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Adam Duffy Gordon

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**Evolution of Body Size and Sexual Size Dimorphism
in the Order Primates:
Rensch's Rule, Quantitative Genetics, and Phylogenetic Effects**

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**Evolution of Body Size and Sexual Size Dimorphism
in the Order Primates:
Rensch's Rule, Quantitative Genetics, and Phylogenetic Effects**

by

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Dedication

For my brothers, who gave me my first lessons in primate behavior,
and for my parents, who got me excited about learning in the first place.

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**Evolution of Body Size and Sexual Size Dimorphism
in the Order Primates:
Rensch's Rule, Quantitative Genetics, and Phylogenetic Effects**

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Rensch's rule, positive scaling of sexual size dimorphism (SSD) with body size, has been shown to be present in the evolutionary history of Primates. However, in some radiations there is negative or absent scaling of size and dimorphism. Lande's (1980) quantitative genetics model predicts (1) positive scaling (Rensch's rule) when selection acts more intensely on male body size than female body size, (2) no scaling when selection acts equally on both sexes, and (3) negative scaling when selection acts more intensely on female body size.

Presented here is a combined response model which describes how sex-specific means and relative variabilities of continuous traits respond to sex-specific selection pressures. Model predictions are compared to data from extant primate populations to identify likely sources of unequal sex-specific selection pressures. Evolution of size and dimorphism within primate radiations is discussed in the context of a new conceptual model for the evolution of various scaling patterns of size and SSD.

Under sexual selection by male competition or female mate choice, male body size is expected to be the primary target of selection. Under sexual selection by female competition or male mate choice, or natural selection by resource limitation, female body size is expected to be the primary target of selection. Because any of these forces may be in operation at any particular point in time, surveys of recent evolutionary changes in dimorphism capture positive and negative scaling patterns of SSD and size, and thus Rensch's rule does not emerge. However, the phylogenetic history of living taxa is not representative of all taxa that ever lived, but only of those taxa that have living descendants. Species subject to intense resource scarcity are more likely to go extinct than species that have abundant resources, so phylogenetic history will be biased against the inclusion of resource limited taxa. In the absence of polyandry, positive scaling of size and SSD (Rensch's rule) is the most likely pattern to emerge in radiations characterized by sexual selection on male size. This conceptual framework is used to study sex-specific body size evolution in *Pan* and *Australopithecus afarensis*.

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Chapter 1: Introduction

At the midpoint of the last century, Bernhard Rensch noted that “in numerous animal groups the sexual dimorphism increases with body size” (p. 157, Rensch, 1959, translated from Rensch, 1950). In the intervening fifty-four years since Rensch’s observation and the present, a vast number of studies have demonstrated the presence of Rensch’s rule in many animal radiations (*e.g.*, birds: Wiley, 1974; Sirgurjonsdottir, 1981; Webster, 1992; Fairbairn & Shine, 1993; mammals: Jarman, 1983; Reiss, 1986; reptiles: Schoener, 1970; Berry & Shine, 1980; insects: Fairbairn, 1990; Sivinski & Dodson, 1992; Andersen, 1994), particularly in the Order Primates (Leutenegger, 1978; Ford, 1994; Martin *et al.*, 1994; Mitani *et al.*, 1996; Plavcan & van Schaik, 1997b; Weckerly, 1998; Smith & Cheverud, 2002). However, in some radiations dimorphism does not scale with body size at all (*e.g.*, strepsirhine primates: Kappeler, 1990; Weckerly, 1998; Smith & Cheverud, 2002), or even scales strongly negatively with size, contrary to Rensch’s rule (*e.g.*, owls: Earhart & Johnson, 1970; spiders: Vollrath & Parker, 1992; Head, 1995; Abouheif & Fairbairn, 1997).

Understanding why sexual size dimorphism (often represented as a ratio or log-transformed ratio of mean male body mass divided by mean female body mass) has a non-zero scaling relationship with body size in some taxa is important for a number of reasons. For students of biological processes and their outcomes, Rensch’s rule is bewildering because there is no clear functional constraint to explain why dimorphism should necessarily increase with size (Fairbairn, 1997), nor why the rule applies in some taxa but not others. In studying primates, anthropologists must contend with one of the strongest positive scaling relationships between size and dimorphism yet detected in the animal kingdom (Abouheif & Fairbairn, 1997). Rensch’s rule raises several questions for

anthropologists: is it necessary to remove the effects of size before comparing dimorphism between taxa? Does size constrain dimorphism? Do modern scaling patterns also apply in the fossil record? Paleoanthropologists are particularly troubled by these questions, since interpretations of the fossil record are often based on size difference between specimens (*e.g.*, deciding whether two size morphs represent two sympatric species or two sexes, or attempting to reconstruct behavior for fossil primates based on the degree of dimorphism). Understanding why Rensch's rule applies to primates would go a long way towards resolving these questions.

The reasons behind non-zero scaling patterns of size and dimorphism have remained elusive for the past half-century. Although a number of mechanisms have been proposed (see Fairbairn, 1997 for a thorough review), no mechanism or combination of mechanisms has yet emerged as the definitive source of Rensch's rule. However, one approach to the problem has been gaining support for the past two decades: quantitative genetic modeling. In 1980, Russell Lande published a model that described how male and female means for a continuous trait (such as body mass) respond to selection (Lande, 1980). Since then, a number of conceptual models have built upon a quantitative genetics framework in attempts to explain Rensch's rule (*e.g.*, correlated response of mean size in one sex to selection on another, Wickman, 1992; Reeve & Fairbairn, 1996; size dimorphism resulting from differences in sex-specific additive genetic variance, Leutenegger & Cheverud, 1982; Cheverud *et al.*, 1985; 1985; correlated selection in one sex in response to selection on the other, Zeng, 1988).

This dissertation follows earlier work in attempting to explain Rensch's rule in the context of quantitative genetics. However, I intend to provide a comprehensive model that can accommodate not only Rensch's rule, but also absent and negative scaling patterns of size and dimorphism present in many animal taxa.

In [Chapter 2](#) I present a “combined response model”, in which I derive a generalization of Bulmer’s (1971) model for response of relative variability to selection that is applicable to sex-specific relative variability. Combined with Lande’s (1980) model for response of sex-specific means to selection, predictions regarding the relationship between sex-specific size, size dimorphism, and relative variability ratios are generated based on varying initial selective parameters. Model predictions are compared to observed parameters for closely related primate populations in an attempt to identify selective forces that typically produce change in size and dimorphism within primates. Broad predictions are made regarding the scaling of size and dimorphism under various selective regimes.

[Chapter 3](#) presents an assessment of scaling patterns of size and dimorphism within the Order Primates and their likely causes. Phylogenetic comparative methods and traditional interspecific regression techniques are used to compare relationships of scaling patterns of dimorphism in higher-level taxa (evolutionary relationships at and above the generic level), lower-level taxa (evolutionary relationships below the generic level), and within modern taxa (traditional interspecific scaling between living taxa). Results of these analyses are interpreted in the context of Lande’s (1980) model and the likely selective forces producing size change in various primate radiations.

In [Chapter 4](#) I address the role of sexual selection in producing size dimorphism within primates, and the question of whether it is appropriate to correct for the effect of size on dimorphism before performing comparative analyses of sexual dimorphism. I use traditional and phylogenetic linear models to determine the contributions of size, social structure, and substrate use towards accounting for variance in size dimorphism within major primate radiations. Also, I consider the relationship between size and dimorphism

separately within major primate radiations and within groups expected to experience similar levels of sexual selection.

[Chapter 5](#) explores the possibility that geometric means representing multiple elements of the primate postcranium by an equal number of measurements for each element may produce size variables that scale isometrically with body mass in primate taxa. Such variables may be preferable to body mass measurements in analyses of sexual size dimorphism because they are less susceptible to dramatic change over short time periods. In addition, geometric means of skeletal measurements would be available for any reasonably complete specimen, allowing size to be incorporated at the individual level in morphological analyses of extant and perhaps even extinct taxa.

In an application of all of the preceding work, [Chapter 6](#) investigates the evolution of sex-specific body size in *Pan* and *Australopithecus afarensis*. Size is measured as a geometric mean of linear measurements from the proximal articular surfaces of the femur, tibia, humerus, and radius. All measurements are available for a comparative sample of African apes, humans, and one small (probably female) fossil partial skeleton, A.L. 288-1. Although similarly complete male fossil specimens are not available, a simultaneous death assemblage that is nearly contemporaneous with A.L. 288-1 (A.L. 333) contains two adult size morphs; the larger size morph includes at least one element preserving the necessary morphology for each measurement included in the geometric mean size variable. Resampling procedures (exact randomization and bootstrapping) are used to calculate the probability that a geometric mean calculated for elements from different individuals would fall within the observed range of geometric means based on single individuals for extant taxa. Resampling procedures are then used to identify the confidence limits on phylogenetically independent contrasts of sex-specific body size in *Pan troglodytes troglodytes*, *P. t. schweinfurthii*, *P. paniscus*, and *A. afarensis*. Results

are interpreted in the context of Lande's (1980) quantitative genetics model, observed levels of body size and canine size dimorphism in *Pan* and *Australopithecus*, social structure in chimpanzees, biogeography of living African apes, and paleoreconstructions of early hominid habitats and environmental change in the late Miocene.

Finally, [Chapter 7](#) provides a brief summary of the major findings of this dissertation.

Chapter 2: Quantitative Genetics and the Scaling of Size and Dimorphism in Primates

INTRODUCTION

In many animal radiations, sexual size dimorphism (SSD) scales positively with body size, a concept known as Rensch's rule (Rensch, 1959). A recent study of size and dimorphism by Smith and Cheverud (2002) reviewed previous investigations of Rensch's rule in primates (*e.g.*, Clutton-Brock *et al.*, 1977; Leutenegger, 1978; Leutenegger & Cheverud, 1982; Gaulin & Sailer, 1984; Kappeler, 1990; Ford, 1994; Martin *et al.*, 1994; Abouheif & Fairbairn, 1997; Plavcan & van Schaik, 1997b) and presented a series of new phylogenetic comparative analyses of the scaling of size and SSD within various primate clades. Considered together, these studies generally support the assertion that Rensch's rule is present in haplorhine primates, but absent in strepsirhines.

However, it is not clear why there should be a positive scaling relationship between size and dimorphism at all. Several different explanations for Rensch's rule have been proposed over the years, which Fairbairn (1997) grouped into eight categories. These eight categories can be generalized into three types of explanations: (1) increases in body size cause or facilitate increases in SSD, (2) correlations of genetics and/or selection pressures between sexes cause changes in dimorphism and body size of both sexes when selection is applied to the size of one sex, and (3) natural selection applies differential sex-specific selection pressures resulting in changes in size and dimorphism.

Models that propose a causal role for body size in the determination of SSD are poorly supported in primates (Mitani *et al.*, 1996; Plavcan & van Schaik, 1997b; Plavcan, 2001; Smith & Cheverud, 2002). Indeed, the absence of scaling of size and dimorphism in strepsirhines is in itself a rebuttal to arguments posing an obligatory

relationship between size and dimorphism (Godfrey *et al.*, 1993). As Fairbairn (1997) points out, there is no *a priori* reason such as biomechanical constraint to suppose that dimorphism must scale positively with size.

Alternatively, some models predict that size and dimorphism both change in response to sex-specific differences in selection pressure or additive genetic variation; these models generate explicit predictions regarding the scaling of size and dimorphism (*e.g.*, Lande, 1980; Zeng, 1988). Differences in sex-specific selection pressures can result from sexual selection, in which large size is advantageous in competition between members of one sex for access to mating opportunities (intra-sexual competition) or large size is a character actively sought out in potential mates (inter-sexual competition) (Darwin, 1871; Andersson, 1994); selection differences can also arise from natural selection due to sexual niche separation, predation, or resource pressures (Selander, 1966; Ralls, 1976; Slatkin, 1984; Shine, 1989; Andersson, 1994). Within primates, sexual selection is usually thought to produce sexual size dimorphism (*e.g.*, Clutton-Brock *et al.*, 1977; Gaulin & Sailer, 1984; Clutton-Brock, 1985; Rodman & Mitani, 1987; Ford, 1994; Martin *et al.*, 1994; Mitani *et al.*, 1996; Plavcan & van Schaik, 1997b; Lindenfors & Tullberg, 1998; Plavcan, 1999; Barton, 2000; Plavcan, 2001). The relationship between SSD and sexual selection is of particular interest to anthropologists because of the potential to infer social and/or mating behaviors of extinct primates based on body size dimorphism in the fossil record (*e.g.*, Wolpoff, 1976; Schroder, 1993; McHenry, 1994a; Kappelman, 1996; Plavcan & van Schaik, 1997a; Plavcan, 2002; Reno *et al.*, 2003).

This paper addresses specific predictions for scaling of size and SSD based on a quantitative genetics approach. Unless otherwise specified, SSD is represented here by the logarithm of mean male size divided by mean female size ($\log [M/F]$) (Smith, 1999). Lande (1980) developed a model that predicts the response to selection of male and

female means of a continuous character (*e.g.*, body mass or canine size). As Smith and Chevrud (2002) point out, Lande's model predicts the following: with a genetic correlation of 0.9 between sexes for body mass, selection acting on male body size alone will produce positive scaling of size dimorphism and female body size with a slope nearly identical to that observed for haplorhine primates (Smith & Cheverud, 2002). Positive scaling results from the fact that body size in females is correlated to that of males, so large increases in male size produce smaller increases in females even when selection does not act on female body size.

The idea that Rensch's rule could result from a correlated response to selection has been around for some time (Maynard Smith, 1977; Leutenegger, 1978; Zeng, 1988; Webster, 1992; Fairbairn & Preziosi, 1994), and a formal mathematical description of how correlated selection would work has been available since Lande published his model over twenty years ago (Lande, 1980). Lande himself thought that natural selection for female optimum body size would counteract the correlated response of female body size, in which case there would be no scaling of size and dimorphism once female size had returned to its optimum (Lande, 1980; Zeng, 1988; Emerson, 1994; Fairbairn, 1997).

However, this scenario makes assumptions that may not be true. For one, it requires that the initial selection pressure acts only on male body size; in some circumstances selection may act on both sexes with greater selection pressure applied to one sex. Perhaps more importantly, Lande's scenario also assumes that constraints defining optimum body size for females remain stable long enough for a return to previous optimum body size at equilibrium, making no allowance for environmental change or the emergence of a new optimum in response to new conditions (Smith & Cheverud, 2002). For example, larger females may be able to move into new dietary niches with larger optimum body size; also, birthing constraints on delivering larger

infants may select against small size in females, increasing optimum body size as male and female body size increases. Evidence for such correlated selection on female size in response to selection on male size (distinct from correlated response in females to selection on males alone) has been found in birds and mammals (Ralls, 1976; Cabana *et al.*, 1982; Clutton-Brock *et al.*, 1988; Webster, 1992). Thus Lande's model is not applied here as a strict correlated response model, as correlated selection most likely acts to redefine optimum body size in both sexes when initial selection pressure acts only on one sex.

