that may be necessary to offset

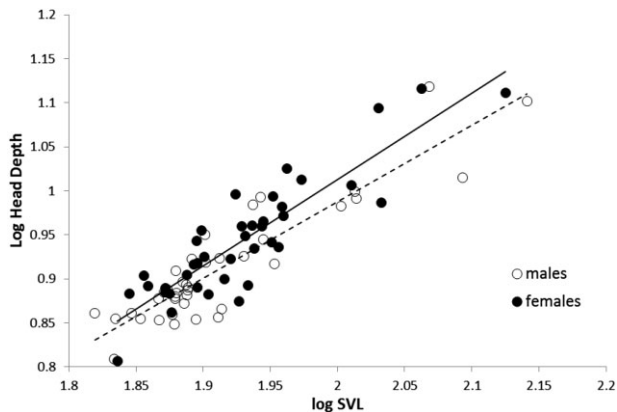


Figure 4. Head size plotted against snout–vent length (SVL) in male (open circles, dashed line) and female (closed circles, solid line) *Draco* species. Values are species averages, not phylogenetically corrected values. Least-squares regression lines are shown for illustrative purposes.

gliding costs of gravidity, males likely undergo selection against an increasingly large head for their body size that may destabilize them during gliding (Shine *et al.*, 1998). Consistently smaller heads in males compared with females is a unique phenomenon among lizards, and we return to this below.

As predicted, being in a sympatric assemblage of congeners versus being a solitary *Draco* species, has a great impact on the magnitude and pattern of SSD. Whereas most solitary species are female-larger, sympatric species exhibit mixed SSD, with some species having much larger males (Fig. 2B). When the two groups of species are examined separately, the sympatric species supported Rensch's rule with the slope of \log_{10} (male size) versus \log_{10} (female size) significantly greater than one. The isolated species, which mostly show female-biased SSD (Fig. 1), also supported Rensch's rule. These mostly female-larger species had an estimated slope less than one. Thus, the two groups of species apparently have different patterns of SSD due to the presence or absence of competitive pressure (past or current) with congeners. Thus, the two different patterns of SSD observed within *Draco* are driven by the large *Draco* species that occur only in sympatric assemblages (Inger, 1983; McGuire, 2003). Larger species have SSD that is reversed from the majority of *Draco* species. The causal factors leading to this are not clear, but the most likely scenario is that resource competition led to divergence in body size, which included the evolution of large species, reminiscent of 'crown-giant' *Anolis* (Losos, 2009). Large *Draco* species are more constrained to upper levels of the forest canopy due to the large ballistic dives required for them to attain lift

for gliding, and this large body size and overall poor gliding ability may have relaxed or eliminated the small-male advantage for gliding performance, and potentially allowed directional selection toward larger body size instead, which is common in non-flying lizards (Stamps, 1983; Cox *et al.*, 2007). Future work on the sympatric assemblages will illuminate whether there is variation in social organization or territoriality among sympatric species as is seen in the well-studied Caribbean anoles (e.g., Losos, 1990; Johnson, Revell & Losos, 2010).

An alternative explanation of our results is that differences in SSD between isolated and sympatric species are due to state of isolation being confounded by phylogenetic relatedness. Most of the sympatric species (62%) are in the 'dorsal nostril-*fimbriatus*' clade (McGuire & Kiew, 2001), and none of the species in that clade are isolated species. Conversely, the isolated species are primarily (94%) in the '*lineatus-volans*' clade, and only 30% of that clade are in sympatric assemblages. Further, even though sympatric species appear to have more male-biased SSD, the significant difference in SSD between isolated and sympatric species (ANOVA: $F_{1,37} = 10.48$, $P = 0.003$) disappears after phylogenetic correction (phylogenetic $P = 0.10$) by using a phylogenetic ANOVA (Garland *et al.*, 1993). Thus, there is the possibility that sexual selection and its consequences are fundamentally different in these two clades. Indeed, if SSD is plotted against maximum SVL (regardless of sex), then the two clades have very different patterns of SSD that follow Rensch's rule in opposing ways. The dorsal nostril-*fimbriatus* clade has a positive relationship (analysis of contrasts, $\beta = 0.276$, $P = 0.01$), whereas the *lineatus-volans* clade has a negative relationship (analysis of contrasts, $\beta = -0.61$, $P = 0.01$; Fig. 5). Examination of the RMA regression slopes of contrasts of male and female SVL for these two clades (dorsal nostril-*fimbriatus* $\beta = 1.27$; *lineatus-volans* $\beta = 0.92$) parallels the comparison above between isolated and sympatric species. It is unclear why the two major *Draco* clades might differ in their intensity of sexual selection, or their response to it, but future studies should consider these patterns as potential constraints.

