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## The static allometry of sexual and non-sexual traits in vervet monkeys

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### Abstract

Sexual traits vary tremendously in static allometry. This variation may be explained in part by body size-related differences in the strength of selection. We tested this hypothesis with in two populations of vervet monkeys, using estimates of the level of condition dependence for different morphological traits as a proxy for body size-related variation in the strength of selection. In support of the hypothesis, we found that the steepness of allometric slopes increased with the level of condition dependence. One trait of particular interest, the penis, had shallow allometric slopes and low levels of condition dependence, in agreement with one of the most consistent patterns yet detected in the study of allometry, that of genitalia exhibiting shallow allometries.

### ADDITIONAL KEYWORDS

*Chlorocebus*; primate; scaling relationships; sexual selection

### INTRODUCTION

Think about different athletes that interest you, and you will probably visualize differences in bodily proportions. How does this variation in proportions arise? This question may be asked with the quantitative framework of allometry, the study of how structure sizes scale on body size (Huxley 1932). The main descriptor of scaling is the allometric slope ( $b$ ), which is obtained from log-log regressions of trait size on body size. When traits have  $b = 1$ , they vary in proportion to body size (they exhibit isometry). Traits with  $b > 1$  are

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disproportionately large in large individuals and exhibit positive allometry (also known as hyperallometry). And traits with  $b < 1$  are disproportionately small in large individuals and exhibit negative allometry (also known as hypoallometry). We refer to variation between  $b > 1$  and  $b < 1$  in terms of steep vs. shallow allometries, respectively.

Allometry can be studied at various levels: between species or higher taxa (in what is known as evolutionary allometry); within species among developmental stages (ontogenetic allometry); and within species among individuals of the same developmental stage (static allometry). At any level, variation in allometric patterns challenges biologists to provide explanations in terms of sources of selection and developmental constraints (Huxley 1932; Gould 2002; Eberhard *et al.*, 2009). Here we focus on variation in static allometry.

Perhaps the greatest amount of variation in static allometry occurs in sexual traits. Some ornaments and weapons have very steep allometries (Kodric-Brown *et al.*, 2006; Bonduriansky, 2007). But sexual ornaments may also show isometry, or even quite shallow allometries (Cuervo & Møller, 2001; Bonduriansky, 2007; Schulte–Hostedde *et al.*, 2011). And it does not seem simple to predict which ornament will have what kind of allometry. The spectacular tail coverts of male resplendent quetzals, for example, scale shallowly with body size (with  $b = 0.38$ ), whereas the apparently more modest central tail feathers of male common tailor birds scale very steeply with body size ( $b = 9.01$ ; Cuervo & Møller, 2001). And then there is a large class of sexual traits, genitalia, that predominantly exhibit shallow allometries (Eberhard *et al.*, 1998; Eberhard, 2009).

Why would sexual traits vary so much in their static allometry? Here we focus on a hypothesis that posits an interplay between the form of selection (stabilizing vs. directional) and body size-related differences in the net benefit of trait size increase (Bonduriansky, 2007; Eberhard *et al.*, 2009; and see also Green, 1992; Eberhard *et al.*, 1998; Bonduriansky & Day, 2003). According to this hypothesis, stabilizing selection on trait size favors shallow allometries (Eberhard *et al.*, 1998, 2009). By contrast, the effect of directional selection varies according to whether the net benefits of increase in trait size vary with body size — i.e., according to whether the strength of net directional selection varies with body size (Bonduriansky, 2007; Eberhard *et al.*, 2009). This is because selection favoring larger ornaments should result in isometry if males of all sizes benefit equally from larger ornaments; but it should result in steeper allometries if larger males benefit to a greater extent from larger ornaments; and it should result in shallower allometries if smaller males are the ones that most benefit from bearing larger ornaments (Eberhard *et al.*, 2009; cf. Bonduriansky & Day, 2003; Bonduriansky, 2007).

This hypothesis will be challenging to test in full, because this would require measuring the form and strength of selection, asking whether the latter varies with body size, and assembling a collection of such measures for a number of species. Nevertheless, partial tests of the hypothesis are possible. There is evidence that traits under stabilizing selection have shallower allometries than traits under directional selection (Rodríguez & Al-Wathiqui, 2012a; Rodríguez *et al.*, 2014a). Another test approximated body size-related variation in the net benefits of trait increase with variation in the level of condition dependence of different traits, finding that more highly condition dependent traits under directional

selection have steeper allometries (Rodríguez *et al.*, 2014a). This test used behavioral traits, however, and it remains to be seen whether morphological traits follow the same patterns.