When an assumption of constant female optimum size and a necessary return to that optimum is *not* imposed, Lande's (1980) equations predict that body size dimorphism will scale positively with sex-specific body size whenever selection acts more intensely on males than females; the predicted slope is independent of selection intensity and whether selection acts to increase or decrease size (Figure 2.1). However, Lande's model also predicts that selection acting more intensely on female size will produce a negative scaling relationship, contrary to Rensch's rule (Figure 2.1). When selection pressures are equal, body size will change but no change is expected in dimorphism. Lande's model also predicts that differences in sex-specific additive variance will produce change in dimorphism, even in the presence of equal selection pressure on both sexes.

Thus Lande's (1980) quantitative genetics model predicts positive scaling of size and SSD for certain starting conditions, but it also predicts negative scaling or an absence of scaling altogether under other conditions. Two questions arise: (1) what combination of sex-specific selection pressures and relative variability occur in primates, and (2) can quantitative genetics models accommodate those combinations and the observed scaling patterns of size and SSD in primates?

The first question can be addressed by an extension of Lande's model. Bulmer (1971) devised a model for monomorphic populations that predicts the response to selection of relative variability for continuous traits. This paper derives a generalization of Bulmer's model to separately predict response for males and females ([Appendix A](#)). Lande's model can be used to distinguish between selection primarily acting on males and selection primarily acting on females; a combined model describing sex-specific responses of mean size and relative variability to selection can be used to identify whether selection acts to increase or decrease size. Observed parameters for groups of closely related extant populations can then be compared to model predictions to identify the specific combination of selection pressures that are expected to have acted on particular primate populations.

The second question is best addressed by considering scaling patterns of size and SSD within different primate clades in conjunction with the selection pressures that are most likely operating within those clades. Due consideration must also be given to time depth; *i.e.*, more recent scaling patterns may overlay older, different scaling patterns.

Model Predictions

Leutenegger and Cheverud (1982; 1985) presented equations for the response to selection of mean male size, mean female size, and SSD based on Lande's (1980) quantitative genetics model, where "response" is a proportional change in size or dimorphism ([Appendix B](#)). When heritabilities are equal between the sexes, these equations predict that positive correlations of size and dimorphism will result when selection acts primarily on males, and negative correlations will result when selection acts primarily on females. If selection acts to increase the size of one sex and decrease the size of the other, male size will be positively correlated with SSD and female size will

be negatively correlated with SSD, regardless of which sex increases and which sex decreases in size. These predicted relationships are shown in [Table 2.1](#).

Leutenegger and Cheverud's (1982; 1985) equations can be combined with equations describing a generalization of Bulmer's (1971) model ([Appendix C](#)). This combined response model predicts a negative correlation between SSD and a ratio of sex-specific relative variability when selection acts to increase size, and a positive correlation when selection acts to decrease size ([Table 2.1](#)). These predictions are generated by consideration of equations [C.11](#) and [C.12](#) in [Appendix C](#). A verbal description follows.

Bulmer's (1971) model, which has been supported by a number of simulation studies (Bulmer, 1976; Robertson, 1977; Sorensen & Kennedy, 1984; van der Werf & de Boer, 1990), predicts that additive genetic variance decreases in response to directional or stabilizing selection. For example, if only the largest animals in a population reproduce, the descendant population will have fewer small animals and thus be less variable than the parental population. This decrease in variance in response to selection is known as the Bulmer Effect (Falconer & Mackay, 1996). The generalized Bulmer Effect derived here predicts that when selection is more intense on one sex than the other, additive variance in the offspring generation is reduced proportionally more in the sex under greater selection. For example, if males are subjected to greater selection for increasing size than females, male additive variance will reduce more than female additive variance. Thus a ratio of male relative variability divided by female relative variability will have a lower value in offspring than in parents.

The combined response model takes into account the effect of sex-specific selection pressures on relative variation, sex-specific body size, and SSD. When selection pressure acts to increase male body size, male size increases and female size increases to a lesser degree, resulting in an increase in SSD. In this situation female size

may increase due to the genetic correlation between sexes or correlated selection pressure on females (Andersson, 1994; Reeve & Fairbairn, 1996; Fairbairn, 1997; Smith & Cheverud, 2002). Because selection is more intense on males than females, male relative variability decreases more than that of females, and so relative variability ratio decreases. Thus the changes in SSD and relative variability ratio are negatively correlated ([Table 2.1](#)).

A negative correlation also results from selection acting to increase female size. Both sexes increase in size, although male size increases to a lesser degree, resulting in a decrease in SSD. Because selection is more intense on females than males, female relative variability decreases more than that of males, and so relative variability ratio increases. Changes in SSD and relative variability ratio are negatively correlated. Thus selection for increased size is associated with negative correlations of these ratios, regardless of which sex is subject to more intense selection pressure ([Table 2.1](#)).

In contrast, decreases in size are always associated with positive correlations of SSD and relative variability ratio. When selection acts to decrease male size more than female size, SSD decreases. Because more intense selection pressure is applied to males than to females, male relative variability decreases more than that of females, and so relative variability ratio also decreases. Thus changes in SSD and relative variability ratio are positively correlated. It can be shown that when selection acts to decrease female size more than male size, both SSD and relative variability ratio increase, and so change in these two ratios is also positively correlated for this combination of selection pressures ([Table 2.1](#)).

Selection may also act to increase size in one sex and decrease size in the other. In this case the relationship between SSD and relative variability ratio depends on the relative strength of selection on both sexes. Correlations may be negative or positive.

However, correlations of sex-specific body size and SSD can be used to distinguish this case from instances where selection acts in the same direction on both sexes (Table 2.1).

It has also been suggested that when sex-specific selection intensities are equal and non-zero, SSD may result solely from differences in sex-specific relative variability (*i.e.*, variance dimorphism, Leutenegger & Cheverud, 1982; Cheverud *et al.*, 1985; Leutenegger & Cheverud, 1985). When size dimorphism results from variance dimorphism alone, relative variability ratios are predicted to remain constant because selection intensities are equal on both sexes, and thus sex-specific relative variabilities decrease by the same proportion in both sexes. Thus changes in dimorphism should have a zero correlation with changes in relative variability ratio.

Taken together, Lande's (1980) model and the combined response model described here generate mutually exclusive sets of predictions for changes in dimorphism produced by (1) selection acting primarily to increase male size, (2) selection to increase female size, (3) selection to decrease male size, (4) selection to decrease female size, (5) selection to increase size in one sex and decrease size in the other, and (6) equal sex-specific selection operating on variance dimorphism.

Model Limitations

The predictions described above and listed in Table 2.1 are for correlations between changes from an ancestral state. Because primates have relatively long life spans, body mass data collected over the course of multiple generations is available for very few (if any) wild primate populations. Also, the Bulmer Effect persists only as long as selection pressures are maintained, and maximum reductions of additive variance are reached within small numbers of generations (Bulmer, 1971). Thus comparisons between the most closely related subspecies, perhaps separated by only a few hundred or thousand generations, are unlikely to produce meaningful results using the combined

response model. Although when Lande's (1980) model is applied by itself it is not constrained in this way, Lande's model cannot determine the direction of size change without incorporating the Bulmer Effect.

One way in which the combined response model can be applied is to compare closely related populations of the same taxon. Populations that live in close proximity in space and time are likely to be closely related, particularly because individuals transfer between groups in many primate species. In order to maximize the probability that populations share a common genetic heritage within the past few generations, populations should be selected that are geographically close enough for potential mates to have transferred between populations. Populations that fall within this area can be considered recent descendants of a common ancestral population. Thus heritabilities, genetic correlations, mean size, and relative variability should be identical for the recent ancestral state of all populations under consideration, and the only parameters that vary are sex-specific selection pressures. Because change in all populations is measured from the same state, correlations among changes in variables are identical to correlations in the variables themselves. In addition, comparison between populations separated by at most a few generations ensures that, should a hypothetical constant optimum female body size exist, selection will not have had enough time to restore female body size to its optimum and thus interfere with scaling patterns. Correlations of body size, SSD, and relative variability ratio can therefore be compared to model predictions to identify the selection pressures most likely to have modified size and dimorphism in these taxa. Populations that share consistent patterns can then be compared on the basis of social and ecological variables in order to assess the likelihood of differences in dimorphism resulting from predicted relative selection pressures.

SAMPLE AND METHODS

Sample

The combined response model has strict criteria. Sex-specific mean size and standard deviation data are needed from multiple populations (at least three in order to calculate correlations) of the same taxon, situated close together in space and time. Each population should include at least four adult individuals of each sex to minimize sampling effects on means and standard deviations. Such data have been published for very few primate taxa.

Published data for four populations each of three taxa are presented here: *Papio anubis*, *Saguinus mystax*, and *Chlorocebus pygerythrus* (= *Cercopithecus aethiops pygerythrus*) (Table 2.2). Each taxon is used to illustrate a particular combination of predicted selection direction (increase or decrease) and the sex targeted by more intense selection (males or females).

Methods

Sex-specific body size is measured as base 10 logarithm of sex-specific mean body mass in kilograms. SSD is calculated as $\log_{10}[M]-\log_{10}[F]$, which is equivalent to $\log_{10}[M/F]$ (where M and F are male and female mean sex-specific body mass in kilograms). Variability in body mass is usually reported as standard deviation or variance of raw data, not of logged data as required by the combined response model. However, Wright (1968) showed that the standard deviation of logged data can be closely approximated by the following formula:

$$s' = \sqrt{0.4343 \times \log_{10}(1 + C^2)}$$

where s' is estimated standard deviation and C is the coefficient of variability (standard deviation of raw data divided by the mean). Relative variability ratio is calculated here as

$\log_{10}[s'M]-\log_{10}[s'F]$, which is equivalent to $\log_{10}[s'M/s'F]$. These values are identical to logged ratios of coefficient of variation at two significant figures for all populations in this study, and for some populations are identical at three or more significant figures.

Correlations of (1) female body size and SSD, (2) male body size and SSD, and (3) SSD and relative variability ratio are calculated for each taxon. Due to small sample sizes (four populations in all cases), significance level is considered less important than strength of correlation as measured by coefficient of determination. Correlations are compared to [Table 2.1](#) to identify the predicted direction and primary target of selection in each taxon.

In addition, sex-specific body size in each population is compared against a baseline as a further check on the determination of the sex that is the primary target of selection. The difference in log sex-specific mean body size between populations and baseline is used to calculate difference as a percentage of baseline size. Ideally, baseline size represents body size in the last common ancestor of all populations for a particular taxon. In taxa in which positive correlations of size and body size ratio indicate that male size is the primary target of selection, male size should have changed proportionally more than female size, and thus percentage changes from baseline should be greater for males than females. Negative correlations of size and body size ratio indicate that female size is the primary target, in which case percentage changes from baseline should be greater for females than males.

In practice, ancestral body size for any group of populations cannot be determined definitively unless that ancestral population was weighed. In this study, ancestral body size is approximated by the population with the smallest body size in the case of taxa characterized by selection for increasing size, and by the population with the largest body size in the case of taxa characterized by selection for decreasing size. (Note: comparison

of proportional differences in this study yields similar results regardless of which extreme of mass is selected as baseline for each taxon.) These baseline populations have themselves responded to selection pressures since the last common ancestor of all populations for a given taxon, so differences from baseline are *not* changes from ancestral state, and should not be viewed as definitive indicators of the sex that is targeted by selection. However, since differences from baseline do not involve relative variation, they can independently support or contradict results from correlation analyses of dimorphism in body size and relative variation.

Correlations and baseline comparisons are used to identify the most likely set of selection pressures modifying size and dimorphism for each group of populations. Ecological and social data associated with each population and/or taxon as a whole are then considered in conjunction with (1) predicted patterns of selection pressures and (2) theoretical predictions of sexual and natural selection theory in order to identify the most likely source of selection pressures. Results are generalized for various selection patterns acting on primates.

RESULTS

Prediction: Positive Selection on Male Size

Female and male body size are both positively correlated with body size ratio in four Kenyan populations of *Papio anubis*, consistent with Rensch's rule (Fig. 2.2a, Table 2.3). Body size ratio and relative variability ratio are negatively correlated in wild populations consistent with selection for larger body size (Fig. 2.2b, Table 2.3). Mean sex-specific body size differences are calculated between a baseline population (population A, with the lowest mean body size) and all other populations (expressed as percentages of population A in Table 2.2). When male and female differences are compared, males in population B and D are greater than baseline size by a larger

proportion than females are greater than baseline. Male and female difference from baseline are approximately equal in population C.

Prediction: Positive Selection on Female Size

Female and male body size are both negatively correlated with body size ratio in four Peruvian populations of *Saguinus mystax*, contrary to Rensch's rule (Fig. 2.3a, Table 2.3). Body size ratio and relative variability ratio are negatively correlated, consistent with selection for larger body size (Fig. 2.3b, Table 2.3). Mean sex-specific body size differences expressed are calculated from a baseline population (population A, with the lowest mean body size) (Table 2.2). When male and female differences are compared, females in population C and D are greater than baseline size by a larger proportion than males are greater than baseline. Male and female difference from baseline are approximately equal in population B.

Prediction: Negative Selection on Female Size

Female and male body size are both negatively correlated with body size ratio in three Kenyan populations of *Chlorocebus pygerythrus*, contrary to Rensch's rule (Fig. 2.4a, Table 2.3). Body size ratio and relative variability ratio are positively correlated, consistent with selection for smaller body size (Fig. 2.4b, Table 2.3). Mean sex-specific body size differences expressed are calculated from a baseline population (population A, with the highest mean body size) (Table 2.2). When male and female differences are compared, females in population B, C, and D are smaller than baseline size by a larger proportion than males are smaller than baseline.

Other Selection Patterns

No examples were found of populations matching conditions consistent with selection primarily for small male size, selection in different directions for each sex, or size dimorphism resulting from variance dimorphism alone.

DISCUSSION

Positive Selection on Male Size

The positive scaling of size and SSD in both sexes of *P. anubis* is consistent with predictions for selection acting primarily on male body size under Lande's (1980) model. Differences from baseline, in which males are proportionally larger than baseline than are females, support the assertion that selection is stronger on males than females in these populations. The negative correlation of SSD and relative variability ratio indicates that selection has acted to increase size.

