

Scaling of Morphological Characters across Trait Type, Sex, and Environment: A Meta-analysis of Static Allometries

Kjetil Lysne Voje*

Department of Biosciences, Centre for Ecological and Evolutionary Synthesis, University of Oslo, P.O. Box 1066, Blindern NO-0316, Oslo, Norway

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ABSTRACT: Biological diversity is, to a large extent, a matter of variation in size. Proportional (isometric) scaling, where large and small individuals are magnified versions of each other, is often assumed to be the most common way morphological traits scale relative to overall size within species. However, the many traits showing nonproportional (allometric) scaling have motivated some of the most discussed hypotheses on scaling relationships in biology, like the positive allometry hypothesis for secondary sexual traits and the negative allometry hypothesis for genitals. I evaluate more than 3,200 allometric parameters from the literature and find that negative allometry, not isometry, is the expected scaling relationship of morphological traits within species. Slopes of secondary sexual traits are more often steeper compared with other traits, but slopes larger than unity are also common for traits not under sexual selection. The steepness of the allometric slope is accordingly a weak predictor of past and present patterns of selection. Scaling of genitals varies across taxonomic groups, but negative allometry of genitals in insects and spiders is a consistent pattern. Finally, I find indications that terrestrial organisms may have a different scaling of morphological traits overall compared with aquatic species.

Keywords: allometry, isometry, sexual selection, genitals, evolution.

Introduction

The study of how features of organisms scale with overall body size has been one of the most successful attempts in describing general trends within biology (Schmidt-Nielsen 1984; West et al. 1997, 1999). Such scaling relationships are often well described by power functions, commonly referred to as allometric equations. They have the form $Y = aX^b$, where b is the scaling exponent that describes how the trait Y relates to changes in the overall size variable X . The detection of various power laws in physiological (Kleiber 1947; Schmidt-Nielsen 1984), life-history (Calder 1984; Charnov

1993), ecological (Peters 1986; Reiss 1989), and morphological traits (Huxley 1932; Gould 1966) has triggered numerous hypotheses on adaptation and constraints on the evolution of phenotypic diversity. For example, explanations of the close fit of the allometric model to across-species data generally fall in two broad classes: those interpreting the model parameters as reflections of functional adaptation between traits and those that interpret the fit of the model as representing developmental and structural constraints on trait evolution (Pélabon et al. 2014; Voje et al. 2014).

Most studies of morphological scaling relationships have focused on the scaling exponent in the allometric model. An exponent of 1 is known as isometric (proportional) scaling, meaning large and small individuals are magnified versions of each other. Natural selection is recognized to cause allometric (nonproportional) scaling of morphological traits due to, for example, biomechanical and physiological reasons. For example, since Galileo (1638), we have understood that big terrestrial animals need disproportionately thicker bones, compared with those of smaller terrestrial animals, to support their greater body weight. However, bones of organisms that are less constrained by gravitational forces on their body mass, like whales and fish, can show isometric scaling with body size (Schmidt-Nielsen 1984). Convincing examples of allometric scaling ($b \neq 1$) of morphological traits that cannot be explained by general biomechanical principles have accordingly been argued to be special cases in need of explanation (Tomkins et al. 2010; Shingleton and Frankino 2013). A test of a significant deviation from isometry is indeed a common procedure in studies of morphological allometry within species (e.g., Hills et al. 1983; Johnson 1995; Grandjean et al. 1997; Flores and Negreiros-Fransozo 1999; Schmitz et al. 2000; Sørensen et al. 2003; Aisenberg et al. 2010).

Some of the most popular hypotheses regarding within-species (static) allometric scaling of morphological traits (the intraspecific allometric relationship observed across

* E-mail: k.l.voje@ibv.uio.no.

individuals in the same developmental stage; Gould 1966; Cheverud 1982) are inspired by observations of non-proportional scaling. One example is the positive allometry hypothesis, which claims secondary sexual traits almost universally exhibit positive static allometry (Green 1992; Petrie 1992). Traits that function as weapons or signal traits are often under directional sexual selection and many of them turn into exaggerated structures, like the antlers of the extinct Irish Elk *Megaloceros giganteus* (Gould 1974) and the eye span of stalk-eyed flies (Burkhardt and la Motte 1983). According to the positive allometry hypothesis, a steep allometric exponent will be the result of sexual selection if an increased relative trait size yields increased mating success (e.g., when the cost of producing a larger trait is condition dependent; Bonduriansky 2007). Positive static allometry ($b > 1$) has accordingly been suggested as an indicator of whether a trait is under sexual selection (e.g., Green 1992; Petrie 1992), a claim that has inspired theoretical investigations of the conditions for when sexual selection may result in steep allometries (Bonduriansky and Day 2003; Kodric-Brown et al. 2006; Fromhage and Kokko 2014). Another popular idea inspired by a pattern of non-proportional scaling is the negative allometry hypothesis of spider and insect genitalia (Eberhard et al. 1998; Eberhard 2009). Male genitals in these two groups often have a static allometric exponent less than 1, a pattern often explained by the advantage of males having genital sizes that are appropriately adjusted to the most common size or internal genital structures of females in the population (Eberhard et al. 1998; Eberhard 2009).