When all of our results are considered together, we can hypothesize a scenario explaining the evolution of SSD in *Draco*. The typical condition for *Draco* appears to be moderate body size and female-larger SSD, most likely because of selection for small-male size for improved gliding performance during territory defense, combined with selection for increased female size to minimize negative impacts on gliding performance while gravid. Increased mass during gravidity is likely a larger problem for smaller species than for larger species. Thus, being a larger female in the

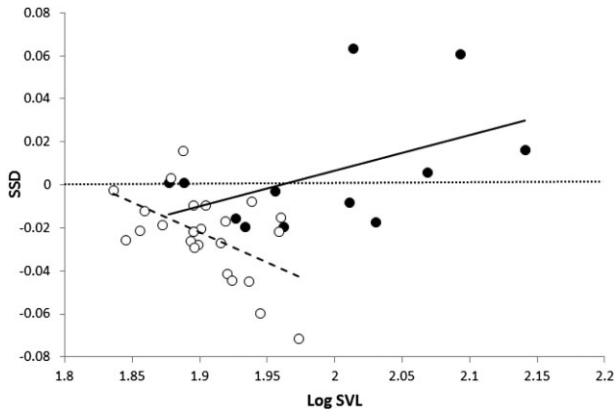


Figure 5. Sexual size dimorphism (SSD) (male – female value) in *Draco* lizards in relation to maximum snout–vent length (SVL) for each species. Maximum SVL was the largest for the species, regardless of sex. Species in the dorsal nostril-*fimbriatus* clade (solid circles, solid line) show a positive relationship, whereas species in the *lineatus-volans* clade (open circles, dashed line) show a negative relationship. Dotted line at SSD = 0 represents no sexual dimorphism. Figure shows species averages for aesthetics, but analyses were performed on phylogenetic independent contrasts (see text for details).

small- to moderate-sized *Draco* species would be at a selective advantage because it would reduce relative clutch mass and improve gliding while gravid (Shine *et al.*, 1998). As body sizes of species increase, as occurs in sympatric assemblages, the impact on gliding imposed by gravity should diminish, resulting in less selection favoring larger females. At the same time, as body size increases, and gliding performance decreases, there would be a shift in selection on males away from gliding performance (i.e., a reduction in the small-male advantage) and toward larger body size via other mechanisms of sexual selection, resulting in male-larger SSD. In other words, selection for large females is likely greater than selection for large males at the smaller end of the size continuum, whereas this relationship reverses for larger species. In larger species, there may be less selection pressure for large females, whereas males are no less territorial and experience no such reduction in selection pressure. This scenario predicts differences along the body-size continuum in how males defend territories (gliding versus fighting) and whether small or large body size is favored by sexual selection.

The evolution of residual head size may also be driven by aerodynamic constraints, but without an intersexual transition in relative selection pressures along the body-size continuum as is the case for SSD. Rather, we propose that residual head size imposes a gliding performance constraint on both sexes at all

body sizes. All else being equal, *Draco* head sizes should be small to minimize body mass and maximize gliding performance. However, for females, there is the added aerodynamic problem of maintaining center of body mass when carrying a payload of eggs, resulting in the need for relatively larger heads in females than for equivalent-sized males of the same species. At larger body sizes, the residual head sizes of *Draco* species become progressively smaller in both sexes, but the residual size of the head in females remains larger than for males of the same species reflecting the continued egg payload constraint. Our findings suggest that selection on aerodynamic performance trumps sexual selection on male head size and associated biting performance that characterizes the vast majority of lizard species.