Sexual selection theory predicts that group-living, polygynous populations like those present in *P. anubis* should allow individual males to improve their relative fitness by winning competitions with other males for mating opportunities; females may also choose to mate with larger males (Brown, 1975; Ralls, 1977; Andersson, 1994). Thus sexual selection is expected to act primarily on male size, granting a selective advantage to larger males in polygynous taxa. The patterns observed in these wild *P. anubis* populations are consistent with the theoretical expectations of sexual selection theory. In general, when selection increases male size more than female size in primates, it is expected to usually result from male competition for mating opportunities within multi-male and uni-male polygynous primate populations (Brown, 1975; Plavcan, 2001).

Positive Selection on Female Size

Negative scaling of size and SSD in both sexes of Peruvian *S. mystax* is consistent with predictions for selection acting primarily on female body size under Lande's (1980) model. Differences from baseline, in which females are proportionally larger than baseline than are males, support the assertion that selection is stronger on females than males in these populations. The negative correlation of SSD and relative variability ratio indicates that selection has acted to increase size in these populations.

Sexual selection theory predicts that group-living, polyandrous populations with high paternal investment like those seen in *S. mystax* should promote competition between females for mates, as well as male choice for large, fecund females (Ralls, 1976; Petrie, 1983; Gwynne & Simmons, 1990; Gwynne, 1991; Parker & Simmons, 1996; Cunningham & Birkhead, 1998). Thus sexual selection is expected in this case to act primarily on female size, granting a selective advantage to larger females. The patterns observed in these *S. mystax* populations are consistent with theoretical expectations of sexual selection theory. In general, when selection increases female size more than male size in primates, it will most likely usually result from sexual selection acting within polyandrous groups.

Negative Selection on Female Size

Negative scaling of size and SSD in both sexes of Kenyan *C. pygerythrus* is consistent with predictions for selection acting primarily on female body size under Lande's (1980) model. Differences from baseline, in which females are proportionally smaller than baseline than are males, support the assertion the selection is stronger on females than males in these populations. The positive correlation of body size ratio and relative variability ratio indicates that selection has acted to decrease size in these populations.

In most cases, sexual selection theory does not predict that small size is advantageous for either sex in gaining access to reproductive opportunities (although see below). However, natural selection pressures can select for smaller size, particularly through resource pressures. In the case of the *C. pygerythrus* populations in this study, while all populations were multimale-multifemale groups, significant differences in ecological conditions existed between populations (Turner *et al.*, 1997). The population with the largest female mean body size (population A) was living in a lakeside grassland

with the highest rainfall levels of all populations and had access to human crops; the other populations were living in dry grassland and thornscrub (B and C) or woodland and savannah (D) where access to food was much more irregular (Turner *et al.*, 1997). Due to the short time period likely separating vervet populations in this study (at most a few generations), it is possible that individuals belonging to populations in the more marginal habitats can trace their recent ancestry to populations living with more reliable resources (*i.e.*, access to cropland).

In general, natural selection pressures may be applied equally to males and females, but when resource pressures are present they are expected to be stronger on females because of the energetic costs associated with reproduction (Ralls, 1976; Emlen & Oring, 1977; Wrangham, 1980; van Schaik, 1989; Isbell, 1991; Mitchell *et al.*, 1991; van Hooff & van Schaik, 1992; Isbell & Pruett, 1998; Boinski *et al.*, 2002). Thus natural selection may act to decrease female body size more than male size when resources are scarce. Work on human dimorphism in Native Americans suggests that small body size is advantageous for mothers when resources are scarce during lactation (Hamilton, 1975; cited in Ralls, 1977). Because larger females have absolutely greater metabolic costs than small females, small females should be better able to develop an energetic surplus for reproduction during periods of resource scarcity. Larger females will be less likely to reproduce than small females in times of scarcity because of the required greater investment of internal reserves (and thus, greater risk) on the part of larger females; hence, a decrease in expectation of future offspring (Pianka & Parker, 1975; Pianka, 1976). Empirical evidence from Darwin's finches supports these predictions, showing that small females breed more often than larger females in variable environments (Downhower, 1976).

Niche separation, in which optimum body size differs between the sexes due to adaptation for different feeding niches, could also account for sex-differences in natural selection pressures (Selander, 1966; Ralls, 1976; Slatkin, 1984; Shine, 1989; Andersson, 1994). However, Clutton-Brock and Harvey (1977) point out that although there are sex-specific dietary differences associated with size dimorphism in primates (*e.g.*, Clutton-Brock, 1977; Demment, 1983; Kamilar, 2003), there is no evidence of sex differences in feeding apparatus such as is seen some birds (Selander, 1972), indicating that dietary differences are probably a product of size dimorphism rather than a cause. In contrast, a recent review of primate community structure and resource availability concluded that many primates do encounter food shortages (Janson & Chapman, 1999). Thus negative selection on female size will usually be the product of natural selection, most likely in the form of resource limitation. Although other forms of natural selection can select for small size (*e.g.*, small size and crypsis as a result of predation pressure), these selection pressures are not necessarily expected to affect females more than males.

Other Selection Patterns

In my search through the limited data available to provide examples for this study, I was unable to find any instances of negative selection acting primarily on male size. The absence of such an example does not necessarily reflect the absence of this pattern in primate evolution. However, it probably *does* reflect the low likelihood of such a pattern. Sexual selection, which is expected to act primarily on male size in many primate populations, should generally increase body size rather than decrease it unless female choice targets small males (Andersson, 1994). It is true that alternative mating strategies exist that favor small male size. For example, some adult orangutan males resemble juveniles in size and appearance; these males are able to enter other males' territories for covert mating, often coerced from females (MacKinnon, 1974; Galdikas, 1985; Mitani,

1985; Schürmann & van Hooff, 1986; Utami *et al.*, 2002). However, such strategies act to increase variability in male size rather than decrease overall size: the orangutan strategy described above is termed “alternative” because other males are very large, presumably as a result of competitive sexual selection and/or female choice (Schürmann & van Hooff, 1986; Rodman & Mitani, 1987). Thus sexual selection is unlikely to act to decrease body size, leaving only natural selection as a downward force on body size. When sex differences exist in natural selection pressures within primates, the most likely source is resource limitation, which is expected to affect females more than males. Therefore it is unlikely that male size is often the target of more intense negative selection than female size.

I was also unable to find examples of mixed patterns in which selection acts to increase the size of one sex and decrease the size of other. Since it is unlikely that male size is often the primary target of negative selection, it is extremely unlikely that male size is negatively selected and female size is positively selected – particularly since negative selection on body size may often be a product of resource limitation, which should act more strongly on females than males. The opposite pattern is more likely to occur, as selection for increased size in males and decreased size in females could result from natural selection pressures selecting for smaller body size in both sexes combined with male competition and female choice selecting for larger male size. It remains to be seen how often in such situations that positive selection on male size as a result of sexual selection is more intense than negative selection on male size due to natural selection, resulting in overall positive selection on male size.

Finally, I did not identify any set of populations in which the relative variability ratio remained constant as predicted for SSD resulting from variance dimorphism alone. Studies of dimorphism in canine size and cranial dimensions have also failed to find

evidence of variance dimorphism influencing size dimorphism (Plavcan & Kay, 1988; Plavcan, 1990; 2000b). It may be the case that variance dimorphism mediates the effects of sex-specific selection differentials by reinforcing or counteracting selection differences, but it is unlikely that differences in relative variability often produce size dimorphism in the absence of differences in selection intensity.

Implications for Rensch's Rule

The examples presented above demonstrate that selection can act to increase or decrease size within primates, and it can act primarily on males or primarily on females. Also, selection can be applied equally to both sexes to change size without changing dimorphism: this can be attested to by the existence of the suborder Strepsirhini, in which body size spans more than two orders of magnitude (nearly four orders of magnitude when sub-fossil lemurs are included, Godfrey, 1988; Jungers, 1990a; Godfrey *et al.*, 1993; 1995; 1997; Jungers *et al.*, 2002) without any appreciable size dimorphism at all (Kappeler, 1990; 1991; Godfrey *et al.*, 1993).

When selection pressures do differ between males and females, those differences will probably most often result from the forces described above: sexual selection on males, sexual selection on females, or resource limitation preferentially affecting females. Under the predictions of Lande's (1980) quantitative genetics model (which by itself is not limited to closely related populations of the same taxon), positive scaling of body size and SSD (Rensch's rule) should result when males are the primary target of selection, and negative scaling should result when females are the primary target. The direction of selection (increase or decrease) does not affect this scaling relationship.

Scaling relationships of size and dimorphism within haplorhine primates are generally consistent with Rensch's rule (Clutton-Brock *et al.*, 1977; Mitani *et al.*, 1996; Plavcan & van Schaik, 1997b; Smith & Cheverud, 2002). However, there are haplorhine

primates for which sexual selection probably acts primarily to increase female body size (*e.g.*, polyandrous callitrichid populations), and many primate communities encounter food shortages (Janson & Chapman, 1999) which should generate negative selection acting primarily on female size. Is it possible to reconcile the presence of Rensch's rule and selection on female size using a quantitative genetics framework?

Yes. A large amount of unexplained variation exists in relationships between size and dimorphism in primates (Smith & Cheverud, 2002), which allows for the possibility of localized negative trends superimposed on overall positive trends. Such a pattern occurs if relationships between higher-level taxa (subfamilies, families, superfamilies, *etc.*) for size and SSD are primarily positive, while lower-level taxonomic relationships include positive and negative trends.

If trends differ between higher-level and lower-level taxonomic comparisons, there may be bias in the preservation of lineages in primate ancestry. Only a small percentage of the species that were alive at any particular point in time in the past have left descendant species that are alive today, and thus selection pressures that acted on ancestral lineages are not necessarily representative of the full range of selection pressures that acted on primates at any given point in the past. Extinction in vertebrates is correlated with high resource requirements, slow population recovery rate, and specialization (Diamond, 1984; Brown, 1995). Thus populations subject to intense resource limitation (producing negative scaling of body size and SSD) are more likely to go extinct than populations subject to sexual selection. Because polygyny is much more common than polyandry in haplorhines, selection for increased male size will be the most common type of sexual selection preserved in haplorhine lineages. It follows that haplorhine ancestry is likely biased towards preserving lineages in which size and dimorphism increase together, resulting in Rensch's rule, although at any particular point

in time there may be many primate populations in which resource limitation is acting contrary to Rensch's rule.

The relatively strong positive scaling of size and SSD observed in Primates as compared to other mammalian orders (Abouheif & Fairbairn, 1997) may result in part from the relative rarity of primates. Primates as a whole are rare mammals as measured in a variety of ways (Dobson & Yu, 1993; Yu & Dobson, 2000). Because rare taxa are more likely to go extinct than common taxa (Diamond, 1984), resource limited populations in Primates may go extinct with a higher relative frequency than resource limited populations of more common mammals. If so, negative scaling patterns are less likely to be preserved in Primates than in more common mammalian orders, generating a stronger positive scaling signal in Primates.

Other Evidence from Non-Primate Radiations

Although Rensch's rule (unlike Lande's model) does not depend upon the sex under selection, a review of studies of Rensch's rule across major animal radiations considered taxa where males are usually larger than females separately from taxa where the reverse is true (Abouheif & Fairbairn, 1997). Rensch (1959) himself stated his rule differently for these two cases, but only because of the way he chose to define SSD: as the absolute value of relative size difference, rather than relative difference of a particular sex from the other (*i.e.*, $|\log[M]-\log[F]|$ rather than $\log[M]-\log[F]$). When SSD is defined as the latter, Rensch's rule states that SSD should scale positively with body size, regardless of the larger sex.

However, Abouheif and Fairbairn's (1997) study of size and scaling in 21 radiations of mammals, reptiles, birds, insects, and arachnids using phylogenetically independent contrasts found that the probability of a particular clade following Rensch's rule decreases as the size of males relative to females decreases. If sexual selection most

commonly acts to increase size rather than decrease it, males will usually be larger than females when sexual selection targets male size, and females will usually be larger than males when sexual selection targets female size. Thus when male size is small relative to female size, females are more likely to be the target of sexual selection, in which case Lande's (1980) model predicts that SSD should scale negatively with size (counter to Rensch's rule). As Abouheif and Fairbairn (1997) point out, scaling relationships were significantly positive in only one radiation in which females are larger than males: water striders, a taxon in which sexual selection appears to favor large male size (Fairbairn, 1990; Arnqvist, 1992; Sih & Krupa, 1992; Krupa & Sih, 1993; Fairbairn & Preziosi, 1994; Rowe *et al.*, 1994), and thus is predicted by Lande's model to follow Rensch's rule. In other radiations female body size is thought to be the target of fecundity selection (*e.g.*, owls, spiders); in these cases, SSD scales negatively with body size as predicted by Lande's model (Earhart & Johnson, 1970; Vollrath & Parker, 1992; Head, 1995; Abouheif & Fairbairn, 1997). In general, Abouheif and Fairbairn's (1997) results show that scaling of SSD and size in non-primate radiations are in agreement with predictions based on Lande's (1980) model, but only agree with Rensch's rule when the predictions of Lande's model overlap with Rensch's rule.

Future Directions in Primate Research

Future work can further explore the possibility that recent negative scaling patterns are layered on top of older positive scaling patterns within Primates. For example, comparisons of size and SSD scaling patterns between primate clades can test explicit predictions based on Lande's (1980) model. One such prediction is that scaling patterns in the Callitrichidae should be more negative than patterns in other clades due to the presence of polyandry in some callitrichid populations. Support for this prediction is found in analyses of size and SSD that show that positive scaling of SSD is relatively

weak in platyrrhines (Ford, 1994), particularly when compared to catarrhines (Smith & Cheverud, 2002). Finer-grained approaches can explicitly test the difference between Callitrichidae and other New World monkeys.

In addition, phylogenetic analyses that identify differences between modern scaling patterns, recent evolutionary patterns, and ancient evolutionary patterns can determine whether ancient phylogenetic relationships (*i.e.*, between higher-level taxa) preserve different evolutionary signals than more recent relationships (*i.e.*, between lower-level taxa), and whether modern relationships primarily reflect the influence of one or both of these sets of patterns. Phylogenetically independent contrasts (Felsenstein, 1985; Garland *et al.*, 1992; Garland & Ives, 2000) can be partitioned into separate analyses of contrasts between higher- and lower-level taxa, which can in turn be compared to modern scaling patterns as measured by traditional inter-specific regression analyses. Studies of this type will allow primatologists to identify the types and relative strengths of selective pressures that have produced the variation in sex-specific body size and SSD that is present in living primates.

The next chapter undertakes just such an analysis for three major radiations within the Order Primates: Strepsirhini, Platyrrhini, and Catarrhini.