At the same time that there are many examples of positive allometric scaling of secondary sexual traits, it is far from clear whether such traits have a steeper slope more often than other traits (Bonduriansky 2007). An analysis comparing static allometric parameters across studies is one way to test the generality of proportional scaling within species and to assess the extent to which primary and secondary sexual traits show nonproportional scaling more often than expected. One challenge in performing such an analysis is the mixture of statistical models used in estimating relevant allometric parameters (Houle et al. 2011; Pélabon et al. 2014; Voje et al. 2014). For example, the commonly used reduced major axis (RMA) line-fitting technique estimates the slope as the ratio of the standard deviations of the trait and body size, which is not statistically equivalent to the slope parameter estimated from an ordinary least squares regression that depends on the covariation between the traits (e.g., Voje et al. 2014). Earlier reviews of the negative allometry hypothesis (Eberhard 2009) and the steep allometry of the secondary sexual traits hypothesis (Kodric-Brown et al. 2006; Bonduriansky 2007; Tomkins et al. 2010) reported allometric exponents estimated from different statistical models, which makes the slope estimates nonequiv-

alent and difficult to compare in a meaningful way. A second challenge is that many studies do not evaluate or discuss to what extent the allometric model fit their data. We are therefore running the risk of letting noninformative scaling parameters inform the debate on allometric hypotheses.

I evaluate more than 3,200 statistically equivalent static allometric parameters reported in the literature to test several hypotheses regarding static allometric scaling of morphological traits. Statistically equivalent means, in this context, that all allometric slopes I collected have been estimated using the same statistical model, which implies that all have the same biological interpretation. In this study, static allometry refers to the allometric relationship between a trait and overall size (both on log scale) observed across individuals of the same species and the same developmental stage (Gould 1966; Cheverud 1982). I first assess whether isometric scaling is generally more common than allometric scaling for morphological characters scale differently across trait types, sex, and environments, including to what extent primary and secondary sexual traits show allometric scaling more often compared with other traits (nonprimary or nonsecondary sexual traits). Last, I evaluate to what extent reported allometric parameters have been estimated on traits that fit the allometric model.

Material and Methods

Data

I surveyed all matches in Google Scholar for “static allometry” for within-species allometric exponents estimated for animal morphological traits (date of search: September 20, 2014; $N = 831$). Also, estimates of the coefficient of determination (R^2), the sample size, and the standard error of slope estimates were collected whenever this information was available. I also investigated citations in previous reviews on static allometries (Eberhard et al. 1998; Kodric-Brown et al. 2006; Bonduriansky 2007; Eberhard 2009; Tomkins et al. 2010; Voje et al. 2014). I included allometric slopes from only those studies that estimated the allometric model on bivariate data to avoid running the risk of adding slopes from multiple regressions where the sexes had not been allowed to have separate slope estimates. Available data sets were also reanalyzed in some cases to increase the sample size of allometric parameters. When detecting allometric parameters estimated on the same data but reported in different studies, I removed all but one of the identical slope estimates. Articles that reported allometric parameters matching my criteria (see below) are listed in the electronic supplement (table S1, available online). The data reported in this article have been deposited in the Dryad Digital Repository (<http://dx.doi.org/10.5061/dryad.d78c5>; Voje 2015).

To test whether allometric slopes differ systematically across different types of traits, I sorted traits into the following categories on the basis of information in the article that they were collected from: primary sexual traits, secondary sexual traits, and traits that did not fit either of these two categories (referred to as “naturally selected traits”). A trait was recognized as a secondary sexual trait only if the authors specifically claimed that intra- or interspecific sexual selection operated on the trait. A sexual dimorphic trait was therefore not automatically categorized as a secondary sexual trait, because such dimorphism may, for example, result from a general size difference between the sexes. Traits could in some cases be fitted into more than one category. For example, a genital trait may also function as a secondary sexual trait, and many traits may be under both natural and sexual selection. In these cases, genitals were always categorized as a primary sexual trait, and nongenital traits under intra- or interspecific sexual selection were always categorized as secondary sexual traits.

Comparing allometric exponents across studies is meaningful only if the parameters have been estimated on data on equivalent scales and have the same statistical interpretation. In line with the original work on allometric scaling relationship in morphology (Huxley 1924, 1932; Gould 1966), I therefore considered only studies that estimated the allometric parameters on a log scale using least squares regression, which is equivalent to the equation for a straight line $\log(Y) = a + b\log(X)$, where b is the allometric exponent. All allometric exponents estimated using other line-fitting methods were excluded, including studies that fitted the allometric power function ($Y = aX^b$) to data on an absolute scale, because this model deviates from the logarithmic version in assuming absolute rather than multiplicative errors. The least squares slope coefficient is equal to the slope estimated using reduced major axis (RMA) regression multiplied with the correlation coefficient of the variables. I therefore calculated least squares exponents from articles that reported these two parameters. I included only studies that estimated the allometric parameters on traits of equal dimensionality (e.g., length vs. length and area vs. area), which means isometry always equals a coefficient of 1.

Statistical Analyses

I calculated empirical cumulative distribution functions for distributions of within-species allometric exponents to get an overview of the variation in morphological scaling relationships within species. These distributions were used to estimate the likelihood of such coefficients falling within different slope ranges. Nonparametric bootstrapping (10,000 replicates) was used to estimate the uncertainty in the median of the distributions, and I report these as estimates (\pm SE). Only slopes from allometric relationships that had

been estimated on the basis of at least 20 individuals and where the allometric model explained at least 25% of the trait variation were included in the analyses. Applying these cut-off values ensures that inferences are based on only those allometric parameters that show a certain fit to the data that they describe. Allometric models fitted to noncorrelating traits are commonplace in the literature, and including slopes from such models would have made the distributions of within-species allometric exponents bimodal, with one of the peaks centering around zero, and would skew the median toward more shallow slopes.

I fitted generalized linear mixed-effect models using the lme4 (Bates et al. 2014) and effects (Fox 2003) packages in R, version 3.0.2 (R Development Core Team 2015) to conduct a meta-analysis of static allometries. Only allometric slopes with reported standard errors and where the allometric model explained at least 25% of the trait variation were part of the analyzed data. Slope estimates were given weights depending on their estimated reliability using the inverse of the sampling variance. “Study” and “species” were always included as random effects to account for potential study- and species-level autocorrelation. Slope distributions were assumed to follow a normal distribution. Mixed-effect models were used to estimate a baseline static allometric slope expectation across all traits and investigate whether allometric scaling differs across sexes, trait types, and environments (table 1). The number of taxonomic levels that could be included in the various models was limited by sample size.