Here we focus on body size-related variation in the net benefits of trait increase, and we test its role with morphological traits. We approximate this body size-related variation in the net benefits of trait increase with variation in the level of condition dependence of different traits. The rationale for this proxy is that traits whose expression is related to individual condition are likely to have greater costs of expression for smaller individuals (Bonduriansky, 2007; see also Rowe & Houle, 1996; Shingleton *et al.*, 2007). In other words, we reason that the expression of costly traits (those related to condition) should be relatively cheaper for larger individuals, and thereby bring them higher benefits.

This rationale leads to the prediction that there should be a positive relationship between the level to which different structures are related to individual condition and the steepness of their allometry. This is a simplistic prediction, as it assumes that all traits are under directional selection. Nevertheless, support for the prediction would help explain variation in allometry, although lack of support would be inconclusive.

We tested this prediction with a suite of morphological traits in two populations of vervet monkeys, *Chlorocebus aethiops* (Primates: Cercopithecidae) (Fig 1). We tested the prediction in three ways. First, we assessed the relationship between  $b$  and condition dependence across all traits. Second, we categorized traits according to expected differences in  $b$  and condition dependence, and we tested for a relationship between  $b$  and condition dependence across categories (Table 1). We placed each sexual trait in its own category to explore variation in condition dependence and  $b$  among them, as follows: (i) The penis. We focus on vervet penes because genitalia predominantly exhibit shallow static allometries (Eberhard *et al.*, 1998; Eberhard, 2009; Voje *et al.*, 2014). An apparent exception in vertebrates may be due to mixing of adult age groups (Eberhard, 2009; Rodríguez *et al.*, in review), and our  $b$  estimates account for this. Also, genitalia tend to show low condition dependence (Arnqvist & Thornhill, 1998; House & Simmons, 2007; Rodríguez & Al-Wathiqui, 2011). (ii) The testes. Both the penis and the testes are part of a colorful sexual display (Cramer *et al.*, 2013) (Fig. 1). (iii) The canines. The other categories correspond to: (iv) non-sexual body traits (e.g., thigh length); and (v) non-sexual body traits involving girth measurements (e.g., thigh girth), which are closely related to condition (Rutenberg *et al.*, 1987). Third, a difference in overall condition between populations (Table 1) allowed us to test for an effect on the expression of trait allometries. We reasoned that the relationship between condition dependence and  $b$  should be stronger in the population in better condition, where variation in trait developmental architecture should be emphasized, whereas such variation would be curbed in the population in worse condition.

These tests rely on variation among trait types to address the problem of variation in sexual allometries. We consider this to be a strength — if correct, the hypothesis identifies a general rule about the evolution and expression of allometry.

## MATERIALS AND METHODS

We worked with two populations of vervet monkeys, representing two subspecies. We chose these two populations from a broader project (The International Vervet Research Consortium) because they offered the largest sample sizes for the traits in which we were interested. We sampled sexually mature males of *C. a. sabaesus* at a colony at St. Kitts and Nevis, and of *C. a. pygerythrus* at South Africa. Measurements were taken by researchers who were members of the International Vervet Research Consortium. In our analyses, we took measurer ID into account to reduce the potential for among-measurer differences to influence our results. Vervets were wild-caught according to the procedure described by Grobler & Turner (2010). Briefly, vervets were anesthetized while in traps, and measurements were taken from the anesthetized individuals. Vervets remained anesthetized for approx. 30 min, and were then freed and allowed to return to the wild after data collection. Individual micro-chipping ensured that each male was measured only once. Researchers used measuring tape to take linear measures of seven body traits, three sexual traits (including penis length), and measures of the girth of three body parts (Table 1) (details in Turner *et al.*, 1997). Sample sizes vary among traits (Table 1) because it was not always possible to take all measurements for all individuals — vervets were measured only while sedation lasted, and they were never given additional sedation to complete measures. Our sample included three age categories of sexually mature vervet males (with fully developed testes). Individuals were assigned to one of the three age categories (subadult, mature adult, older adult) according their stage in the dental eruption sequence (details in Cramer *et al.*, 2013).