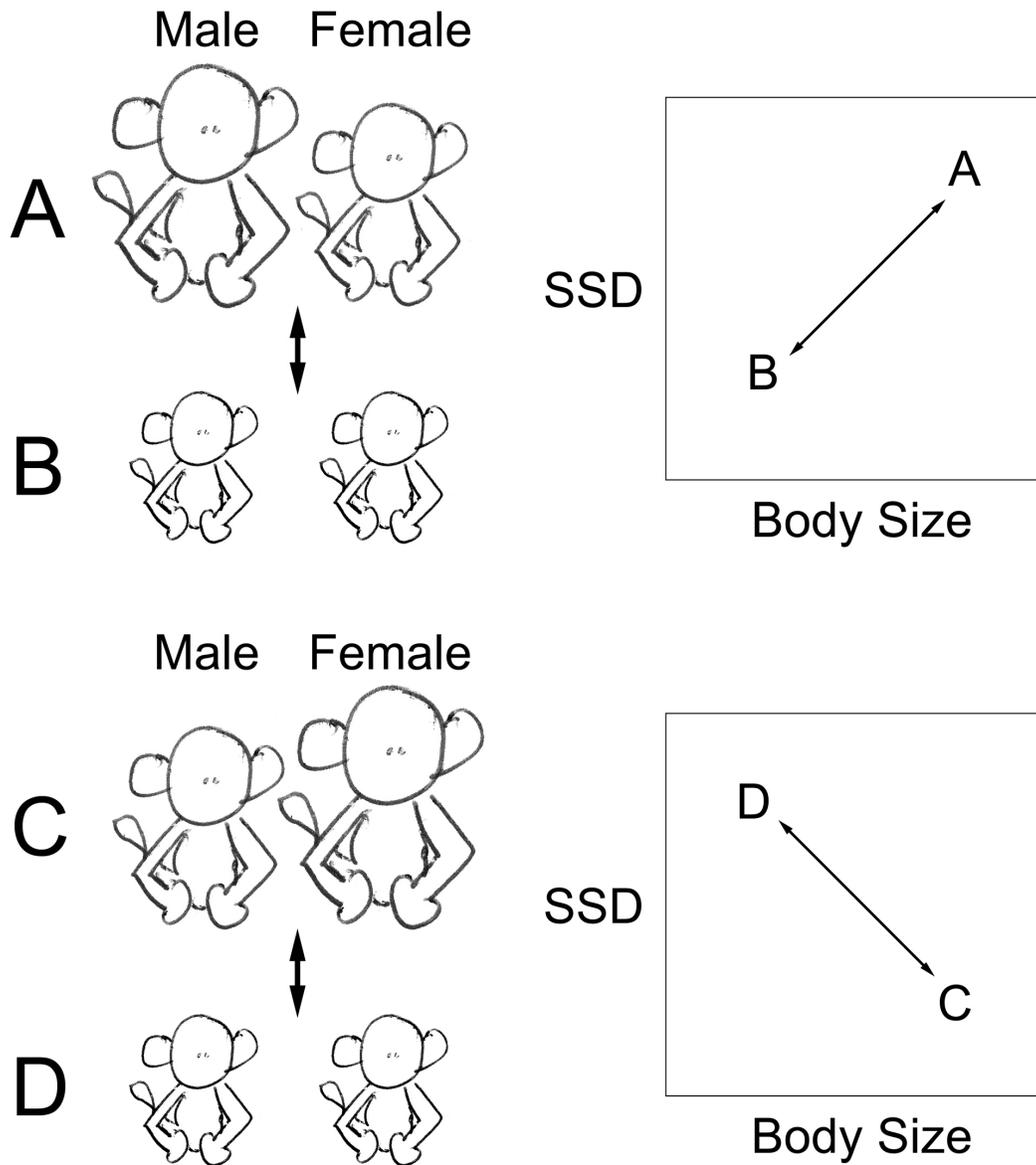


Figure 2.1. Scaling relationships of size and SSD associated with changes in sex-specific size.

When selection acts primarily on males, male size will increase (B to A) or decrease (A to B) more than female size, resulting in positive scaling of SSD and body size. When selection acts primarily on females, female size will increase (D to C) or decrease (C to D) more than male size, resulting in negative scaling of SSD and body size.

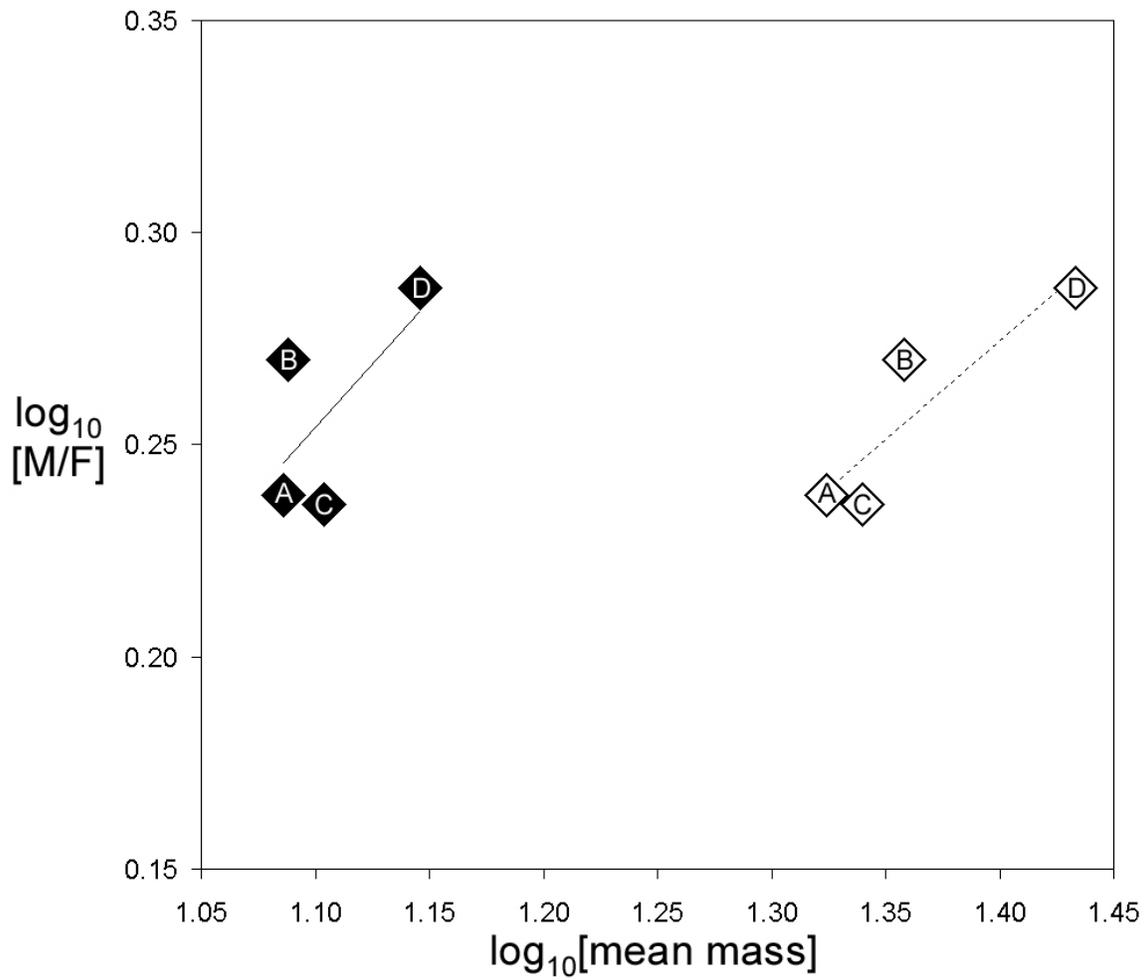


Figure 2.2a. Scaling of sex-specific body size and body size ratio in Kenyan populations of *Papio anubis*.

Closed symbols are females, open symbols are males. Letters correspond to populations in Table 2.2. Trend lines: solid, female; dotted, male. Correlations are positive in both sexes, consistent with Rensch's rule.

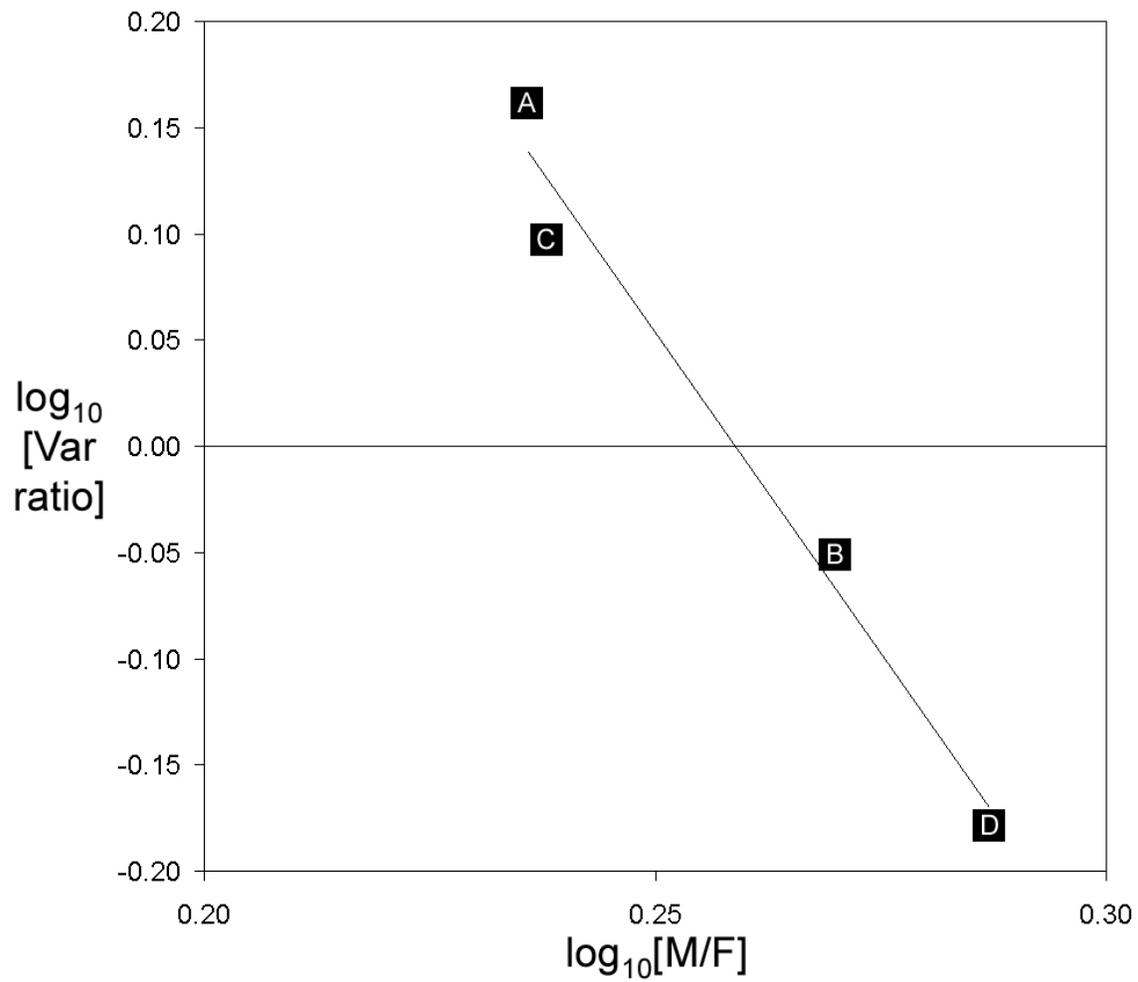


Figure 2.2b. Bivariate plot of body size ratio and relative variability ratio in Kenyan populations of *Papio anubis*.

Correlation among all populations is negative, consistent with selection for increasing size.

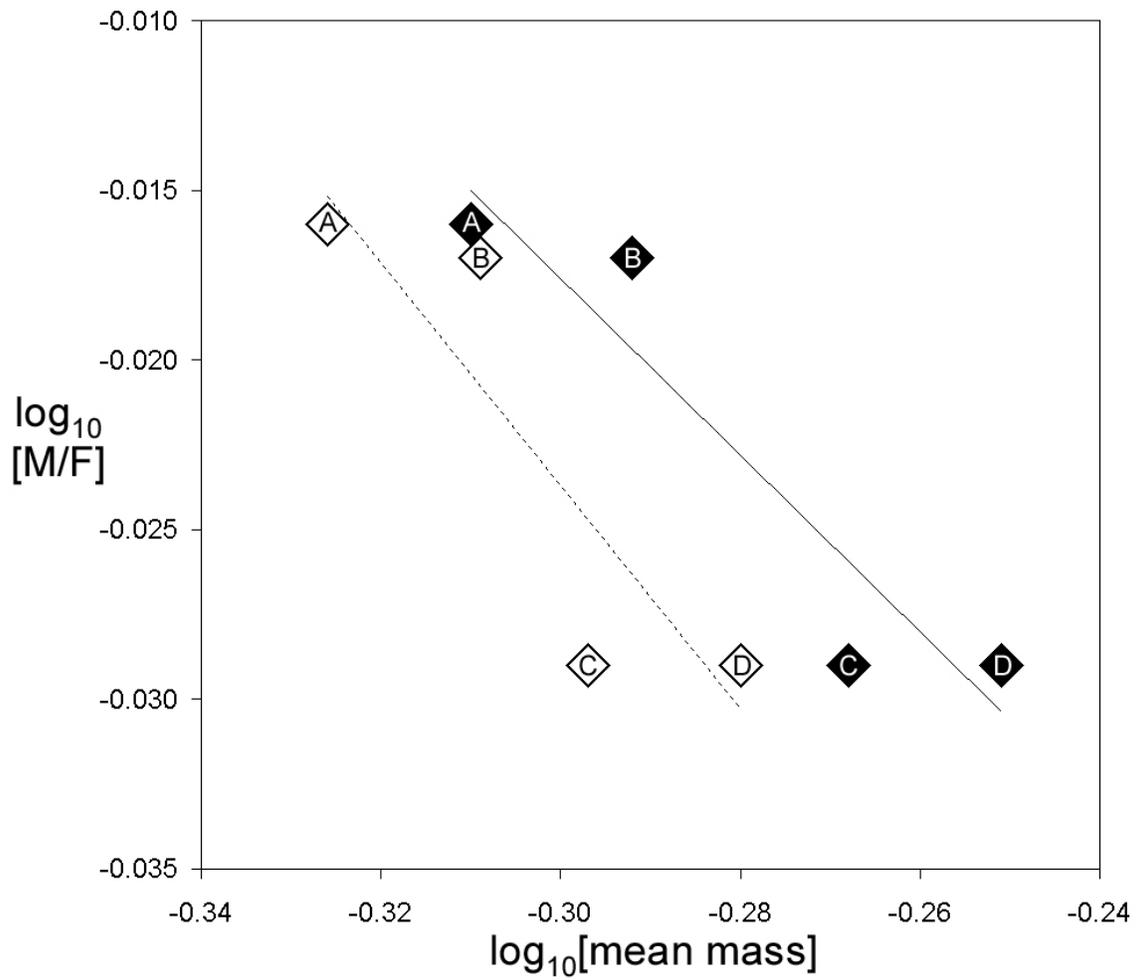


Figure 2.3a. Scaling of sex-specific body size and body size ratio in four Peruvian populations of *Saguinus mystax*.