A linear least squares regression was used to test whether the fit of the static allometric model (R^2) predicts the steepness of the static allometric slope. I consider this a test of the general fit of the allometric model to morphological traits. The sampling uncertainty in the regression model was assessed by nonparametric bootstrapping (10,000 replicates) and is reported as estimate (\pm SE). R scripts containing all analyses are available online.

Results

Data

I found 3,269 within-species allometric slopes in the literature that fulfilled my criteria for being statistically equivalent and accordingly meaningful to compare. The slopes come from 119 studies and cover 510 different species from several animal classes, including mammals, birds, insects, ray-finned fish, reptiles, and amphibians.

Slope Distributions

A total of 928 of the 3,269 allometric relationships (coming from 75 studies) explained at least 25% of the trait

Table 1: Linear mixed-effect models

Model	Response	Fixed effect(s)	Random effects
1	All allometric slopes	Intercept only	Study and species
2	All allometric slopes	Sex	Study and species
3	All allometric slopes	Trait type	Study and species
4	Slopes from genitals and naturally selected traits	Sex × trait type	Study and species
5	Slopes of genital traits	Taxa	Study and species
6	Slopes from traits under sexual selection	Taxa	Study and species
7	Slopes from traits under natural selection	Taxa	Study and species
8	Slopes from traits under natural selection	Habitat	Study and species
9	Slopes from traits under natural selection	Habitat × sex	Study and species
10	Slopes from secondary sexual traits	Habitat	Study and species

variance and had been estimated on the basis of at least 20 measured individuals. The distribution of the 928 slopes (fig. 1A) shows that many morphological traits scale proportionally with overall size. The median of the distribution is $0.94 (\pm 0.01)$, and 42.1% of the slopes are expected to have a steeper slope than 1. The variation in allometric slopes is large, ranging from 0.15 in the male genital length of the beetle *Dorcus reichei* (SE not available; $R^2 = 0.64$; Kawano 2004) to 4.80 (95% confidence interval [CI], 3.9–5.7; $R^2 = 0.80$), which is how the bacular thickness (a genital trait) at mid-shaft changes with body length in the Harp seal (*Pugophilus groenlandicus*; Miller and Burton 2001). The distribution containing only naturally selected traits (i.e., nonprimary and nonsecondary sexual traits; $N = 669$; fig. 1B) has a median (\pm SE) of 0.95 ± 0.01 , and 41.4% of the slopes are larger than 1. The majority of the secondary sexual traits (fig. 1C) show a positive allometric scaling with overall size ($N = 131$; median slope, 1.20 ± 0.06), and 70.2% of the slopes are larger than 1. The great majority of the 138 genital traits show a negative allometric scaling relationship with overall size (fig. 1D). The median of the distribution is 0.52 ± 0.04 , and 19.6% of the slopes are larger than 1.

Meta-analysis

Parameter estimates from the linear mixed-effect models are reported in table 2. The expected baseline static allometric slope estimated from the intercept-only model is 0.86 (95% CI, 0.77–0.94). Males and females differ in predicted slope of approximately 0.09 units, but their confidence intervals show a large overlap. Genitals, secondary sexually selected traits, and naturally selected traits have nonoverlapping 95% CIs (fig. 2; table 2). The expected slope for genitals shows strong negative allometry (0.59), whereas secondary sexual traits show strong positive allometry (1.30). The expected slope of naturally selected traits is 0.87, and the confidence interval does not include isomet-

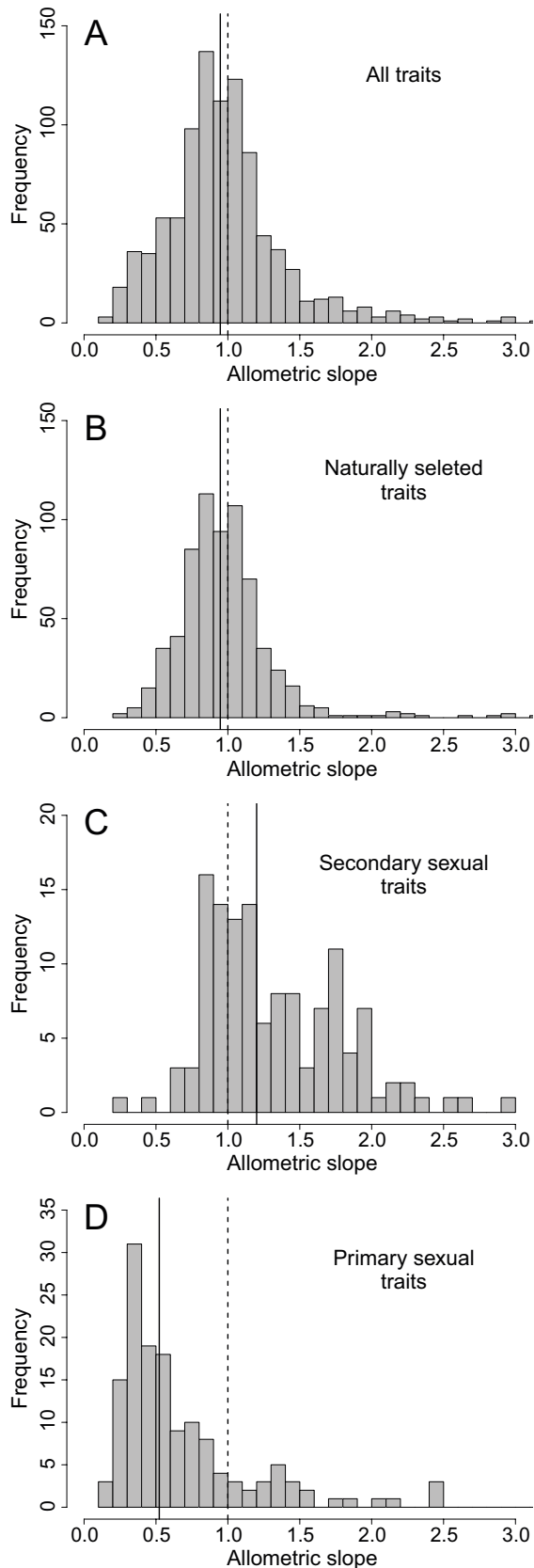
ric scaling. There is no clear difference in how genitals and naturally selected traits scale in males and females, but note the small sample size of slopes for female genitals.