### Estimating allometric slopes ( $b$ )

We conducted all analyses in JMP (v. 7.0.1) (SAS Institute, Cary, NC, USA). We used OLS regression of  $\log_{10}$ - $\log_{10}$  data to estimate  $b$ . There has been debate about the use of OLS regression in studies of allometry, due to the concern that it may bias estimates of  $b$  downwards by not taking into account measurement error in the  $x$ -axis (e.g., Green, 1999). However, recent work shows that OLS regression does not underestimate  $b$  unless measurement error is very large (Al-Wathiqui & Rodríguez, 2011; Kilmer & Rodríguez, in prep.). Further, a popular alternative (RMA regression) confounds scaling with dispersion (it estimates  $b$  with the ratio of the standard deviations in  $x$  and  $y$ ; Eberhard *et al.*, 1999), and it may force apparent isometry ( $b = 1$ ) due to the variance-homogenizing effect of the log-log transformation. OLS regression is therefore indicated for allometric studies (Eberhard *et al.*, 1999; Voje & Hansen 2013; Cassidy *et al.*, 2014; Voje *et al.*, 2014; Kilmer & Rodríguez, in prep.).

We approximated body size ( $x$ -axis in allometric plots) with the body measurement that we considered to have the best-defined landmarks, lower leg length (Table 1). We were concerned that body length (Table 1) might not have such strictly defined landmarks. Lower leg length was significantly correlated with body length and mass (Pearson product-moment correlation pooling across all individuals:  $r = 0.28$  and  $0.50$ , respectively;  $P < 0.0001$  in both cases), and thus offers a good proxy for body size. Since there is no concern that measurement error in  $y$  may bias OLS regression, we retained body length as a  $y$ -axis trait.

To include testes volume in allometric analyses we used the  $\log_{10}$  of the cubic root of the volume measures.

Our estimates of  $b$  had to account for two potential confounding factors, for which we added terms to the basic standard least squares statistical model used to estimate  $b$ , as follows: To account for potential measurer differences, we included terms for measurer ID and its interaction with the  $x$ -axis (random terms, REML method). We also needed to account for variation in the age of the adult vervets sampled. In animals that continue to grow at least some structures during adulthood, as in vertebrates, mixing individuals of different adult ages confounds static allometry with ontogenetic allometry and may overestimate  $b$  (Eberhard, 2009; Rodríguez *et al.*, in review). For example, if genitalia reach full size at an intermediate adult age, they might appear to have a steeper allometry across adult ages than among adults of comparable age. We therefore included terms for age and its interaction with the  $x$ -axis. An alternative is to use only individuals of one adult age category (results of which we also report), but our approach better prevents overestimation of  $b$  (Rodríguez *et al.*, in review).

We show examples of the raw data and  $b$  estimates in Fig. 2. These  $b$  values then became the data for our tests. We use  $b$  estimates regardless of whether they are significantly different from zero, because we view them as descriptors of relative allometric steepness (cf. Eberhard *et al.*, 1998). This approach emphasizes effect sizes rather than statistical significance (Nakagawa & Cuthill, 2007).

We also tested for population differences in trait allometries and sizes. To test for differences in  $b$ , we added to the above models a population  $\times$  lower leg length interaction. We do not report these full models to save space; instead, we focus on the interaction. To test for population differences in trait means, we used models with each trait as the dependent variable and the following independent variables: population, measurer ID (random term, REML method), and adult age category. This is analogous to testing for differences in trait intercepts in allometry plots, but focusing on means. We report population term from these models.

### Testing for a relationship between $b$ and condition dependence

**Estimating individual condition and trait levels of condition dependence**—To estimate the level of condition dependence for each trait, we first calculated individual condition for each male, and we then related variation in condition to variation in trait sizes. We consider individuals that are relatively heavy for their size to be in better condition than individuals that are light for their size. This view of condition is based on resources acquired and carried on the body (e.g., muscle and fat; Hunt *et al.*, 2004), rather than on the health of cellular processes (Hill, 2011). Both views are important, but our measure allowed field sampling with minimal disturbance for the vervets. Alternatives such as experimental manipulation of condition with diet treatments (Kotiaho, 1999; Tomkins *et al.*, 2004) were not an option for this study.

We tested several alternatives for describing mass relative to body size. These included the residuals of an OLS regression of mass on body length; human and primate body mass

indices (BMIs); and the girth of the chest, upper arm and thigh (Table 1). All of these measures were highly correlated with each other. For example, the mean for Pearson's correlation between the mass~body length residuals and the other condition measures was  $r = 0.77 \pm 0.02$  (averaging within and then across populations). We selected the mass~body length residuals as our measure of individual condition. We are aware of debate around this measure (Jakob *et al.*, 1996; Green, 2001; Tomkins *et al.*, 2004; Peig & Green, 2009, 2010). But we consider that it is well suited for our purposes. It has been validated as a metric of general applicability (Schulte–Hostedde *et al.*, 2005). Also, of particular relevance for our study, the girth of the upper arm correlates well with lean muscle mass in primates (Rutenberg *et al.*, 1987), and indeed this was one of the measures that correlated highly with our metric (see above). We used the mass~body length residuals rather than upper arm girth itself because the former is more widely used.