Symbols and lines follow Figure 2.1a. Correlations are negative in both sexes, contrary to Rensch's rule.

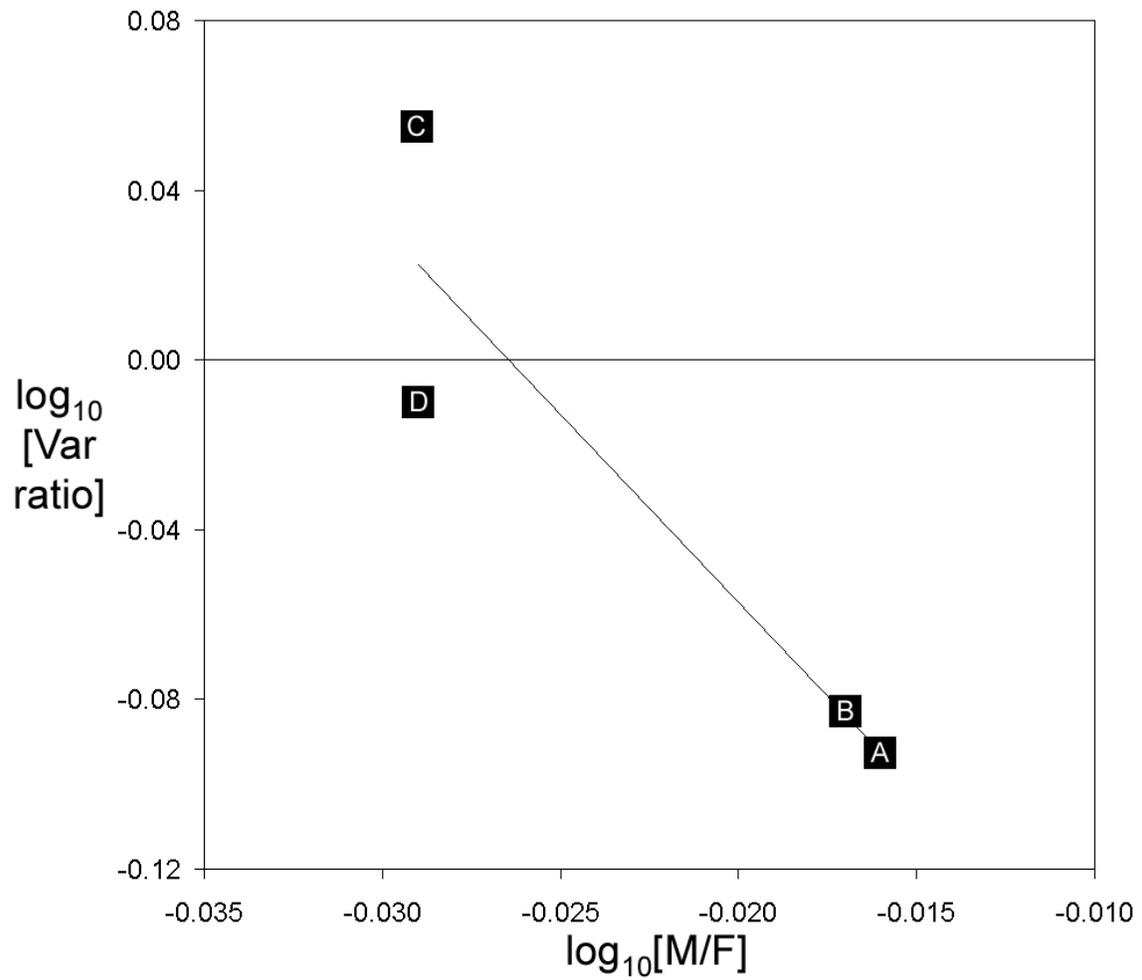


Figure 2.3b. Bivariate plot of body size ratio and relative variability ratio in four Peruvian populations of *Saguinus mystax*.

Correlation among all populations is negative, consistent with selection for increasing size.

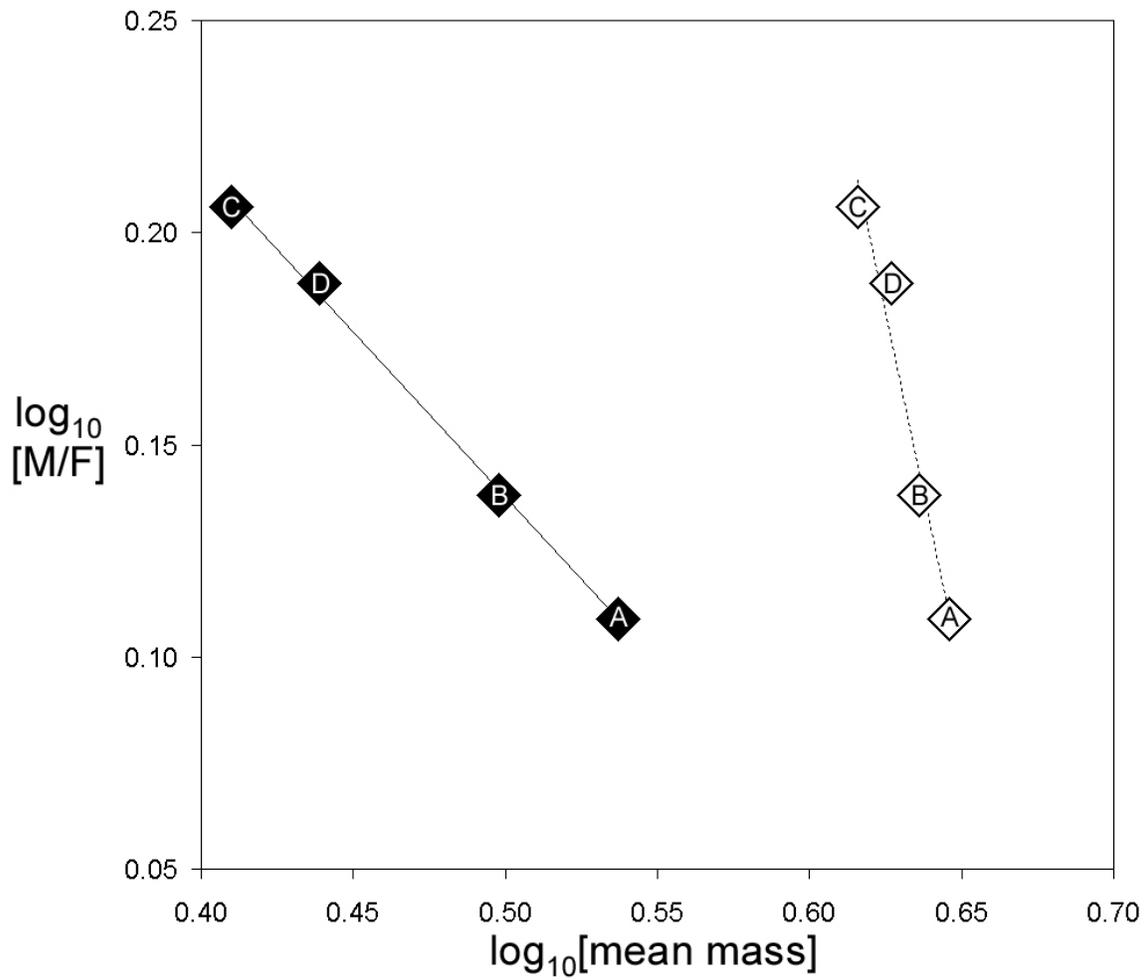


Figure 2.4a. Scaling of female body size and body size ratio in four Kenyan populations of *Chlorocebus pygerythrus*.

Symbols and lines follow Figure 2.1a. Correlations are negative in both sexes, contrary to Rensch's rule.

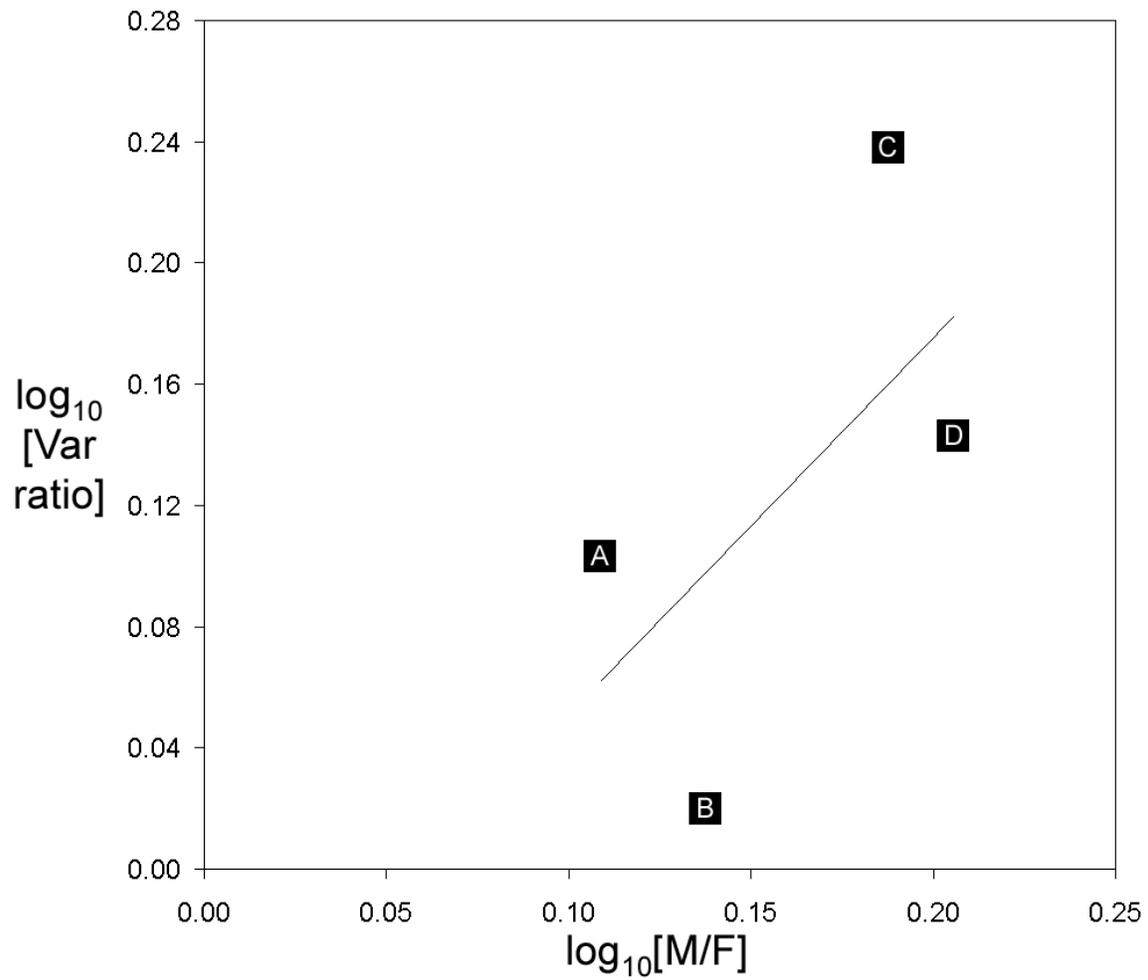


Figure 2.4b. Bivariate plot of body size ratio and relative variability ratio in four Kenyan populations of *Chlorocebus pygerythrus*.

Correlation among all populations is positive, consistent with selection for decreasing size.

| Primary Target of Selection | Direction of Size Selection | Female Body Size - Size Ratio Correlation | Male Body Size - Size Ratio Correlation | Size Ratio - Var. Ratio Correlation |
|--------------------------------|--------------------------------|---|---|---|
| Male | Increase | + | + | - |
| Female | Increase | - | - | - |
| Male | Decrease | + | + | + |
| Female | Decrease | - | - | + |
| Both* | Both* | - | + | any |
| | ** | any | any | 0 |

Table 2.1. Correlations of body size, size ratios, and relative variability ratios resulting from sex differences in selection intensity.

* If selection acts to increase the body size of one sex and decrease the other, correlations will follow the pattern above regardless of which sex increases and which sex decreases in size. Any correlation between body size ratio and relative variability ratio is possible in that scenario, depending on the relative strength of selection on each sex. See text for details. ** This case describes differences due to variance dimorphism alone; selection intensity is equal and non-zero for both sexes, and changes in dimorphism result from selection applied to differences in sex-specific relative variability.

| Population | Male Female | | M (kg) | F (kg) | log [M] | log [F] | log [M]- log[F] | log[VM]- log[VF] | Change Change | | Locality | Reference |
|-------------------------|-------------|-----|--------|--------|---------|---------|--------------------|---------------------|---------------|--------|--------------------------|-----------------------------|
| | N | N | | | | | | | M | F | | |
| <i>P. amubis</i> A | 177 | 237 | 21.1 | 12.2 | 1.324 | 1.086 | 0.238 | 0.097 | - | - | Laikipia District, Kenya | Berger (1972) |
| <i>P. amubis</i> B | 10 | 39 | 22.8 | 12.3 | 1.358 | 1.088 | 0.270 | -0.052 | 8.1% | 0.5% | Nairobi, Kenya | Popp (1983) |
| <i>P. amubis</i> C | 18 | 18 | 21.9 | 12.7 | 1.340 | 1.104 | 0.236 | 0.161 | 3.8% | 4.2% | Athi Plain, Kenya | Gest & Siegel (1983) |
| <i>P. amubis</i> D | 54 | 23 | 27.1 | 14.0 | 1.433 | 1.146 | 0.287 | -0.179 | 28.5% | 14.8% | Mara, Kenya | Popp (1983) |
| <i>S. mystax</i> A | 48 | 30 | 0.472 | 0.490 | -0.326 | -0.310 | -0.016 | -0.093 | - | - | Tapiche, Loreto, Peru | Soini & Soini (1990) |
| <i>S. mystax</i> B | 95 | 80 | 0.491 | 0.511 | -0.309 | -0.292 | -0.017 | -0.083 | 4.0% | 4.2% | Rio Yarpa, Loreto, Peru | Moya <i>et al.</i> (1990) |
| <i>S. mystax</i> C | 34 | 26 | 0.505 | 0.540 | -0.297 | -0.268 | -0.029 | 0.055 | 6.9% | 10.2% | Tahuayo, Loreto, Peru | Soini & Soini (1990) |
| <i>S. mystax</i> D | 79 | 48 | 0.525 | 0.561 | -0.280 | -0.251 | -0.029 | -0.010 | 11.2% | 14.6% | Manitú, Loreto, Peru | Soini & Soini (1990) |
| <i>C. pygerythrus</i> A | 12 | 31 | 4.43 | 3.44 | 0.646 | 0.537 | 0.109 | 0.103 | - | - | Naivasha, Kenya | Turner <i>et al.</i> (1997) |
| <i>C. pygerythrus</i> B | 18 | 15 | 4.33 | 3.15 | 0.636 | 0.498 | 0.138 | 0.020 | -2.3% | -8.6% | Kimana, Kenya | Turner <i>et al.</i> (1997) |
| <i>C. pygerythrus</i> C | 26 | 36 | 4.13 | 2.57 | 0.616 | 0.410 | 0.206 | 0.143 | -6.7% | -25.4% | Samburu, Kenya | Turner <i>et al.</i> (1997) |
| <i>C. pygerythrus</i> D | 4 | 10 | 4.24 | 2.75 | 0.627 | 0.439 | 0.188 | 0.238 | -4.3% | -20.2% | Mosiro, Kenya | Turner <i>et al.</i> (1997) |

Table 2.2. Body size and differences in log size, log relative variability, and difference from extreme size.