Only a few taxa had a sufficient sample size to test whether trait types scaled differently across groups of species. The estimated expectation for static allometric scaling of genitals in insects, spiders, and mammals is negative (table 2), but neither spiders nor mammals are represented by very large sample sizes. The expected slope of secondary sexually selected traits in insect is 1.32, whereas it is 0.89 for spiders. However, both taxa show very wide confidence intervals, and the sample size of spiders is low. Mammals, insects, spiders, and reptiles have expected slope estimates between 0.86 and 0.88 for naturally selected traits, whereas the expectation for crustaceans is close to isometry (1.07).

Terrestrial and aquatic animals differ in their expected slope of naturally selected traits (0.83 vs. 1.02), although the 95% CIs overlap (fig. 3). The difference in expected slope is not explained by different scaling across the sexes, which is overall very similar within each environment (table 2). No difference was detected for sexually selected traits between terrestrial and aquatic animals, whereas small sample sizes prevented a similar test for genitals.

Fit of the Allometric Model

The coefficient of determination (R^2) was reported for 1,297 allometric relationships estimated on at least 20 measured individuals (from 93 studies). Huge variation exists in how much the size of a trait covaries with the chosen measure of body size. The distribution of R^2 has one peak around 0 and another close to 1 (fig. 4A), with a median of 0.56. The R^2 is a weak predictor of the steepness of the allometric slope (fig. 4B); the slope of the linear relationship between R^2 and allometric slope is 0.81 ± 0.04 , and $22.8\% \pm 3.5\%$ of the variation in static slopes is explained.



Discussion

The study of scaling relationships in biology has been successful in revealing regularities of growth, evolutionary trends, and underlying constraints on phenotypic diversification (Huxley 1932; Gould 1977; Schmidt-Nielsen 1984; Brown and West 2000). Isometric scaling of morphological traits has been argued to be the default way morphological traits scale within species (e.g., Shingleton and Frankino 2013), and the many examples of deviations from proportional scaling have inspired some of the most popular hypotheses on static allometric scaling (Green 1992; Petrie 1992; Eberhard et al. 1998, 2009). The current survey of the literature finds support for some of these hypotheses, finds mixed support for others, and reveals indications of environment-dependent regularities of morphological scaling.

Proportional (Isometric) Scaling May Not Be the Rule

The distributions of empirically estimated static allometric slopes show a large variation in how morphological traits scale with overall size within species. The grand mean slope expectation from the linear mixed-effect model is 0.86, and the 95% confidence interval does not include 1. Also, the median of the empirical slope distribution was less than 1. Together, this indicates that weakly negative allometry, not isometry, might be the most common way traits scale with overall size within species. The biological implications of such a change in expected slope may, to some extent, be dependent on the organism in question, but assuming a slightly wrong slope can have a substantial effect on the predicted trait variation if the variation in body size is large. However, even if weak allometry is the most common way traits scale, this does not imply that it is wrong to test for a significant deviation from isometry in studies of morphological allometry. There are many reasons why it is interesting to know whether a trait scales proportionally with changes in overall size. But the use of isometry as a null hypothesis based on the assumption that this is the default way morphological traits scale is not supported by the data presented in this study.

The conclusion that weakly negative allometry, and not isometry, is the most common way morphological traits scale comes with some caveats. First, it is hard to rule out an effect of publication bias on the global slope expectation.

Figure 1: Distributions of allometric slopes. All traits (A), naturally selected traits (B), secondary sexual traits (C), and primary sexual traits (D; genitals). The dotted line represents isometric scaling, whereas the unbroken line represents the median of the distribution. Note the differences in the Y-axis across panels. The X-axis is identical in all four panels to ease comparison, but two naturally selected traits and three primary sexual traits have larger slopes than 3.0 and are not shown.

Table 2: Results of the linear mixed-effect models

Model (traits analyzed)	Sample size	Slope estimate (\pm SD)	95% CI
1 (All traits):			
Grand mean	553	.86 (1.00)	.77–.94
2 (All traits):			
Females	196	.78 (.71)	.68–.88
Males	344	.87 (1.61)	.77–.96
3 (All traits):			
G	74	.59 (.37)	.50–.68
SSST	90	1.30 (.39)	1.20–1.39
NST	389	.87 (.52)	.79–.94
4 (Genitals and naturally selected traits):			
Female:			
G	9	.65 (.25)	.48–.81
NST	60	.94 (.62)	.87–1.02
Male:			
G	187	.52 (1.10)	.44–.60
NST	194	.89 (1.13)	.82–.96
5 (Genitals):			
Insects	36	.47 (.24)	.39–.55
Mammals	12	.81 (.45)	.56–1.06
Spiders	17	.45 (.30)	.33–.57
6 (Secondary sexually selected traits):			
Insects	54	1.32 (1.44)	.86–1.78
Spiders	21	.89 (2.78)	–.41 to 2.18
7 (Naturally selected traits):			
Crustaceans	72	1.07 (.91)	.84–1.30
Insects	147	.87 (1.43)	.77–.97
Mammals	21	.86 (.71)	.64–1.08
Reptiles	103	.88 (2.06)	.40–1.36
Spiders	43	.88 (.97)	.68–1.08
8 (Naturally selected traits):			
Terrestrial	463	.83 (2.56)	.74–.92
Aquatic	90	1.02 (1.05)	.79–1.25
9 (Naturally selected traits):			
Female:			
Terrestrial	46	.89 (.77)	.80–.98
Aquatic	30	1.15 (.57)	.92–1.37
Male:			
Terrestrial	208	.87 (.37)	.79–.95
Aquatic	166	1.05 (.52)	.84–1.27
10 (Secondary sexually selected traits):			
Terrestrial	79	1.28 (3.53)	.90–1.67
Aquatic	14	1.24 (1.37)	.48–1.99

Note: Model numbers refer to the models defined in table 1. CI = confidence interval; G = genital traits; NST = naturally selected traits; SD = standard deviation of slope estimate; SSST = secondary sexually selected traits.