If the problem of gliding while gravid diminishes with increasing size, and if SSD increases with size, then you would expect SSD and residual head depth to be negatively correlated as we found. This relationship is likely due to a diminishing need for a counterbalancing head in larger species, though it would be more advantageous for females when gravid than males, perhaps explaining their different allometries (Fig. 4). Future work can help to test these hypotheses, and we offer specific guidance. First, one could test directly whether eggs represent a larger percentage of total mass in larger versus smaller species, as we have assumed. Second, one could compare the wing loadings of gravid and non-gravid females across a diversity of species. Third, one could quantify in a field study whether gravid females are less inclined to glide than non-gravid females (which we strongly suspect based on our field observations). Proportionally greater wing loadings, and a lower probability of using gliding, in gravid versus non-gravid females at the smaller end of the size spectrum would be congruent with our hypothesized evolutionary scenario.

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REFERENCES

- Abouheif E, Fairbairn DJ. 1997.** A comparative analysis of allometry for sexual size dimorphism: assessing Rensch's rule. *American Naturalist* **149**: 540–562.

- Alcala AC. 1967.** Population biology of the 'flying' lizard, *Draco volans*, on Negros Island, Philippines. *Natural and Applied Science Bulletin* **20**: 335–372.
- Andersson M, Norberg RA. 1981.** Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. *Biological Journal of the Linnean Society* **15**: 105–130.
- Andersson MB. 1994.** *Sexual selection*. Princeton, NJ: Princeton University Press.
- Bell G. 1980.** The costs of reproduction and their consequences. *American Naturalist* **116**: 45–76.
- Berry JF, Shine R. 1980.** Sexual size dimorphism and sexual selection in turtles (order Testudines). *Oecologia* **44**: 185–191.
- Bidau CJ, Martí DA, Castillo ER. 2013.** Rensch's rule is not verified in melanopline grasshoppers (Acrididae). *Journal of Insect Biodiversity* **1**: 1–14.
- Blanckenhorn WU, Dixon AFG, Fairbairn DJ, Foellmer MW, Gibert P, van der Linde K, Meier R, Nylin S, Pitnick S, Schoff C, Signorelli M, Teder T, Wiklund C. 2007a.** Proximate causes of Rensch's rule: does sexual size dimorphism in arthropods result from sex differences in development time? *American Naturalist* **169**: 245–257.
- Blanckenhorn WU, Meier R, Teder T. 2007b.** Rensch's rule in insects: patterns among and within species. In: Fairbairn DJ, Blanckenhorn WU, Székely T, eds. *Sex, size & gender roles: evolutionary studies of sexual size dimorphism*. Oxford: Oxford University Press, 60–70.
- Bohonak AJ. 2002.** *Software for reduced major axis regression, V.1.17*. San Diego: San Diego State University.
- Butler MA, Sawyer SA, Losos JB. 2007.** Sexual dimorphism and adaptive radiation in *Anolis* lizards. *Nature* **447**: 202–205.
- Butler MA, Schoener TW, Losos JB. 2000.** The relationship between sexual size dimorphism and habitat use in Greater Antillean *Anolis* lizards. *Evolution* **54**: 259–272.
- Carothers JH. 1984.** Sexual selection and sexual dimorphism in some herbivorous lizards. *American Naturalist* **124**: 244–254.
- Ceballos CP, Adams DC, Iverson JB, Valenzuela N. 2013.** Phylogenetic patterns of sexual size dimorphism in turtles and their implications for Rensch's rule. *Evolutionary Biology* **40**: 194–208.