Change variables measure percentage difference in raw body size for both sexes from the smallest or largest population mean (see text for details).

| log[F] and log[M/F] | | | | |
|--------------------------------|----------|----------|-----------------------|----------|
| Species | <i>N</i> | <i>r</i> | <i>r</i> ² | <i>p</i> |
| <i>Papio anubis</i> | 4 | 0.665 | 0.443 | 0.335 |
| <i>Saguinus mystax</i> | 4 | -0.936 | 0.876 | 0.064 |
| <i>Chlorocebus pygerythrus</i> | 4 | -0.999 | 0.998 | 0.001 |

| log[M] and log[M/F] | | | | |
|--------------------------------|----------|----------|-----------------------|----------|
| Species | <i>N</i> | <i>r</i> | <i>r</i> ² | <i>p</i> |
| <i>Papio anubis</i> | 4 | 0.902 | 0.814 | 0.098 |
| <i>Saguinus mystax</i> | 4 | -0.882 | 0.777 | 0.118 |
| <i>Chlorocebus pygerythrus</i> | 4 | -0.979 | 0.958 | 0.021 |

| log[M/F] and log[VM/VF] | | | | |
|--------------------------------|----------|----------|-----------------------|----------|
| Species | <i>N</i> | <i>r</i> | <i>r</i> ² | <i>p</i> |
| <i>Papio anubis</i> | 4 | -0.988 | 0.976 | 0.012 |
| <i>Saguinus mystax</i> | 4 | -0.924 | 0.853 | 0.076 |
| <i>Chlorocebus pygerythrus</i> | 4 | 0.612 | 0.374 | 0.388 |

Table 2.3. Correlations of body size, body size ratio, and relative variability ratio.

Chapter 3: Evolution of Rensch's Rule in Primates

INTRODUCTION

In many animal radiations, sexual size dimorphism (SSD) scales positively with body size, a concept known as Rensch's rule (Rensch, 1959). A recent study of size and dimorphism by Smith and Cheverud (2002) reviewed previous investigations of Rensch's rule in primates (*e.g.*, Clutton-Brock *et al.*, 1977; Leutenegger, 1978; Leutenegger & Cheverud, 1982; Gaulin & Sailer, 1984; Kappeler, 1990; Ford, 1994; Martin *et al.*, 1994; Abouheif & Fairbairn, 1997; Plavcan & van Schaik, 1997b) and presented a series of new phylogenetic comparative analyses of the scaling of size and SSD within various primate clades. Considered together, these studies generally support the assertion that Rensch's rule is present in haplorhine primates, but absent in strepsirhines.

However, it is not clear why there should be a positive scaling relationship between size and dimorphism at all. Several different explanations for Rensch's rule have been proposed over the years, which Fairbairn (1997) grouped into eight categories. These eight categories can be generalized into three types of explanations: (1) increases in body size cause or facilitate increases in SSD, (2) correlations of genetics or selection pressures between sexes cause changes in dimorphism and body size of both sexes when selection is applied to the size of one sex, and (3) natural selection applies differential sex-specific selection pressures resulting in changes in size and dimorphism.

Models that propose a causal role for body size in the determination of SSD are poorly supported in primates (Mitani *et al.*, 1996; Plavcan & van Schaik, 1997b; Plavcan, 2001; Smith & Cheverud, 2002). Indeed, the absence of scaling of size and dimorphism in strepsirhines is in itself a rebuttal to arguments posing an obligatory relationship between size and dimorphism. As Fairbairn (1997) points out, there is no *a*

priori reason such as biomechanical constraint to suppose that dimorphism must scale positively with size.

Alternatively, some models that suggest that size and dimorphism both change in response to sex-specific differences in selection pressure or additive genetic variation make explicit predictions regarding the scaling of size and dimorphism (*e.g.*, Lande, 1980; Zeng, 1988). Differences in sex-specific selection pressures can result from sexual selection, in which large size is advantageous in competition between members of one sex for access to mating opportunities (intra-sexual competition) or large size is a character actively sought out in potential mates (inter-sexual competition) (Darwin, 1871; Andersson, 1994); selection differences can also arise from natural selection due to sexual niche separation or resource pressures (Selander, 1966; Ralls, 1976; Slatkin, 1984; Shine, 1989; Andersson, 1994). Within primates, sexual selection is usually thought to produce sexual size dimorphism (*e.g.*, Clutton-Brock *et al.*, 1977; Gaulin & Sailer, 1984; Clutton-Brock, 1985; Rodman & Mitani, 1987; Ford, 1994; Martin *et al.*, 1994; Mitani *et al.*, 1996; Plavcan & van Schaik, 1997b; Lindenfors & Tullberg, 1998; Plavcan, 1999; Barton, 2000; Plavcan, 2001). The relationship between SSD and sexual selection is of particular interest to anthropologists because of the potential to infer social and/or mating behaviors of extinct primates based on body size dimorphism in the fossil record (*e.g.*, Wolpoff, 1976; Schroder, 1993; McHenry, 1994a; Kappelman, 1996; Plavcan & van Schaik, 1997a; Plavcan, 2002; Reno *et al.*, 2003).

This study analyzes a large database of primate taxa using traditional interspecific analyses along with phylogenetic comparative techniques to identify modern, recent, and ancient patterns in the scaling of body size and SSD in primates. Modern patterns are those relationships present in extant primates as measured by traditional regression analyses. Recent and ancient evolutionary patterns are relationships preserved in the

phylogeny of living primates. All three types of scaling patterns are compared to each other and are used to identify a model for the evolution of Rensch's rule that can accommodate all observed relationships within primates, most notably the presence of Rensch's rule in Haplorhini and absence in Strepsirhini. Modern, recent, and ancient scaling patterns in strepsirhines, platyrrhines, and catarrhines are interpreted in the context of this model, and implications for the reconstruction of behavior from the fossil record are discussed.

SAMPLE AND METHODS

Sample

When building samples for broad comparative studies, there are two competing objectives: represent as many taxa as possible, and restrict sample inclusion to reliable data. While exclusionary data sets may be more reliable in terms of the accuracy of mass measurements, they often have built in biases. For example, body mass measurements for a large number of wild primates are much less likely to be available for small solitary cryptic nocturnal species than for larger-bodied, group living diurnal species. In this study I analyze two data sets: a full data set in which taxonomic inclusion is maximized, and a reduced data set in which only taxa with body mass measurements from at least 4 individuals of each sex ([Table 3.1](#)).

In most cases species are the basic taxonomic unit of consideration (*i.e.*, one mean is calculated for all populations of a species), although subspecies are treated as separate taxa when sample sizes meet the reduced data set criteria and sex-specific means differ considerably between subspecies. The full sample is composed of 221 taxa representing 194 species in the Order Primates, including 29 Lemuroidea, 15 Lorisioidea, 4 Tarsioidea, 61 Ceboidea, 70 Cercopithecoidea, and 15 Hominoidea. The reduced sample is made up

of 157 taxa representing 143 species in the Order Primates, including 19 Lemuroidea, 10 Lorisoidea, 3 Tarsioidea, 47 Ceboidea, 53 Cercopithecoidea, and 11 Hominoidea.

Methods

Measuring Size and SSD

Past studies of scaling of size and SSD in primates have generally analyzed either the relationship between female size and male size (*e.g.*, Clutton-Brock *et al.*, 1977; Leutenegger, 1978; Martin *et al.*, 1994; Lindenfors & Tullberg, 1998; Weckerly, 1998), or the relationship between female size and an index of dimorphism (*e.g.*, Kappeler, 1990; Ford, 1994; Plavcan & van Schaik, 1997b; Smith & Cheverud, 2002). As Smith (1999) points out, regression slopes of $\log [M]$ against $\log [F]$ are exactly equal to regressions slopes of $\log [M/F]$ against $\log [F]$ plus 1 (M and F refer to mean male mass and mean female mass, respectively). Intercepts are identical for both regressions, as are standard errors and confidence intervals for slopes and intercepts. The reason for these relationships is that $\log [M/F]$ is equal to $\log [M] - \log [F]$. Therefore the regression of $\log [M/F]$ against $\log [F]$ can be restated as the regression of $\log [M]$ against $\log [F]$ plus the regression of $\log [F]$ against $\log [F]$. The regression of a variable against itself will always result in a slope of one and intercept of zero, with standard errors of zero about both parameters.

In general, $\log [M]$ is preferred over $\log [M/F]$ as the dependent variable in regression analyses because dimorphism is a function of female size and male size, not a property independent of male size. Thus standard errors and confidence intervals should be interpreted as applying to $\log [M]$, not $\log [M/F]$, although those parameters are the same regardless of the choice of dependent variable.

However, it is much easier to see differences between positive scaling and negative scaling of size and dimorphism on a plot of $\log [M/F]$ against $\log [F]$ (where

SSD scaling trends appear as lines with positive and negative slopes, respectively) than on a plot of $\log [M]$ against $\log [F]$ (where SSD scaling trends appear as lines with slopes greater than one and less than one, respectively). Because the regression parameters are identical between these two types of regressions (with the addition or subtraction of 1 to slopes), $\log [M/F]$ is used as the dependent variable in this study in order to maximize the visual impact of bivariate plots, with the caveat that standard errors should be understood to apply to the log of male size and not SSD. Coefficients of determination (r^2) differ between the two types of regression, and are calculated here with $\log [M/F]$ as the dependent variable.

Both base 10 and base e (the natural logarithm) logarithms have been used in the primate literature, and although individual values will differ depending on the logarithmic transformation used, slopes will be identical. Base 10 logarithms are used here simply for ease of estimation of untransformed values (*i.e.*, 10 raised to a particular power rather than e raised to that power). Logarithmic transformations are applied to published and unpublished sex-specific body mass means for 221 primate taxa (Table 3.1). Because mean body size varies between populations, species means are calculated as the mean of population averages when all constituent populations have at least 4 members of each sex (denoted by the letter P in Table 3.1). When all populations do not meet that criterion, species means are calculated as a weighted mean of each population average with the number of individuals as weights (denoted by the letter W in Table 3.1).

Smith and Jungers' (1997) compilation of primate body mass data serves as the source for much of the mass data in Table 3.1. I also draw mass data from other published sources as well as unpublished data generously shared with me by field workers in Madagascar. Eric Delson supplied museum numbers and body mass data from a recent review of size in extant and extinct cercopithecoids (Delson *et al.*, 2000)

that are used to calculate sex-specific means for geographically distinct populations identified in the *Catalogue of Primates in the British Museum (Natural History) and Elsewhere in the British Isles* (Napier, 1981; 1985). In general, mass data from wild populations and large populations are preferred over data from captive and small populations, but means from captive and/or small groups are included if no other data are available for a particular primate species. Because I prefer to give equal weight to populations rather than individuals, population means are reported separately within [Table 3.1](#) whenever possible.

Traditional Regressions

This study attempts to determine if an evolutionary relationship between size and dimorphism exists, a question properly tested using techniques that take into account the evolutionary history of the traits in question – *i.e.*, phylogenetic comparative methods. However, it is appropriate to consider the relationship between size and SSD as it exists among extant taxa using traditional regression techniques for two reasons. First, it represents the present state of affairs (modern scaling patterns), and any explanation of Rensch’s rule must accommodate the observed data. Second, it serves as a benchmark against which phylogenetic analyses can be compared.

Ordinary least squares (OLS) regressions are preferred in this study over Model II regressions for two reasons. The first reason is that although residuals are not a subject of analysis here, previous studies have analyzed residuals from regressions of SSD against size (Ford, 1994; Martin *et al.*, 1994; Mitani *et al.*, 1996; Plavcan & van Schaik, 1997b). Although the appropriateness of using residuals in studies of SSD has been questioned (*e.g.*, Plavcan & van Schaik, 1997b; Smith & Cheverud, 2002), residuals from an OLS regression line of $\log [M/F]$ against $\log [F]$ are meaningful in one sense: they are log-transformed ratios of observed dimorphism divided by expected dimorphism for a

given size. Because Model II regressions minimize the distance between data points and the regression line for all variables rather than for the Y-variable alone, it is inappropriate to calculate a residual from a Model II regression parallel to the Y-axis. Thus Model II residuals lose what little biological meaning OLS residuals may have. The second reason that OLS is preferred is that phylogenetic regressions are performed using the phylogenetic generalized least squares (PGLS) framework, and thus are directly comparable to OLS regressions but not to Model II regressions.

Phylogeny

Phylogenetic relationships may affect comparative analyses of size and SSD in two main ways. First, scaling patterns may differ between major clades. For example, strepsirhines and haplorhines may exhibit very different patterns in the scaling of size and dimorphism. Second, closely related taxa may share similar values for dependent and independent variables because of shared evolutionary history rather than due to a functional relationship between variables.

In order to address the first phylogenetic concern, I follow Smith and Cheverud (2002) in analyzing major primate clades separately. I first consider relationships within Primates as a whole, then analyze Strepsirhini and Haplorhini separately, and finally analyze Platyrrhini and Catarrhini individually. To address the second phylogenetic concern I supplement traditional OLS regression with phylogenetic regression techniques, discussed further below.

The various phylogenetic analyses of this study are conducted using a branching sequence and divergence dates based on Purvis' (1995; 1999) composite primate phylogeny, which is a "supertree" compiled from many published phylogenies for various primate taxa. The Purvis supertree is modified through a series of stages to

produce the set of trees used in this study ([Appendix D](#)). NEXUS code is available for the complete supertree ([Appendix E](#)).