Biologists have a fascination for unusually exaggerated morphologies in their study objects (Bonduriansky 2007), leading to a bias toward steep slopes reported in the literature.

The focus on allometric scaling of genital traits may also have biased the literature, but in the opposite direction, toward more shallow allometric slopes. However, the distribution of empirical slope estimates from naturally selected traits only (i.e., nonprimary or nonsecondary sexual traits) has almost the same mode and median as the full distribution, and publication bias toward extreme scaling relationships cannot explain the similarity between these two distributions. Also, the estimated mean slopes from naturally selected traits in males and females from the mixed-effect models (0.87 and 0.89, respectively) are very similar to the estimated grand mean (0.86). A second source of error that will shift the slope expectation toward a shallower slope is measurement error in the predictor (body size) variable. Measurement error in the body size variable causes a downward bias in the allometric slope proportional to the amount of variation in the predictor variable that is due to measurement error (Fuller 1987). The current analysis therefore suggests weakly negative allometry as the most common scaling relationship overall, but future studies that correct for measurement error in the predictor variable in their estimates of static allometries will be important tests of this conclusion.

Support for a Link between Sexual Selection and Positive Allometry

Sexual selection has been suggested to favor disproportionately larger traits in larger individuals. Such positive allometry may, for example, evolve when the relative costs of expressing a large trait are lower for larger individuals (e.g., Petrie 1992) or when larger trait size confers a direct advantage in sexual competition, resulting in stronger directional selection on trait size than on body size (e.g., Green 1992). The results of the mixed-effect models show an overall strong support for the positive allometry hypothesis; secondary sexual traits have a slope expectation much steeper than both naturally selected traits and genitals. Tests of whether the hypothesis holds within different taxa were limited by small sample size; however, the hypothesis is supported in insects, although less so in spiders.

It is important to remember that support for a link between secondary sexual traits and positive allometry does not make the steepness of the allometric slope a particularly reliable indicator of the type of selection (natural vs. sexual selection) that has operated on the trait. First, and as pointed out by Bonduriansky (2007), there are examples of negative slopes of traits under secondary sexual selection, such as forceps of certain species of earwigs (Simmons and Tomkins 1996), forelegs in the fly *Chymomyza exophthalma* (Eberhard 2002), and forelimb length in *Rana clamitans* and *Bufo americanus* (Shulte-Hostedde et al. 2011). Second, even though naturally selected traits have an expected slope of less than 1, more than 40% of slopes of naturally selected

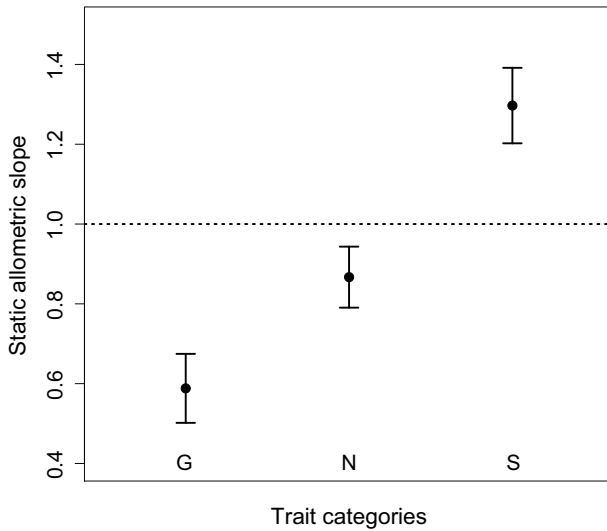


Figure 2: Differences in expected static allometric slope across trait types as predicted from a linear mixed-effect model (model 3 in table 1). The mean predicted slope (\pm SD) is 0.59 ± 0.37 ($N = 74$) for genitals (G), 0.87 ± 0.52 ($N = 389$) for naturally selected traits (N), and 1.30 ± 0.39 ($N = 90$) for secondary sexually selected traits (S). The dotted horizontal line represents proportional (isometric) scaling. Error bars represent 95% confidence intervals, which do not overlap across any of the three trait categories. See model 3 in table 2 for more details.

traits are larger than 1 based on the empirical slope distributions. Because there are many more naturally selected traits than secondary sexually selected traits reported in the literature, this means that only approximately 25% of the traits showing positive allometry in this study represent secondary sexual traits. The steepness of the slope alone has accordingly limited predictive power when trying to infer whether a character is a secondary sexually selected trait. How different types of selection affect the allometric slope is poorly known (reviewed in Pelabon et al. 2014). However, one way to strengthen the argument of whether a certain trait is under secondary sexual selection might be to compare scaling relationships between the sexes. There are few reasons to expect differences in slopes between the sexes if the same selection pressures operate on the trait in both males and females. Male eye span is a secondary sexual trait in many stalk-eyed flies (Burkhardt and la Motte 1983; Wilkinson et al. 1998), and a steeper static allometric slope is commonly observed in males than in females (Voje and Hansen 2013). Similarly, sexual dimorphism in facial morphology in *Anolis* lizards is sometimes caused by a steeper allometric slope in males than females, although it is more common to observe a shift in only the allometric intercept (Sanger et al. 2013). However, correlated trait evolution across the sexes due to strong selection on the trait in only one of the sexes can potentially cause both male and female al-

lometric slope to change in the same direction, which is one possible explanation for why many female stalk-eyed flies show positive allometry (Voje and Hansen 2013). Comparisons of homologous allometric slopes between the sexes should therefore focus on the relative slope difference and not the steepness of one of the slopes alone.