- Colwell RK. 2000.** Rensch's rule crosses the line: convergent allometry of sexual size dimorphism in hummingbirds and flower mites. *American Naturalist* **156**: 495–510.
- Cox RM, Butler MA, John-Alder HB. 2007.** The evolution of sexual size dimorphism in reptiles. In: Fairbairn DJ, Blanckenhorn WU, Székely T, eds. *Sex, size & gender roles: evolutionary studies of sexual size dimorphism*. Oxford: Oxford University Press, 38–49.
- Cox RM, Skelly SL, John-Alder HB. 2003.** A comparative test of adaptive hypotheses for sexual size dimorphism in lizards. *Evolution* **57**: 1653–1669.
- Dale J, Dunn PO, Figuerola J, Lislevand T, Székely T, Whittingham LA. 2007.** Sexual selection explains Rensch's rule of allometry for sexual size dimorphism. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **274**: 2971–2979.
- Darwin C. 1871.** *The descent of man, and selection in relation to sex*. London: John Murray.
- Fairbairn DJ. 1997.** Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. *Annual Review of Ecology & Systematics* **28**: 659–687.
- Fairbairn DJ. 2007.** Introduction: the enigma of sexual size dimorphism. In: Fairbairn DJ, Blanckenhorn WU, Székely T, eds. *Sex, size & gender roles: evolutionary studies of sexual size dimorphism*. Oxford: Oxford University Press, 1–10.
- Fairbairn DJ, Blanckenhorn WU, Székely T. 2007.** *Sex, size & gender roles: evolutionary studies of sexual size dimorphism*. Oxford: Oxford University Press.
- Felsenstein J. 1985.** Phylogenies and the comparative method. *American Naturalist* **125**: 1–15.
- Foellmer MW, Moya-Laraño J. 2007.** Sexual size dimorphism in spiders: patterns and processes. In: Fairbairn DJ, Blanckenhorn WU, Székely T, eds. *Sex, size & gender roles: evolutionary studies of sexual size dimorphism*. Oxford: Oxford University Press, 71–81.
- Frydlová P, Frynta D. 2010.** A test of Rensch's rule in varanid lizards. *Biological Journal of the Linnean Society* **100**: 293–306.
- Garland T Jr, Dickerman AW, Janis CM, Jones JA. 1993.** Phylogenetic analysis of covariance by computer simulation. *Systematic Biology* **42**: 265–292.
- Garland T Jr, Harvey PH, Ives AR. 1992.** Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Systematic Biology* **41**: 18–32.
- Garland T Jr, Midford PE, Ives AR. 1999.** An introduction to phylogenetically based statistical methods, with a new method for confidence intervals on ancestral states. *American Zoologist* **39**: 374–388.
- Henningsen JP, Irschick DJ. 2012.** An experimental test of the effect of signal size and performance capacity on dominance in the green anole lizard. *Functional Ecology* **26**: 3–10.
- Herrel A, De Grauw E, Lemos-Espinal JA. 2001a.** Head shape and bite performance in xenosaurid lizards. *Journal of Experimental Zoology* **290**: 101–107.
- Herrel A, Spithoven L, Van Damme R, De Vree F. 1999.** Sexual dimorphism of head size in *Gallotia galloti*: testing the niche divergence hypothesis by functional analyses. *Functional Ecology* **13**: 289–297.
- Herrel A, Van Damme R, Vanhooydonck B, De Vree F. 2001b.** The implications of bite performance for diet in two species of lacertid lizards. *Canadian Journal of Zoology* **79**: 662–670.
- Husak JF, Fox SF. 2008.** Sexual selection on locomotor performance. *Evolutionary Ecology Research* **10**: 213–228.
- Husak JF, Lappin AK, Fox SF, Lemos-Espinal JA. 2006.** Bite-force performance predicts dominance in male Venerable Collared Lizards (*Crotaphytus antiquus*). *Copeia* **2006**: 301–306.