Once we estimated individual condition, we calculated the level of condition dependence of each trait. We used models with condition as the independent variable, and z-scores for each trait as the dependent variable. With z-scores, the slope of the trait~condition relationship is equivalent to Pearson's correlation ( $r$ ). This  $r$  was the measure of condition dependence for each trait. Note that our measure of condition is independent of body size — a male can be in good or poor condition irrespective of his size — and therefore independent of our description of allometry; e.g., a male can bear a relatively large or small trait irrespective of whether he is relatively heavy or light for his size. Thus, the  $b$ ~condition dependence relationship asks whether relatively heavy or light males produce larger or smaller traits across body sizes.

**Testing the condition dependence prediction**—We tested this prediction in three ways. First, we asked if  $b$  varied with the level of condition dependence of each trait. The statistical model included  $b$  as the dependent variable, and the following independent variables: condition dependence, population, and their interaction (Table 2). In this test, the data ( $b$  and condition dependence) come from traits that are correlated with each other, which introduces the risk of spurious significance. But the usual correctives are not appropriate for our study. Generating suites of uncorrelated traits with Principal Components Analysis would detract from our focus on traits of interest (e.g., the penis). And corrections against spurious significance compromise statistical power (Nakagawa, 2004). But note that this problem is likely to be minor in our tests: our data involve allometric scalings and relationships between scalings and condition dependence, which are more likely to be independent of each other than the traits themselves. Also, correlations between traits were often weak: range:  $r = 0.03$ – $0.86$ ; mean:  $r = 0.40$ ; median:  $r = 0.41$ ; and 75% were below 0.53. Nevertheless, we took advantage of a pattern in these correlations to assess the risk of spurious significance. Correlations between traits on the same limb were higher (mean  $r = 0.64$ ) than correlations between traits on different body parts (mean  $r = 0.38$ ) ( $F_{1,153} = 5.16$ ,  $P = 0.024$ ). We therefore repeated the above test with only one trait per limb. Results robust to this exclusion would suggest that our analysis is not unduly affected by data obtained from correlated traits.

Second, we assessed the relationship between condition dependence and  $b$  across categories for different trait types: penis; testes; canines; body traits; and girth body traits. We tested

for differences in  $b$  and condition dependence among these trait types with standard least squares models including the following independent variables: trait type, population, and their interaction (Table 3). We obtained least square mean  $\pm$  SE values for condition dependence and  $b$  for these trait types from these models, and we calculated Pearson's correlation ( $r$ ) between the mean values for  $b$  and condition dependence.

Third, we tested for population differences in the relationship between  $b$  and condition dependence. This difference is tested by the condition dependence  $\times$  population interaction in the above model (Tables 2).

## RESULTS

We tested for a positive relationship between a trait's level of condition dependence and the steepness of its allometric slope ( $b$ ). We found this relationship in both populations (Table 2; Fig. 3A). Excluding the non-significant interaction did not alter the result (term for condition dependence:  $F_{1,21} = 8.39$ ,  $P = 0.0086$ ). The pattern also remained when we repeated the test including only one trait per limb, although the term for condition dependence became marginally-significant ( $F_{1,13} = 4.39$ ,  $P = 0.056$ ) due to lowered power. Thus, the pattern that we detect is not forced by correlated traits. The result was also the same with males of only one age category (mature adults): term for condition dependence:  $F_{1,20} = 5.11$ ,  $P = 0.035$ .

We then assessed the  $b$ -condition dependence relationship across trait types. Both  $b$  (y-axis in Fig. 3B) and condition dependence (x-axis in Fig. 3B) varied significantly among trait types (Table 3). Populations varied in how  $b$  (but not condition dependence) differed among trait types (compare interaction terms in Table 3; Fig. 3A). Across trait types, the  $b$ -condition dependence relationship was strong and positive (Fig. 3B). The correlation between the least square mean values for  $b$  and condition dependence among trait types was  $r = 0.87$ ,  $P = 0.058$ ; marginal significance is due to low power with  $n = 5$  data points, but the relationship is of large effect size (Nakagawa & Cuthill, 2007).

The  $b$ -condition dependence relationship differed between populations, with  $b$  having a broader range in the population in better condition (St. Kitts and Nevis) (Fig. 3A). However, this difference was not significant (interaction term in Table 2).