Although it is hoped that the phylogenetic branching sequence used here is an accurate representation of the ancestral-descendant relationships within primates, there are likely to be some errors in the topology. A number of studies have shown that results of phylogenetic methods are not compromised by some inaccuracies in branching sequence and branch length (Martins & Garland, 1991; Martins, 1996b; Diaz-Uriarte & Garland, 1998; Martins & Housworth, 2002). It has been suggested that in absence of knowledge of the true phylogeny, analyses should be performed on a large number of random trees (Martins, 1996a), and that partial knowledge of phylogenies can be used to constrain random trees so that random branching sequences are generated only for the unknown portion of the phylogeny (Housworth & Martins, 2001). However, Symonds (2002) found that random trees do a particularly poor job of estimating the actual evolutionary correlation between characters. Recently it has been suggested that correlation parameters can be calculated by weighting random trees by the probability that they are correct using Bayesian inference to determine tree weights (Huelsenback & Rannala, 2003). Theoretical concerns aside, a recent study of the relationship between competition levels and SSD in primates found that results were not significantly altered when branches were swapped (Plavcan, in press). The tree for the present study is well resolved, and what few inaccuracies in branching sequence exist are unlikely to affect the results of phylogenetic analyses.

Three methods are used to set branch lengths for the primate tree. They are as follows.

Divergence Dates. Under a gradualistic model of character evolution, the amount of evolutionary change within a lineage is expected to be correlated with time (as a proxy

for number of generations). Purvis (1995) provides estimates of divergence dates for various nodes in his supertree using arithmetic means and medians of divergence dates gathered from the various trees he samples to construct the composite phylogeny. When available, Purvis' mean dates are used to assign dates to divergences in the tree used for the present study. However, many divergences are not dated or are resolved differently here than in Purvis' original supertree (Purvis, 1995).

Divergences between subspecies in this study are arbitrarily assigned branch lengths of 0.25 myr unless otherwise noted. In the case of polytomies in the original Purvis (1995) supertree that are resolved, here the first divergence and last divergence of taxa included within the Purvis polytomy are arbitrarily separated by 2 million years (myr) for divergences occurring between 10 and 20 million years ago (mya), 1 myr for divergences between 5 and 10 mya, and 0.5 myr for divergences between 1 and 5 mya. Previously resolved relationships that are now polytomies are dated using a weighted mean of the divergence dates given for the original divergences in Purvis (1995). Weights are the number of trees used to calculate the mean dates for the Purvis supertree. When a divergence date is unavailable for a particular group of species and those species are considered one species by some authorities, an arbitrary divergence date of 1 mya is imposed. When dates are unavailable for other divergences, one of two methods is used. Grafen's (1989) method based on species diversity can be used to scale branch lengths between nodes of known age and tips. In some cases the resulting dates will disagree with younger divergence dates reported in Purvis (1995), or with information from the fossil record. In those cases divergence dates for the undated nodes will be assigned as occurring at half the time from the last dated divergence to the present.

Equal Branch Lengths. Several previous studies of sexual size dimorphism (SSD) in primates have set all branch lengths equal to one (*e.g.*, Mitani *et al.*, 1996; Plavcan &

van Schaik, 1997b; Lindenfors & Tullberg, 1998; Smith & Cheverud, 2002). This procedure has been argued to represent a punctuated equilibrium model of character evolution because each speciation event is expected to produce an equal amount of change (Mitani *et al.*, 1996; Lindenfors & Tullberg, 1998). However, Smith and Cheverud (2002) point out that a true punctuated equilibrium model would only allow change along one branch of a divergence. Equal branch length models allow change to occur along both branches, and thus do not accurately represent punctuated equilibrium (Smith & Cheverud, 2002). Equal branch lengths are used here so that results may be compared between this study and other studies that have used equal branch lengths. Divergences between subspecies are arbitrarily assigned branch lengths of one-half.

Best Branches. Garland *et al.* (1992) state that independent contrast analyses should only be performed with trees in which the absolute value of standardized contrasts are not significantly correlated with their standard deviations. Correlations are significant at $\alpha = 0.05$ for all trees in this analysis with the exception of the reduced Platyrrhini tree based on divergence dates. I use Grafen's (1989) ρ transform to modify branch lengths such that absolute values of standardized contrasts and their standard deviations are uncorrelated. This method scales the height of the entire tree to one, then transforms the height of each node (*i.e.*, the distance between the node and terminal taxa) by raising it to the user-selected positive exponent ρ . Values for ρ are as follows (values are the same for full and reduced data sets): Primates, 0.69; Strepsirhini, 0.38; Haplorhini, 0.69; Platyrrhini, 0.50; Catarrhini, 0.62.

Independent Contrasts and PGLS Regressions

Phylogenetic comparative analyses in this study are performed using Martins and Hansen's (1997) PGLS method and an adaptation of Felsenstein's (1985) phylogenetically independent contrasts method. It has been shown that regression

parameters are identical for PGLS and independent contrasts regressions when the contrast slope is forced to pass through the reconstructed base ancestral state for all characters in the analysis (Garland & Ives, 2000; Rohlf, 2001). Thus it is equivalent to perform either analysis. PGLS is used for bivariate regressions of dimorphism against size because the PGLS method is also used to perform ancestral reconstructions of size and dimorphism.

PGLS analyses work by specifying the covariance matrix for a data set, which is a function of the branching sequence and branch lengths of the sample phylogeny. This study uses the most common evolutionary model, in which the value of a trait at a particular internal node (hypothetical taxonomic unit, or HTU) or tip (operational taxonomic unit, or OTU) is equal to the value of the node directly ancestral to it, plus an error term. Variance of the error term is proportional to branch length between ancestor and descendant, which determines the structure of the covariance matrix (see Rohlf, 2001) for a detailed description of this process). Covariance matrices are constructed and PGLS regressions are performed using code written in the programming language *R* (Ihaka & Gentleman, 1996) ([Appendix F](#)). A previously existing program that performs PGLS regression, Emilia Martins' program *COMPARE* (Martins, 2003), was not used because it requires fully resolved bifurcating trees although the PGLS method itself makes no such restrictions. I tested the results of my program against PGLS regressions in *COMPARE 4.5* and independent contrasts regressions in the *PDAP:PDTREE* (Midford *et al.*, 2002) module of *Mesquite 1.0* (Maddison & Maddison, 2003) using a set of fully resolved trees; in all cases results were identical for all three programs.

Interpreting Phylogenetic Regression Results

Slopes and intercepts produced by traditional OLS regressions will differ from those produced by PGLS and contrasts analyses. Interpretation of phylogenetic analyses

is facilitated by examining how these analyses work. As mentioned above, PGLS regression parameters are identical to independent contrasts regressions in which the contrast slope is forced to pass through the reconstructed base ancestral state for all characters in an analysis (Garland & Ives, 2000; Rohlf, 2001). Independent contrasts are data points generated by calculating differences in traits ($\log [F]$ and $\log [M/F]$ in this study) between sister taxa – observed taxa in the case of tips, and hypothetical taxa in the case of internal nodes. Bivariate PGLS regressions can therefore be thought of a line passing through the ancestral reconstruction of the X and Y variables, weighted away from horizontal by the relationship between the two variables in pairs of sister taxa. If size and dimorphism always increase or decrease together, the regression line will take on a significantly positive slope. If one trait always decreases when the other increases, and vice-versa, the line will take on a significantly negative slope. A combination of both patterns will tend to cancel each other out, resulting in a slope that does not significantly differ from zero. Thus PGLS and independent contrasts regressions produce phylogenetically weighted slopes that measure the association between variables once the relatedness between taxa has been taken into account.

Differences between traditional and phylogenetic regressions can provide important information regarding the evolutionary history of sets of traits. For example, consider the case of an OLS regression that has a significantly positive slope and a PGLS regression performed on the same data that has a slope that does not significantly differ from zero. In that case, the significant positive relationship observed in the OLS regression may result from a pattern occurring at the base of major adaptive radiations, and the lack of a significant relationship in the PGLS analysis could result from the absence of that pattern in more recent relationships. It is possible to directly test for such

differences between ancient and recent patterns by using a particular type of contrasts analysis.

Ancient Phylogeny versus Recent Phylogeny

It has been noted that internal nodes in an independent contrast analysis are not estimates of ancestral states (Smith & Cheverud, 2002). Instead, they are phylogenetically-weighted means of all descendant OTUs. Comparisons of nodes at the base of genera are therefore similar to comparisons of generic arithmetic means except that internal nodes incorporate information regarding the relatedness of species within each genus. Contrasts between deep internal nodes in an accurate phylogeny reflect patterns relating to higher level taxonomic units, and thus relationships among the ancient progenitors of living species, while contrasts between tips and shallow internal nodes reflect recent patterns and variation present in living taxa.

Independent contrasts for a particular data set can be divided into two groups: recent contrasts, which are defined here as contrasts between tips or nodes within the same genus, and ancient contrasts, which are defined as contrasts between tips or nodes that differ at the generic level or higher. Regressions are performed separately on the two groups to identify recent and ancient patterns. Analyses of recent contrasts, which are similar to paired-taxa analyses in which pairs are restricted to congeners, will identify relationships between variables in closely related taxa. Analyses of ancient contrasts will identify phylogenetic signals – *i.e.*, relationships between variables in the ancestors of living primates, the small fraction of earlier species that left descendant taxa that exist today. Recent contrasts can be expected to exhibit more “noise” due to measurement error, sampling error, and stochastic variation, but these factors should only affect the strength of the correlation, not the trend (*i.e.*, slope of the regression). Thus similar slopes in regression analyses of ancient and recent contrasts indicate that the relationship

between variables is consistent across time depths. Differences in slopes may indicate that patterns present in all taxa living at a particular point in the past are different from patterns present in all taxa living at a more recent point in time; alternatively, differences may indicate that patterns in the ancient phylogeny are not representative of all species for a particular point in the past, since many of those taxa do not have living descendants.

PGLS Ancestral Reconstruction Analysis

Another technique for analyzing ancestral scaling patterns of size and dimorphism is to reconstruct size and SSD in ancestral primates using the PGLS method. Values for ancestral nodes are estimated by functions of the covariance matrices for tips and internal nodes, observed data from OTUs, and values for the base node of the phylogeny (Martins & Hansen, 1997). Typically the value of each character for the base node is set as the grand mean of OTU data, weighted by the covariance matrix (Martins & Lamont, 1998; Rohlf, 2001). This method will be referred to as the **grand mean method (GMM)**. An alternative method presented here is the **assigned value method (AVM)**. In some cases the value for the base node may be known, as in the case of tracking the evolution of an experimental viral strain; the value may also be constrained to a range of likely values, as in the case of information from a well documented fossil record; alternatively, a researcher may wish to identify how evolutionary reconstructions differ when the initial value is changed. In any of these cases it is appropriate to use AVM reconstructions. The assigned value method reconstructs values for all other internal nodes based on user-specified values for the base node, OTU values, and the same evolutionary model specified for GMM reconstructions.

Because the computer program *COMPARE* does not perform PGLS reconstructions using the assigned value method, code was written for the programming language *R* that generates GMM and AVM ancestral reconstructions ([Appendix F](#)).

GMM ancestral reconstructions for fully bifurcating trees were compared to reconstructions calculated by the freely available computer packages *Mesquite 1.0* (Maddison & Maddison, 2003, running the PDAP:PDTREE module, Midford *et al.*, 2002) and *COMPARE 4.5* (Martins, 2003). In all cases results were identical, regardless of computer program. Confidence intervals for the reconstructed values are not identical between *PDAP:PDTREE* and *COMPARE*, however. Confidence intervals for the base node calculated here match those of *PDAP:PDTREE*. I follow Garland and Ives (2000) in the calculation of σ^2 (the scaling constant for phylogenetic covariance matrices) and Rohlf (2001) in the calculation of standard errors for all reconstructed nodes ([Appendix F](#)).

GMM reconstructions of $\log_{10}[M]$ and $\log_{10}[F]$ are calculated for the last common ancestor (LCA) of six groups: Primates, Strepsirhini, Haplorhini, Anthropoidea, Platyrrhini, and Catarrhini. Sexual size dimorphism is calculated as $\log_{10}[M]-\log_{10}[F]$ (equal to $\log_{10}[M/F]$) for each HTU. In some cases size reconstructions may differ from expectations based on the fossil record. Fossil evidence suggests that the earliest primates were relatively small. For example, omomyoids ranged in size from about 35 g to 1775 g, and adapoids ranged in size from about 100 g to 7 kg (Covert, 2002). Therefore, AVM reconstructions of size in ancestral primates are also calculated using four initial conditions for the LCA of all primates: 50 g, 100 g, 250 g, and 500g. Change in $\log_{10}[F]$ and $\log_{10}[M/F]$ is calculated between each of the six reconstructed nodes and their direct descendants, standardized by the square root of the branch length between node and ancestor. This procedure results in five standardized changes per variable. OLS regressions are performed on each set of changes in order to determine the relationship between size and dimorphism in ancestral primates.

Body size evolution is modeled in the same way for reconstructions as it is in PGLS regressions: body size in descendant taxa is modeled as the direct ancestor's body size plus an error term with mean zero. Therefore the expected value of body size in descendants is equal to that of ancestors, so the expected value for changes in size and dimorphism is zero. Because of this expectation, regression intercepts are constrained to zero. Forcing the regression to pass through the origin also makes the assumption that scaling of dimorphism is consistent. That is, an increase in size can not be expected to be accompanied by increases in SSD in some cases and decreases in SSD in other cases. If the regression is not constrained to the origin, a positive intercept coupled with a positive slope would indicate that for a particular range of size changes a decrease in size would be accompanied by an increase in dimorphism, while all other decreases in size would be related to decreases in dimorphism (Fig. 3.1a). A negative intercept with a positive slope would indicate that for a particular range an increase in size would lead to a decrease in dimorphism, while all other increases in size would lead to an increase in dimorphism (Fig. 3.1b). Opposite reversals would happen with negative slopes (Fig. 3.1c & 3.1d). Thus regression intercepts must be constrained to the origin in order to identify consistent scaling patterns of size and SSD.

RESULTS

In the reporting of results, all mentions of phylogenetic analyses refer to results using the “best branches” branch lengths unless explicitly noted, although tables report statistics for all three trees. A significance level of $\alpha = 0.05$ is assumed unless otherwise noted.

PGLS and independent contrasts regressions are collectively referred to as phylogenetic regressions in the text because PGLS regression parameters are identical to parameters for independent contrast regressions that have been forced to pass through the

grand mean of OTU data (Garland & Ives, 2000; Rohlf, 2001). PGLS regression parameters reported here are therefore also independent contrast regression parameters. Brief notes regarding degrees of freedom and significant figures in the reporting of results follow below.

Degrees of freedom. Independent contrasts analyses perform regressions which are constrained to pass through the origin, resulting in the loss of one degree of freedom from the number of data points, which in turn is one fewer than the number of species, resulting in $N-2$ degrees of freedom, where N = number of species. PGLS regressions analyze all data points, but do not constrain the regression to pass through the origin, so they too have $N-2$ degrees of freedom. Thus significance tests are identical between PGLS and independent contrasts regressions.