The Law of Negative Scaling of Genitals in Insects and Spiders

I find strong support for negative allometric scaling of genitalia in insects and spiders, whereas the evidence for such a pattern in mammals is less convincing. The selection regimes causing the pattern of shallow genital allometries in insects and spiders probably vary, because a single selection-hypothesis does not fit in all cases (Eberhard 2009; Eberhard et al. 2009). Independent of the precise types of selection creating the pattern, the negative allometric scaling of genitalia in insects and spiders is perhaps the most consistent pattern detected so far of within-species allometric relations.

Different Scaling of Morphological Traits in Terrestrial and Aquatic Organisms

Gravitational forces are different in water relative to on land, which has been found to influence scaling relation-

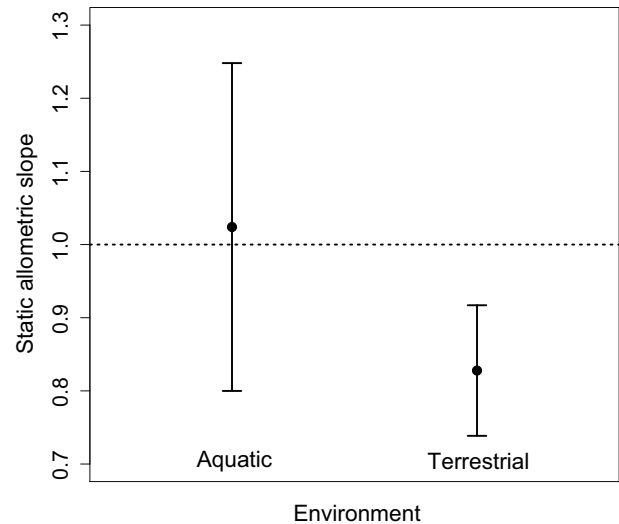


Figure 3: Differences in expected static allometric slope across aquatic and terrestrial animals as predicted from a linear mixed-effect model (model 8 in table 1). Aquatic animals have a predicted slope (\pm SD) of 1.02 ± 1.05 ($N = 90$), whereas the predicted slope for terrestrial animals is 0.83 ± 2.56 ($N = 463$). The dotted horizontal line represents proportional (isometric) scaling. Error bars represent 95% confidence intervals. See model 8 in table 2 for parameter estimates.

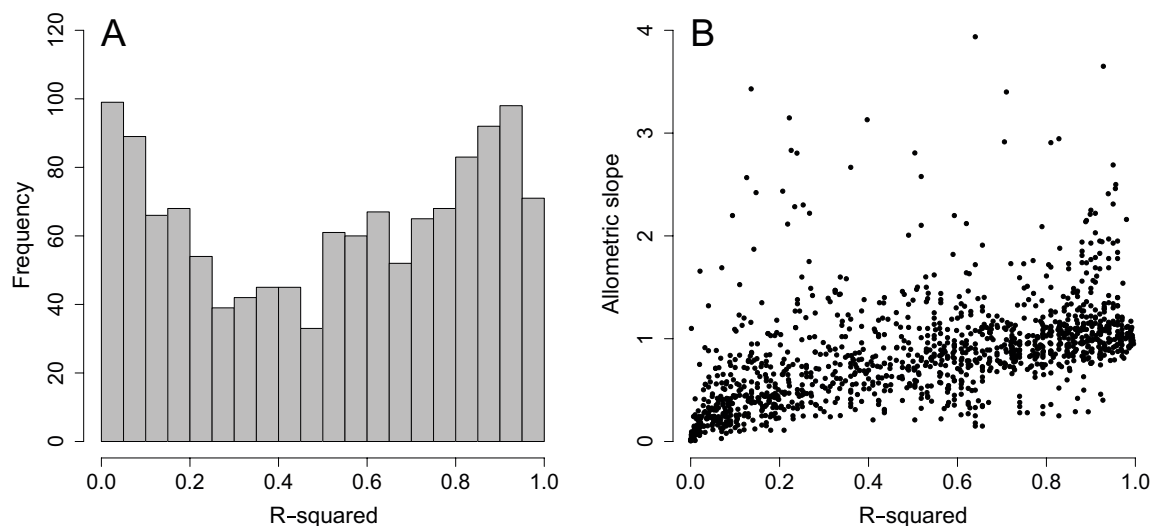


Figure 4: A, Distribution of 1,297 reported R^2 values from within-species (static) allometric relationships. The median of the distribution is 0.56. B, Within-species (static) allometric slope as a function of R^2 , the latter used as a measure of the fit of the allometric model to the data. R^2 explains a mean (\pm SD) of 22.7% (\pm 3.4%) of the variation in allometric slopes, but this trend is to a large extent driven by the large number of allometries with an R^2 close to zero. R^2 explains only 8.7% (\pm 1.9%) of the variation in allometric slopes when only allometric relations with an R^2 larger than 0.25 are considered.

ships of bone mass to total body mass across species in whales and fish compared with how this trait scales across terrestrial animals (Schmidt-Nielsen 1984). The results of this study indicate that morphological traits in aquatic organisms in general scale close to isometry, whereas terrestrial organisms have an expected scaling around 0.87. Also, naturally selected traits in crustaceans showed a mean scaling relationship close to isometry, whereas the expected slope of traits in the same trait category in terrestrial mammals, insects, spiders, and lizards indicated negative allometric scaling. The buoyancy experienced by aquatic organisms therefore seems to have a general impact on how traits scale across life forms living in or out of water.