We found population differences in several traits (Table 1), but little evidence of differences in allometry. The sexual traits varied the most in allometry (Fig. 3), but the lower leg  $\times$  population interaction was significant only for the penis (Table 4), and this variation remained within the realm of negative allometry (red symbols in Fig. 3A). The trait that varied the least in allometry was the head ( $b = 0.18$  for St. Kitts and Nevis;  $b = 0.31$  for South Africa).

## DISCUSSION

Study of the allometry of sexual traits reveals an astounding amount of variation. This variation may be explained in part by an interplay between the form of selection and body size-related differences in the strength of selection (Bonduriansky, 2007; Eberhard *et al.*, 2009). We tested a component of this hypothesis with morphological traits in vervet

monkeys, using trait differences in condition dependence as a proxy for body size-related variation in the net benefits of trait increase. We found support for the prediction that there should be a positive relationship between condition dependence and the steepness of allometry, and this pattern was robust across diverse trait types. But we found only weak support for the prediction that variation in the expression of trait allometries as a function of condition dependence would be greater for a population in better overall condition. We therefore interpret our findings as tentative support for the hypothesis.

We also offer some caveats to this interpretation. First, further work with other study species is required to assess how vulnerable our findings are to problems arising from use of data generated from traits correlated with each other. Second, our test involved oversimplification of the full hypothesis: we lack information about the form of selection, and we approximated body size-related variation in the net benefits of trait increase with the level of condition dependence of different traits. Thus, our test was asymmetric: the support we find is encouraging, but negative results would have been inconclusive. Nevertheless, to date there is agreement among studies using morphological and behavioral traits that both the form of selection and condition dependence have predictable influences allometry (Rodríguez & Al-Wathiqui 2012a; Rodríguez *et al.*, 2014a; this study). Third, we categorized several body traits as non-sexual (Table 1), but vervets exhibit sexual size dimorphism (Turner *et al.*, 1997). Thus, overall male size in vervets reflects the effect of sexual selection (Lindenfors *et al.*, 2007). Although this represents sex differences in intercept rather than slope, it may also influence the evolution of trait allometries. Addressing this interesting question will require further work comparing male and female allometries. Finally, we note that the evolution of allometry is likely to be influenced by many factors. For instance, sexual structures with forceful or coercive functions (e.g., weapons) may evolve steeper allometries than sexual structures that function in other ways (e.g., displays) (Eberhard, 2009; cf. Rodríguez *et al.*, 2014a). Also along those lines, whether structures function by contacting the body of the mating partner or from a distance may also influence allometry (Eberhard *et al.*, 1998; Eberhard, 2002, 2009; Kilmer & Rodríguez, unpub.). The combinations of functions that traits perform (e.g., genitalia have sexually-selected functions such as contact courtship and naturally-selected functions like insemination) may also influence the evolution of allometries (House & Simmons, 2003; Eberhard, 2009; Rodríguez & Al-Wathiqui, 2012a).

Against the background of high diversity in sexual allometries, the predominantly shallow allometry of animal genitalia stands out as a remarkably consistent pattern, with the apparent exception of vertebrate genitalia (Eberhard, 2009). We were thus especially interested in the allometry of vervet penes. After accounting for variation in adult age, which may bias *b* estimates upward (Rodríguez *et al.*, in review), vervet penes showed negative allometries and low condition dependence, in agreement with the overall pattern across animal groups (Eberhard *et al.*, 1998; Eberhard, 2009). This offers insight into potential sources of selection on vervet penes. In spite of their showiness (Fig. 1), they are unlikely to have evolved as indicators of size or condition, or as coercive structures (cf. Eberhard *et al.*, 1998, 2009). The head also had consistently shallow allometries — in agreement with a widespread trend for brain size to exhibit shallow static, developmental, and evolutionary



allometries (Huxley, 1932; Striedter, 2005) — although it did not have especially low levels of condition dependence, being below the 20<sup>th</sup> percentile for *b*, but only below the 48<sup>th</sup> percentile for condition dependence.