- Husak JF, Lappin AK, Van Den Bussche RA. 2009.** The fitness advantage of a high performance weapon. *Biological Journal of the Linnean Society* **96**: 840–845.
- Inger RF. 1983.** Morphological and ecological variation in the flying lizards (genus *Draco*). *Fieldiana Zoology, New Series* **18**: 1–35.
- Johnson MA, Revell LJ, Losos JB. 2010.** Behavioral convergence and adaptive radiation: effects of habitat use on territorial behavior in *Anolis* lizards. *Evolution* **64**: 1151–1159.
- Kavanagh PH, Lehnebach CA, Shea MJ, Burns KC. 2011.** Allometry of sexual size dimorphism in dioecious plants: do plants obey Rensch's rule? *American Naturalist* **178**: 596–601.
- Kratochvíl L, Frynta D. 2002.** Body size, male combat, and the evolution of sexual dimorphism in eublepharid geckos (Squamata: Eublepharidae). *Biological Journal of the Linnean Society* **76**: 303–314.
- Lailvaux SP, Herrel A, Vanhooydonck B, Meyers JJ, Irschick DJ. 2004.** Performance capacity, fighting tactics, and the evolution of life-stage male morphs in the green anole lizard (*Anolis carolinensis*). *Proceedings of the Royal Society of London B* **271**: 2501–2508.
- Lappin AK, Hamilton PS, Sullivan BK. 2006.** Bite-force performance and head shape in a sexually dimorphic crevice-dwelling lizard, the Common Chuckwalla [*Sauromalus ater* (= *obesus*)]. *Biological Journal of the Linnean Society* **88**: 215–222.
- Lappin AK, Husak JF. 2005.** Weapon performance, not size, determines mating success and potential reproductive output in the collared lizard (*Crotaphytus collaris*). *American Naturalist* **166**: 426–436.
- Lindenfors P, Gittleman JL, Jones KE. 2007.** Sexual size dimorphism in mammals. In: Fairbairn DJ, Blanckenhorn WU, Székely T, eds. *Sex, size and gender roles: evolutionary studies of sexual size dimorphism*. 16–26. Oxford: Oxford University Press.
- Losos JB. 1990.** Concordant evolution of locomotor behavior, display rate, and morphology in West Indian *Anolis* lizards. *Animal Behaviour* **39**: 879–890.
- Losos JB. 2009.** *Lizards in an evolutionary tree: ecology and adaptive radiation of anoles*. Berkeley, CA: University of California Press.
- Maddison WP, Maddison DR. 2009.** Mesquite: a modular system for evolutionary analysis. Version 2.72 Available at: <http://mesquiteproject.org>.
- Martins EP, Hansen TF. 1997.** Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *American Naturalist* **149**: 646–667.
- McGuire JA. 1996.** Phylogenetic systematics of crotophytid lizards. Bulletin of the Carnegie Museum No. 32: 1–143.
- McGuire JA. 2003.** Allometric prediction of locomotor performance: an example from Southeast Asian flying lizards. *American Naturalist* **161**: 347–369.
- McGuire JA, Alcalá AC. 2000.** A taxonomic revision of the flying lizards of the Philippine Islands (Iguania: Agamidae: *Draco*), with a description of a new species. *Herpetological Monographs* **14**: 81–138.
- McGuire JA, Brown RM, Mumpuni, Riyanto A, Andayani N. 2007.** The flying lizards of the *Draco lineatus* group (Squamata: Iguania: Agamidae): a taxonomic revision with descriptions of two new species. *Herpetological Monographs* **21**: 180–213.
- McGuire JA, Dudley R. 2005.** The cost of living large: comparative gliding performance in flying lizards (*Draco*). *American Naturalist* **166**: 93–106.
- McGuire JA, Dudley R. 2011.** The biology of gliding in flying lizards (Genus *Draco*) and their fossil and extant analogs. *Integrative and Comparative Biology* **51**: 983–990.
- McGuire JA, Kiew B-H. 2001.** Phylogenetic systematics of Southeast Asian flying lizards (Iguania: Agamidae: *Draco*) as inferred from mitochondrial DNA sequence data. *Biological Journal of the Linnean Society* **73**: 203–229.
- Midford PE, Garland T Jr, Maddison WP. 2005.** PDAP Package of Mesquite. Version 1.07.
- Mori A, Hikida T. 1993.** Natural History Observations of the Flying Lizard, *Draco volans sumatranus* (Agamidae, Squamata) from Sarawak, Malaysia. *Raffles Bulletin of Zoology* **41**: 83–94.
- Mori A, Hikida T. 1994.** Field observations on the social behavior of the flying lizard, *Draco volans sumatranus*, in Borneo. *Copeia* **1994**: 124–130.
- Musters CJM. 1983.** Taxonomy of the genus *Draco* L. (Agamidae, Lacertilia, Reptilia). *Zoologische Verhandlungen* **199**: 1–120.
- Myers P. 1978.** Sexual dimorphism in size of vespertilionid bats. *American Naturalist* **112**: 701–711.
- Pincheira-Donoso D, Tregenza T. 2011.** Fecundity selection and the evolution of reproductive output and sex-specific body size in the *Liolaemus* lizard adaptive radiation. *Evolutionary Biology* **38**: 197–207.
- R Development Core Team. 2011.** *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.
- Raihani G, Székely T, Serrano-Meneses MA, Pitra C, Goriup P. 2006.** The influence of sexual selection and male agility on sexual size dimorphism in bustards (Otididae). *Animal Behavior* **71**: 833–838.
- Rensch B. 1950.** Die Abhängigkeit der relativen Sexualdifferenz von der Körpergröße. *Bonner Zoologische Beiträge* **1**: 58–69.
- Rensch B. 1960.** *Evolution above the species level*. New York, NY: Columbia University Press.
- Revell LJ. 2009.** Size-correction and principal components for interspecific comparative studies. *Evolution* **63**: 3258–3268.
- Revell LJ. 2010.** Phylogenetic signal and linear regression on species data. *Methods in Ecology and Evolution* **1**: 319–329.
- Revell LJ. 2012.** phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* **3**: 217–223.
- Schoener TW. 1977.** Competition and the niche. In: Gans C, Tinkle D, eds. *Biology of the reptilia, Vol. 4*. New York, NY: Academic Press, 35–136.