Biological and Statistical Fit of the Allometric Model

The literature on within-species allometric scaling relationships is large and challenging to evaluate. One reason is that many studies do not report to what extent their data fit the allometric model. This is a potential problem, because traits often do not covary very strongly with the chosen measure of body size (fig. 4A). Steep allometric slopes do not automatically have a large R^2 , and the coefficient of determination is only a weak predictor of the steepness of the allometric slope (fig. 4B). Without critically assessing whether a particular model fits our data, we are running the risk of letting nonsense parameter estimates inform our hypotheses.

Another source of potential confusion in the literature on within-species allometries comes from the various sta-

tistical models that are used in estimating them. For example, common for the majority of the most extreme slopes of trait and body size relationships is that they have been estimated using reduced major axis (RMA) regression. This statistical model estimates the slope parameter as the ratio of the standard deviations of the trait and body size. Such slopes are regularly referred to and interpreted as allometric slopes but are not comparable to least squares regression estimates, because the latter depend on the covariation between the trait and body size. That horns in males in the beetle species *Onthophagus taurus* has an RMA slope of 15.7 (Tomkins et al. 2005) is therefore not informative regarding how this trait changes with overall size (i.e., allometry), but rather says that the standard deviation in horn size is close to 16 times larger than the standard deviation in body size on a proportional scale. RMA is therefore not the appropriate tool if we want to study how trait changes in concert (Huxley 1932; Savageau 1979; Stevens 2009), which is the foundation of the study of multivariate trait evolution (Lande 1979; Lande and Arnold 1983) and the conventional way allometry has been studied (Huxley 1932; Gould 1966).

Conclusion

Distributions of statistically equivalent static (within-species) allometric slopes reveal huge variation in morphological scaling relationships. Most secondary sexually selected traits show steep allometry, but many traits under

natural selection also have an allometric slope larger than 1. The steepness of the allometric coefficient is therefore not a particularly reliable indicator of the type of selection (natural vs. sexual selection) that has operated on the trait. The overall expected allometric scaling relationship of morphological traits is weak negative allometry, not isometry. Testing for a deviance from isometry can be interesting for many reasons, but such tests should not be conducted only on the basis of the assumption that most traits scale proportionally with overall size. How well the allometric model fits a trait and body size relationship should always be reported. Whether the allometric model accurately describes how a trait changes with overall size is essential information to interpret its parameters in relation to many hypotheses on allometric scaling.

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Literature Cited

- Aisenberg, A., F. G. Costa, M. González, R. Postiglioni, and F. Pérez-Miles. 2010. Sexual dimorphism in chelicerae, forelegs and palpal traits in two burrowing wolf spiders (Araneae: Lycosidae) with sex-role reversal. *Journal of Natural History* 44:1189–1202.
- Bates D., M. Maechler, B. Bolker, and S. Walker. 2014. lme4: linear mixed-effects models using Eigen and S4. R package, version 1.1–7.
- Bonduriansky, R. 2007. Sexual selection and allometry: a critical reappraisal of the evidence and ideas. *Evolution* 61:838–849.
- Bonduriansky, R., and T. Day. 2003. The evolution of static allometry in sexually selected traits. *Evolution* 57:2450–2458.
- Brown, J. H., and G. B. West. 2000. *Scaling in biology*. Oxford University Press, Oxford.
- Burkhardt, D., and I. de la Motte. 1983. How stalk-eyed flies eye stalk-eyed flies: observations and measurements of the eyes of *Cyrtodopsis whitei* (Diopsidae, Diptera). *Journal of Comparative Physiology* 151:407–421.
- Calder, W. A. 1984. *Size, function, and life history*. Harvard University Press, Cambridge, MA.
- Charnov, E. L. 1993. *Life history invariants*. Oxford University Press, New York.
- Cheverud, J. M. 1982. Relationships among ontogenetic, static, and evolutionary allometry. *American Journal of Physical Anthropology* 59:139–149.
- Eberhard, W., A. B. Huber, R. L. Rodriguez, R. D. Briceno, I. Salas, and V. Rodriguez. 1998. One size fits all? relationships between the size and degree of variation in genitalia and other body parts in twenty species of insects and spiders. *Evolution* 52:415–431.
- Eberhard, W., R. L. Rodriguez, and M. Polihronakis. 2009. Pitfalls in understanding the functional significance of genital allometry. *Journal of Evolutionary Biology* 22:435–445.
- Eberhard, W. G. 2002. Natural history and behavior of *Chymomyza mycopelates* and *C. exophthalma* (Diptera: Drosophilidae), and allometry of structures used as signals, weapons, and spore collectors. *Canadian Entomologist* 134:667–687.
- . 2009. Static allometry and animal genitalia. *Evolution* 63:48–66.
- Flores, A., and M. L. Negreiros-Fransozo. 1999. Allometry of the secondary sexual characters of the shore crab *Pachygrapsus transversus* (Gibbes, 1850) (Brachyura, Grapsidae). *Crustaceana* 72:1051–1066.
- Fox, F. 2003. Effect displays in R for generalised linear models. *Journal of Statistical Software* 8:1–27.
- Fromhage, L., and H. Kokko. 2014. Sexually selected traits evolve positive allometry when some matings occur irrespective of the trait. *Evolution* 68:1332–1338.
- Fuller, W. A. 1987. *Measurement error models*. Wiley, New York.
- Gould, S. J. 1966. Allometry and size in ontogeny and phylogeny. *Biological Reviews* 41:587–640.
- . 1974. The origin and function of “bizarre” structures: antler size and skull size in the “Irish Elk,” *Megaloceros giganteus*. *Evolution* 28:191–220.
- . 1977. *Ontogeny and phylogeny*. Belknap, Cambridge, MA.
- Grandjean, F., D. Romain, C. Souty-Grosset, and J. P. Mocquard. 1997. Size at sexual maturity and morphometric variability in three populations of *Austropotamobius pallipes* (Lereboullet, 1858) according to a restocking strategy. *Crustaceana* 70:454–468.
- Green, A. J. 1992. Positive allometry is likely with mate choice, competitive display and other functions. *Animal Behaviour* 43:170–172.
- Hills, M., S. H. Graham, and B. A. Wood. 1983. The allometry of relative cusp size in hominoid mandibular molars. *American Journal of Physical Anthropology* 62:311–316.
- Houle, D., C. Pélabon, G. P. Wagner, and T. F. Hansen. 2011. Measurement and meaning in biology. *Quarterly Review of Biology* 86:3–34.
- Huxley, J. S. 1924. Constant differential growth-ratios and their significance. *Nature* 114:895–896.
- . 1932. *Problems of relative growth*. Dial, New York.
- Johnson, N. F. 1995. Variation in male genitalia of *Merope tuber* Newman (Mecoptera: Meropeidae). *Journal of the Kansas Entomological Society* 68:224–233.
- Kawano, K. 2004. Developmental stability and adaptive variability of male genitalia in sexually dimorphic beetles. *American Naturalist* 163:1–15.
- Kleiber, M. 1947. Body size and metabolic rate. *Physiological Reviews* 27:511–541.
- Kodric-Brown, A., R. M. Sibly, and J. H. Brown. 2006. The allometry of ornaments and weapons. *Proceedings of the National Academy of Sciences of the USA* 103:8733–8738.
- Lande, R. 1979. Quantitative genetic analysis of multivariate evolution, applied to brain: body size allometry. *Evolution* 33:402–416.
- Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. *Evolution* 37:1210–1226.
- Miller, E. H., and L. E. Burton. 2001. It's all relative: allometry and variation in the baculum (os penis) of the harp seal, *Pagophilus groenlandicus* (Carnivora: Phocidae). *Biological Journal of the Linnean Society* 72:345–355.