Implicit in our discussion of the evolution of allometry is the notion that it can be molded by selection. There is, however, debate on whether selection can modify allometry (Eberhard & Gutiérrez, 1991; Emlen & Nijhout, 2000; Frankino *et al.*, 2005; Eberhard *et al.*, 2009), or whether such patterns mainly represent constraints (Gould, 2002; and see Egset *et al.*, 2011, 2012). We take the large amount of variation in sexual allometries (Cuervo & Møller, 2001; Bonduriansky, 2007; Schulte–Hostedde *et al.*, 2011) as suggestive of their potential to be shaped by selection. Also suggestive are the relationship between *b* and condition dependence (this study; Rodríguez *et al.*, 2014a), and variation in allometry according to the form of selection on different traits (Rodríguez & Al-Wathiqui 2012a; Rodríguez *et al.*, 2014a). Further, evidence of genetic variation in how allometry responds to environmental inputs during development — i.e. of genotype × environment interaction in allometry (Rodríguez & Al-Wathiqui, 2012b) — suggests that allometry may respond differently to selection in different environments. Finally, we point to evidence of (slow) evolutionary divergence in allometry (Voje & Hansen, 2013; Voje *et al.*, 2014). In our comparison of two vervet monkey populations, we found that trait sizes varied more commonly than trait allometries. But our sample of only two populations may underestimate the extent of divergence in trait allometries.

We conclude by emphasizing that a complete explanation for the evolution of allometry will likely involve many variables. It is encouraging, however, that approximations such as ours can explain some of the variation observed in trait allometries.

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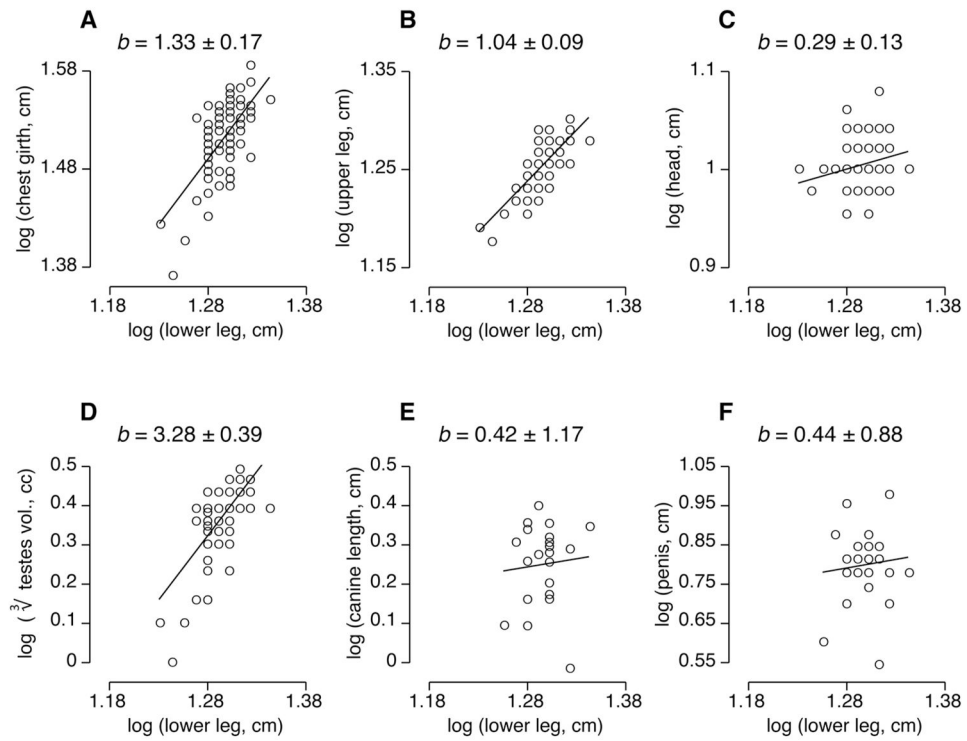
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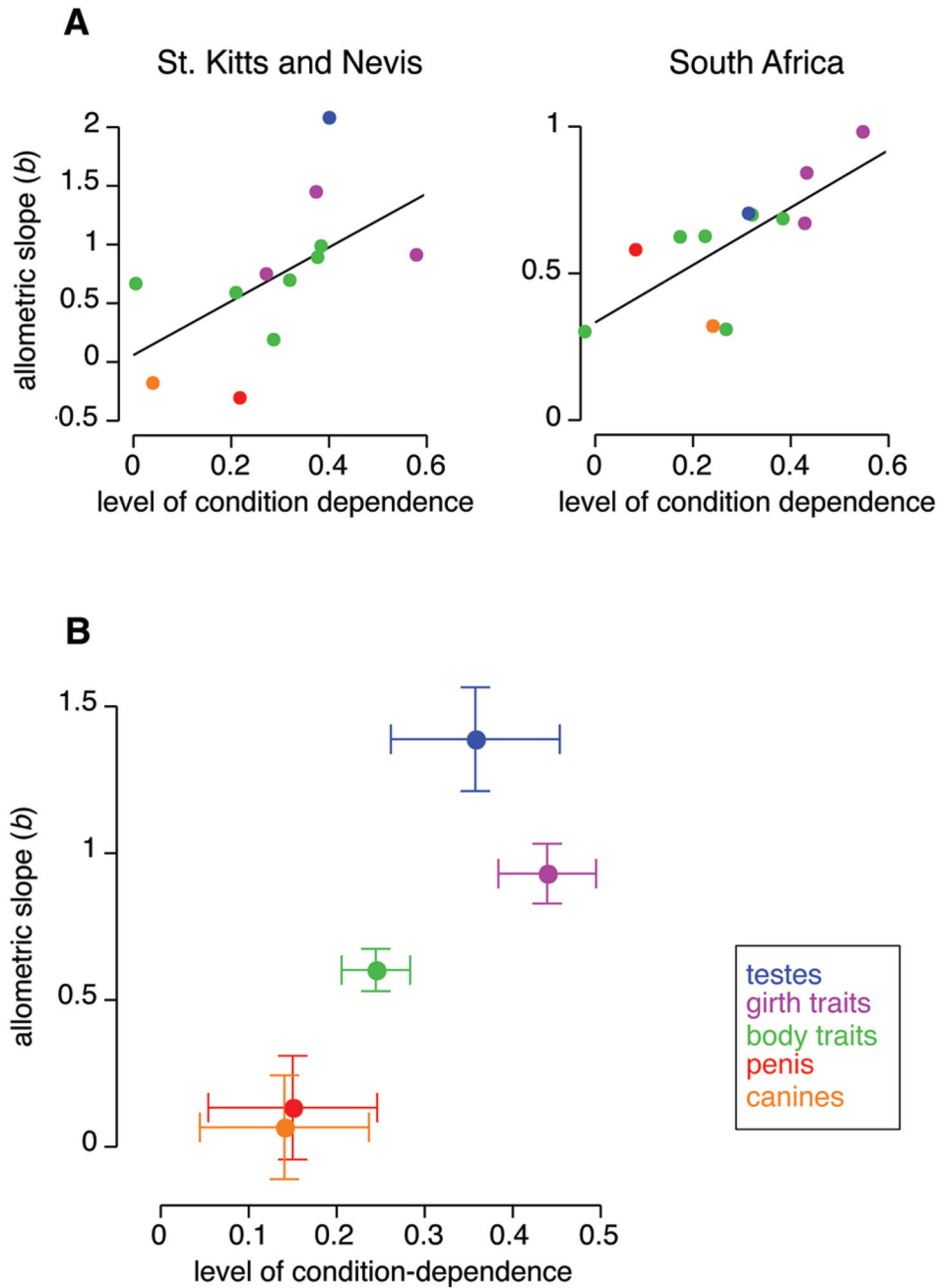
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**Figure 1.**  
An adult male vervet monkey, *Chlorocebus aethiops pygerythrus*, from South Africa. Photo by Jennifer Danzy Cramer.