- Serrano-Meneses MA, Córdoba-Aguilar A, Azpilicueta-Amorín M, González-Soriano E, Székely T. 2008.** Sexual selection, sexual size dimorphism and Rensch's rule in Odonata. *Journal of Evolutionary Biology* **21**: 1259–1273.
- Shine R, Keogh S, Doughty P, Giragossyan H. 1998.** Costs of reproduction and the evolution of sexual dimorphism in a 'flying lizard' *Draco melanopogon* (Agamidae). *Journal of Zoology* **246**: 203–213.
- Sibly RM, Zuo W, Kodric-Brown A, Brown JH. 2012.** Rensch's rule in large herbivorous mammals derived from metabolic scaling. *American Naturalist* **179**: 169–177.
- Smith RJ. 1999.** Statistics of sexual size dimorphism. *Journal of Human Evolution* **36**: 423–459.
- Stamps JA. 1983.** Sexual selection, sexual dimorphism, and territoriality. In: Huey RB, Pianka ER, Schoener TW, eds. *Lizard ecology: studies of a model organism*. Cambridge, MA: Harvard University Press, 169–204.
- Stark RC, Fox SF, Leslie DM Jr. 2005.** Male Texas horned lizards increase daily movements and area covered in spring: a mate searching strategy? *Journal of Herpetology* **39**: 169–173.
- Stuart-Fox D. 2009.** A test of Rensch's rule in dwarf chameleons (*Bradypodion* spp.), a group with female-biased sexual size dimorphism. *Evolutionary Ecology* **23**: 425–433.
- Székely T, Freckleton RP, Reynolds JD. 2004.** Sexual selection explains Rensch's rule of size dimorphism in shorebirds. *Proceedings of the National Academy of Sciences of the United States of America* **101**: 12224–12227.
- Székely T, Lislevand T, Figuerola J. 2007.** Sexual size dimorphism in birds. In: Blanckenhorn W, Fairbairn D, Székely T, eds. *Sex, size & gender roles: evolutionary studies of sexual size dimorphism*. Oxford: Oxford University Press, 27–37.
- Temeles EJ. 1985.** Sexual size dimorphism of bird-eating hawks: the effect of prey vulnerability. *American Naturalist* **125**: 485–499.
- Verwaijen D, Van Damme R, Herrel A. 2002.** Relationships between head size, bite force, prey handling efficiency and diet in two sympatric lacertid lizards. *Functional Ecology* **16**: 842–850.
- Vitt LJ, Cooper WE Jr. 1985.** The evolution of sexual dimorphism in the skink *Eumeces laticeps*: an example of sexual selection. *Canadian Journal of Zoology* **63**: 995–1002.
- Zamudio KR. 1998.** The evolution of female-biased sexual size dimorphism: a population-level comparative study in horned lizards (*Phrynosoma*). *Evolution* **52**: 1821–1833.