- Pélabon, C., C. Firmat, G. H. Bolstad, K. L. Voje, D. Houle, J. Cassara, A. L. Rouzic, et al. 2014. Evolution of morphological allometry. *Annals of the New York Academy of Sciences* 1320:58–75.
- Peters, R. H. 1986. *The ecological implications of body size*. Cambridge University Press, Cambridge.
- Petrie, M. 1992. Are all secondary sexual display structures positively allometric and, if so, why? *Animal Behaviour* 43:173–175.
- R Development Core Team. 2015. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.
- Reiss, M. J. 1989. *The allometry of growth and reproduction*. Cambridge University Press, Cambridge.
- Sanger, T. J., E. Sherratt, J. W. McGlothlin, E. D. Brodie, J. B. Losos, and A. Abzhanov. 2013. Convergent evolution of sexual dimorphism in skull shape using distinct developmental strategies. *Evolution* 67:2180–2193.
- Savageau, M. A. 1979. Allometric morphogenesis of complex systems: derivation of the basic equations from first principles. *Proceedings of the National Academy of Sciences of the USA* 76:6023–6025.
- Schmidt-Nielsen, K. 1984. *Scaling: why is animal size so important*. Cambridge University Press, Cambridge.
- Schmitz, G., K. Reinhold, and P. Wagner. 2000. Allometric relationship between genitalic size and body size in two species of mordellid beetles (Coleoptera: Mordellidae). *Annals of the Entomological Society of America* 93:637–639.
- Schulte-Hostedde, A. I., S. Kuula, C. Martin, C. C. M. Schank, and D. Lesbarrères. 2011. Allometry and sexually dimorphic traits in male anurans. *Journal of Evolutionary Biology* 24:1154–1159.
- Shingleton, A. W., and W. A. Frankino. 2013. New perspectives on the evolution of exaggerated traits. *BioEssays* 35:100–107.
- Simmons, L. W., and J. L. Tomkins. 1996. Sexual selection and the allometry of earwig forceps. *Evolutionary Ecology* 10:97–104.
- Sørensen, K., W. J. Koops, and M. Grossman. 2003. Size allometry in mink (*Mustela vison*) selected for feed efficiency. *Acta Agriculturae Scandinavica* 53:51–57.
- Stevens, C. F. 2009. Darwin and Huxley revisited: the origin of allometry. *Journal of Biology* 8:14.
- Tomkins, J. L., J. S. Kotiaho, and N. R. LeBas. 2005. Matters of scale: positive allometry and the evolution of male dimorphisms. *American Naturalist* 165:389–402.
- Tomkins, J. L., N. R. LeBas, M. P. Witton, D. M. Martill, and S. Humphries. 2010. Positive allometry and the prehistory of sexual selection. *American Naturalist* 176:141–148.
- Voje, K. L. 2015. Data from: Scaling of morphological characters across trait type, sex and environment: a meta-analysis of static allometries. *American Naturalist*, Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.d78c5>.
- Voje, K. L., and T. F. Hansen. 2013. Evolution of static allometries: adaptive change in allometric slopes of eye span in stalk-eyed flies. *Evolution* 67:453–467.
- Voje, K. L., T. F. Hansen, C. K. Egset, G. H. Bolstad, and C. Pélabon. 2014. Allometric constraints and the evolution of allometry. *Evolution* 68:866–885.
- West, G. B., J. H. Brown, and B. J. Enquist. 1997. A general model for the origin of allometric scaling laws in biology. *Science* 276:122–126.
- . 1999. The fourth dimension of life: fractal geometry and allometric scaling of organisms. *Science* 284:1677–1679.
- Wilkinson, G. S., H. Kahler, and R. H. Baker. 1998. Evolution of female mating preferences in stalk-eyed flies. *Behavioral Ecology* 9:525–533.

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