**Figure 2.**

Examples of allometric ( $\log_{10}$ - $\log_{10}$ ) plots, showing how different structures scale relative to the length of lower leg (our estimate of body size) in vervet monkeys. All  $x$ -axes span two log units;  $y$ -axes span two (A–C) or five log units (D–E). (A) Chest girth shows weak positive allometry ( $b > 1$ ). (B) The length of the upper leg shows near perfect isometry ( $b = 1$ ). (C) The head shows negative allometry ( $b < 1$ ). Allometric slopes ( $b$ ) given  $\pm 1$  SE. Data from the St. Kitts and Nevis site for males of all adult ages for illustrative purposes.



**Figure 3.** Relationship between the level of condition dependence of different traits and their allometric slope ( $b$ ), in two vervet monkey populations. (A) Across all traits. (B) Across trait types, showing least square means  $\pm$  1 SE.

**Table 1**

Measures that we used to describe trait allometries in two vervet monkey populations. All traits were measured in cm unless otherwise indicated. We report least square mean  $\pm$  SE values and tests for population differences in trait means (see text). Significant differences in boldface

type of trait	trait	<i>C. a. sabaesus</i> , St Kitts and Nevis (mean $\pm$ SE, <i>n</i> )	<i>C. a. pygerythrus</i> , South Africa (mean $\pm$ SE, <i>n</i> )	<i>F</i> , <i>P</i>
body mass	mass (kg)	5.95 $\pm$ 0.26, 104	5.47 $\pm$ 0.24, 99	<b>10.47, 0.0014</b>
estimate of body size	lower leg length	19.9 $\pm$ 0.3, 89	19.8 $\pm$ 0.2, 99	0.69, 0.41
body traits (lengths)	body	38.9 $\pm$ 1.7, 89	39.4 $\pm$ 1.7, 99	0.61, 0.44
	head (excl. the face)	10.5 $\pm$ 0.3, 89	10.5 $\pm$ 0.3, 89	0.003, 0.96
	upper arm	16.4 $\pm$ 0.4, 89	15.6 $\pm$ 0.4, 98	<b>17.26, &lt; 0.0001</b>
	lower arm	16.2 $\pm$ 0.3, 89	16.0 $\pm$ 0.3, 97	1.64, 0.21
	upper leg (thigh)	18.6 $\pm$ 0.6, 89	18.2 $\pm$ 0.5, 99	3.50, 0.06
	sternal notch-pubic symphysis	36.5 $\pm$ 9757, 80	37.0 $\pm$ 9600, 97	0.00, 1.00
girth traits	chest	35.7 $\pm$ 1.6, 89	32.8 $\pm$ 1.6, 98	<b>43.19, &lt; 0.0001</b>
	upper arm	15.4 $\pm$ 0.8, 84	14.1 $\pm$ 0.8, 98	<b>19.23, &lt; 0.0001</b>
	upper leg (thigh)	22.4 $\pm$ 0.9, 84	21.7 $\pm$ 0.8, 99	2.83, 0.09
body mass indeces	human BMI *	7.9 $\pm$ 0.5, 70	7.2 $\pm$ 0.5, 89	<b>12.62, 0.0005</b>
	primate BMI **	39.9 $\pm$ 4.3, 70	36.0 $\pm$ 4.2, 99	<b>10.35, 0.0016</b>
condition	mass~body length residuals	0.67 $\pm$ 0.38, 89	0.13 $\pm$ 0.37, 94	<b>16.74, &lt; 0.0001</b>
sexual traits	canine length	1.9 $\pm$ 0.2, 22	1.7 $\pm$ 0.03, 87	1.43, 0.34
	testes volume (cc)	15.4 $\pm$ 1.1, 91	15.9 $\pm$ 0.6, 95	0.21, 0.66
	penis length	6.6 $\pm$ 0.4, 32	6.9 $\pm$ 0.3, 88	0.94, 0.33

\* human BMI = mass / (head + body + upper leg + lower leg / 100)<sup>2</sup>

\*\* primate BMI = mass / (body / 100)<sup>2</sup>



**Table 2**

Test of the condition dependence hypothesis to explain variation in trait allometries, with two vervet monkey populations. Significant terms in boldface

<b>factor</b>	<b>df num, denom</b>	<b><i>F, P</i></b>
condition dependence	1, 20	<b>8.54, 0.0084</b>
population	1, 20	0.37, 0.55
condition dependence × population	1, 20	1.38, 0.25

**Table 3**

Comparison of allometric slopes ( $b$ ) and condition dependence among trait types (penis, testes, canines, body traits, girth body traits; see text) in vervet monkeys. Significant terms in boldface

factor	test for differences in $b$		test for differences in condition dependence	
	df num, denom	$F, P$	df num, denom	$F, P$
trait type	4, 14	<b>11.19, 0.0003</b>	4, 14	<b>3.40, 0.038</b>
population	1, 14	0.22, 0.65	1, 14	0.00, 0.99
trait type $\times$ population	4, 14	<b>5.99, 0.005</b>	4, 14	0.58, 0.68

**Table 4**

Test for population differences in vervet monkey allometry. We report only the term that tests for population differences (lower leg  $\times$  population interaction) extracted from the full models detailed in the text. Significant term in boldface

trait	test for the interaction	
	df num, denom	<i>F, P</i>
body	1, 1	3.23, 0.32
head	1, 2.889	0.006, 0.94
upper arm	1, 46.66	0.11, 0.74
lower arm	1, 66.75	0.00, 0.99
upper leg (thigh)	1, 127	0.16, 0.69
sternum-pubis	1, 1	0.09, 0.82
chest girth	1, 162.7	0.62, 0.43
upper arm girth	1, 136	0.84, 0.36
lower leg (thigh) girth	1, 76.33	0.46, 0.50
canine	1, 62.38	0.62, 0.44
testes	1, 171.4	0.20, 0.65
penis	1, 109.4	<b>8.26, 0.005</b>