In this study, branch lengths are transformed to meet the assumption of no relationship between absolute value of standardized contrasts and standard deviations (Garland *et al.*, 1992; Diaz-Uriarte & Garland, 1996). It has been suggested that the transformation process reduces the degrees of freedom in regression analyses by an additional two (Diaz-Uriarte & Garland, 1996; Diaz-Uriarte & Garland, 1998) or three (Smith & Cheverud, 2002) degrees of freedom. In reporting results of phylogenetic analyses, I choose not to reduce the degrees of freedom for branch transformations so that comparisons of significance between traditional and phylogenetic analyses are based on the same degrees of freedom. However, I report standard errors for all parameters so that significance tests can be recalculated and new p -values generated with fewer degrees of freedom if so desired. Sample sizes in this study are large enough that a difference of three degrees of freedom will usually not make a difference in significance tests at $\alpha = 0.05$. The smallest sample in this study, the reduced data set for Strepsirhini, has 33 data points. Thus in the smallest data set, the full degrees of freedom for regression

analyses are 31 and the maximally-reduced degrees of freedom are 28, both of which are relatively large values for comparative analyses of this kind.

Significant figures. Because statistics for analyses of female size and dimorphism are more appropriately interpreted in the context of analyses of female size and male size, regression slopes of $\log [M/F]$ against $\log [F]$ should be interpreted as slopes of $\log [M]$ against $\log [F]$ minus one when deciding how many significant figures are used in reporting regression slopes. For example, with three significant figures a slope would be reported as -0.005 rather than -4.99×10^{-3} , since the appropriate slope is actually 0.995 minus 1. For the sake of symmetry, positive slopes are also reported to the third decimal place (*e.g.*, 0.008 rather than 0.01).

All Primates

Traditional and Phylogenetic Regressions

Two data sets were considered for the Order Primates: a full data set ($N = 221$ taxa) and a reduced data set ($N = 157$ taxa). Slopes for OLS regressions of $\log_{10}[M/F]$ against $\log_{10}[F]$ are virtually identical for the full and reduced samples and are significantly greater than zero, indicating positive scaling of size dimorphism with body size in primates (*i.e.*, Rensch's rule) (Table 3.2). However, slopes for phylogenetic analyses are not significantly different from zero for either data set, and are in fact very close to zero (0.001 and 0.031 for full and reduced data sets, respectively). Coefficients of determination (r^2) are similarly low for the phylogenetic regressions ($r^2 = 0.000$ and 0.012 for full and reduced data sets). Thus the relationship between size dimorphism and body size does not persist in living primates once similarities due to phylogeny have been taken into account (Fig. 3.2a).

Separate analysis of recent (within genera) and ancient (between genera and higher order taxonomic divisions) independent contrasts within primates demonstrates

different scaling patterns (Fig. 3.2b). Ancient contrasts scale with significant positive slopes in both full and reduced data sets, indicating that the evolutionary history of living primates is consistent with Rensch's rule; however, recent contrasts have negative slopes, although not significantly so in the reduced data set (Table 3.3a).

Notice that the recent contrasts regression is heavily leveraged by a single point in the lower right of Figure 3.2b. This is an “artificial” contrast in that it is the contrast at the base of a trichotomy (the divergence of *Semnopithecus entellus entellus*, *S. e. schistacea*, and *S. e. theristes* – this contrast also appears in the haplorhine and catarrhine analyses). In the case of polytomies, branches of near-zero length are arbitrarily inserted into trees in order to force trees to assume the dichotomous branching sequences necessary to generate contrasts. Thus the leverage point in Figure 3.2b does not necessarily represent an actual relationship between sister taxa. Rerunning the recent contrasts regression without that leverage point also produces a significantly negative slope for the full data set but generates a non-significantly positive slope for the reduced data set (Table 3.3b; see Fig. 3.2b).

PGLS Reconstruction

Male and female body size is estimated for the last common ancestors of Primates, Strepsirhini, Haplorhini, Anthropoidea, Platyrrhini, and Catarrhini using PGLS ancestral reconstruction techniques (Table 3.4). Slopes for regressions of standardized change in $\log_{10}[M/F]$ against standardized change in $\log_{10}[F]$ are significantly positive for all reconstructions in both full and reduced data sets, regardless of constraint on initial size (Table 3.5, Fig. 3.3). These results are consistent with results of ancient contrasts analyses for Primates.

Strepsirhini

The two suborders of Primates, Strepsirhini and Haplorhini, are here considered separately. Full and reduced data sets are analyzed for Strepsirhini ($N = 49$ and $N = 33$, respectively). For both data sets, OLS regression slopes of $\log_{10}[M/F]$ against $\log_{10}[F]$ are slightly negative, although not significantly so, as coefficients of determination are quite low (Table 3.2). Similarly, slopes for phylogenetic analyses are not significantly different from zero for either data set (-0.006 and 0.005 for full and reduced, respectively). These results indicate that body size and dimorphism are not related in the Strepsirhini. (Fig. 3.4a).

Slopes for recent and ancient independent contrasts within Strepsirhini do not differ significantly from zero in either data set (Fig. 3.4b), indicating a consistent pattern (or lack thereof) in the relationship between body size and dimorphism over evolutionary time in strepsirhines (Table 3.3).

Haplorhini

Full and reduced data sets are analyzed for Haplorhini ($N = 172$ and $N = 124$, respectively), yielding significantly positive OLS regression slopes for both data sets (Table 3.2). However, slopes for phylogenetic analyses are not significantly different from zero for either data set (although note that PGLS slopes are significantly positive for both data sets using equal branch lengths). These results indicate that although size dimorphism scales positively with body size in living haplorhines, that relationship disappears once similarities due to phylogeny have been taken into account (Fig. 3.5a).

As seen for all primates, size dimorphism scaling patterns in haplorhines differ between ancient and recent contrasts (Table 3.3a). Ancient contrasts regression slopes are significantly positive in both full and reduced data sets, while recent contrasts regression slopes are negative in both data sets, although only significantly so in the full

data set (Fig. 3.5b). When the “artificial” recent contrast is removed, the slope for the full data set remains negative (slope = -0.092, $p = 0.062$) but the slope for the reduced data set becomes positive (slope = 0.084, $p = 0.090$; see Table 3.3b and Fig. 3.5b).

Platyrrhini

The suborder Haplorhini is further divided into the infraorders Platyrrhini and Catarrhini. Full and reduced data sets are analyzed for Platyrrhini ($N = 64$ and $N = 48$, respectively). As seen in haplorhines as a whole, slopes for OLS regressions of $\log_{10}[M/F]$ against $\log_{10}[F]$ are significantly positive for both platyrrhine data sets, while slopes for phylogenetic analyses are not significantly different from zero for either data set (Table 3.2). Thus size dimorphism scales positively with body size in living platyrrhines, but only when similarities due to phylogeny are not considered. Although phylogenetic regression slopes do not differ significantly from zero, the intercepts for phylogenetic regressions on both data sets are significantly greater than zero (Fig. 3.6a). Thus platyrrhines as a group exhibit significant sexual dimorphism, even when phylogeny is taken into account, although that dimorphism does not scale with body size.

In Platyrrhini, ancient and recent contrasts differ, but not in the same manner as in all Primates and Haplorhini. While ancient contrasts slopes are more positive than recent contrast slopes, the pattern of significance differs from that of haplorhines: ancient contrasts slopes are positive in both full and reduced data sets, although not significantly so, and recent contrasts slopes are significantly negative in both data sets (Table 3.3a, Fig. 3.6b). Although slopes for platyrrhine ancient contrasts are not significantly positive, their coefficients of determination ($r^2 = 0.145$ and 0.138 for full and reduced, respectively) are similar in magnitude for those of primate ancient contrasts, which are significantly positive ($r^2 = 0.159$ and 0.117 for full and reduced data sets).

Note that with the exception of two contrasts, ancient SSD contrasts are of relatively low magnitude (vertical displacement from the x-axis in Fig. 3.6b). The large positive contrast is between Callitrichidae (*Callithrix*, *Cebuella*, *Leontopithecus*, and *Saguinus*) and the *Cebus-Saimiri* clade, reflecting the relatively small size and low dimorphism of callitrichids and/or the relatively large size and high dimorphism of the other clade. The large negative ancient contrast is between Atelinae (*Ateles*, *Lagothrix*, and in the full data sample, *Brachyteles*) and *Alouatta*, and is particularly low because of the large size and low dimorphism in the atelines (Fig. 3.6a). Without these two contrasts, ancient regression slopes are slightly lower, but are tighter fits (full: slope = 0.051, $r^2 = 0.287$, $p = 0.072$; reduced: slope = 0.040, $r^2 = 0.247$, $p = 0.120$).

SSD contrasts that have the same sign (positive or negative) as size contrasts are consistent with positive scaling, while contrasts with different signs are consistent with negative scaling. Platyrrhine ancient contrasts are mostly positive in the full data set (8 of 13, or 62%) and equal numbers of positive and negative in the reduced data set (6 of 12). Recent contrasts are mostly negative in both data sets (full: 36 of 50, or 72%; reduced: 26 of 35, or 75%). The clade with the highest percentage of negative recent (intra-generic) contrasts in both data sets is the Callitrichidae (full: 13 of 17, or 77%; reduced: 9 of 11, or 82%).

Catarrhini

The final taxonomic group considered here is Catarrhini ($N = 104$ and $N = 73$ for the full and reduced data sets, respectively). Regression slopes for catarrhines differ from all other non-strepsirhine regressions in this analysis; although the OLS slope is significantly positive for the full data set, it is not significant for the reduced data set (Table 3.2). Also, the catarrhine slope is the lowest slope of all non-strepsirhine OLS regressions in both data sets, but it is the highest phylogenetic slope in both data sets

(although not significantly positive for the phylogenetic analyses) (Fig. 3.7a). Also, the phylogenetic regression slope is higher than the OLS slope in the reduced data set. When the base *Semnopithecus* contrast is removed, the phylogenetic regression slope becomes even steeper and more significant in both data sets (full: slope = 0.088, $R^2 = 0.028$, $p = 0.091$; reduced: slope = 0.173, $R^2 = 0.151$, $p = 0.001$).

As in all other analyses, size dimorphism in Catarrhini scales positively with body size for ancient contrasts and negatively for recent contrasts. Slopes are significantly different from zero for ancient contrasts in both data sets and recent contrasts in the full data set (Fig. 3.7b). Slopes for regressions of recent contrasts are less significantly negative for the catarrhine analysis than for any other non-strepsirhine analysis (Table 3.3a). Also, when the *Semnopithecus* recent contrast is removed, the slope for the full data set remains negative, but no longer significantly so, and the slope for the reduced data set becomes significantly positive, although not as high as the ancient slope (Table 3.3b; see Fig. 3.7b).

Taxonomic Grade Shift

Although regression slopes of $\log_{10}[M/F]$ against $\log_{10}[F]$ do not differ significantly zero in any of the phylogenetic analyses, the intercepts for the Platyrrhini analyses are significantly greater than zero. Superimposing PGLS regression lines for Strepsirhini, Platyrrhini, and Catarrhini on a bivariate plot of the raw data suggests a grade shift in the relationship between size and dimorphism in these taxa (Fig. 3.8). The group with largest mean body size (Catarrhini) also has the highest regression line and thus the highest mean dimorphism, while the group with the smallest mean body size (Strepsirhini) has the lowest regression line. Thus the overall pattern is consistent with the existence of Rensch's rule in the evolutionary history of living primates.

Full versus Reduced Data Sets

In general, results from full and reduced data sets are in agreement. The one analysis for which there is substantial difference of results is recent contrasts regression in Catarrhini. The full catarrhine data set can be split into two groups: (1) those taxa only in the full data set ($N = 31$), and (2) those taxa in both data sets ($N = 73$). Group 1 females are more massive on average than group 2 females (mean $\log_{10}[F] = 0.937$ in group 1 and 0.821 in group 2, $p = 0.106$), but less dimorphic (mean $\log_{10}[M/F] = 0.126$ in group 1 and 0.146 in group 2, $p = 0.362$). Catarrhines are therefore divided non-randomly between these two groups. For example, while all 18 of the guenon taxa (which tend to be relatively small but highly dimorphic) are in both full and reduced data sets, only about half (9 of 16) of *Hylobates* taxa (relatively large and monomorphic) and half (4 of 8) of *Trachypithecus* species (large and low dimorphism) are in both data sets.

DISCUSSION

Particular scaling patterns of size and SSD within major primate radiations were recently reviewed by Smith and Cheverud (2002). The present study aims to extend our knowledge of these scaling patterns by identifying the source of differences between traditional and phylogenetic regression results in an attempt to understand the underlying mechanisms driving SSD in primates.

Effects of Sample Selection and Branch Lengths

Traditional OLS interspecific regression slopes for each of the five taxonomic groups are similar for full and reduced data sets. OLS slopes are also similar to regression slopes calculated in other studies on the same clades (as reported in Smith & Cheverud, 2002). However, slopes for phylogenetic regressions vary considerably: between different data sets for a particular clade, and between analyses using different branch lengths for the same data set.

It is well known that regression analyses can change substantially by adding or removing data points, a recognition that underlies critiques of using residuals from regression lines as data (*e.g.*, Jungers *et al.*, 1995; 1998). This problem is magnified in phylogenetic analyses for two primary reasons. First, because the error structure of a regression is based on the full network of ancestor-descendant relationships between taxa, removal or addition of particular taxa can dramatically alter the covariance matrix. For example, the addition or removal of a few large dimorphic species that are closely related to small monomorphic species will have a much greater effect on a phylogenetic regression than an OLS regression due to the expectation of similarity between closely related species in phylogenetic analyses. Second, different branch lengths will produce different covariance matrices and thus different results. Compare PGLS regression slopes between the three sets of branch lengths in [Table 3.2](#). In all non-strepsirhine cases, divergence dates produce a negative slope, equal branch lengths produce a positive slope, and “best branches” produce a positive slope in-between that of divergence dates and equal branch lengths. However, only “best branches” branch lengths meet Garland *et al.*’s (1992) criterion of uncorrelated absolute values of standardized contrasts and their standard deviations.

Branch lengths that do not meet Garland *et al.*’s (1992) criterion have inflated Type I errors, but errors are much reduced when branch lengths meet that criterion (Diaz-Uriarte & Garland, 1998). Therefore differences in regression parameters due to different branch lengths in this study are not a major concern. The variability in results presented here provide a good example as to why it is important to check branch lengths using Garland *et al.*’s (1992) method.

However, differences in sample composition create a major problem. In phylogenetic analyses, the tradeoff between complete taxonomic representation and good

data is critical. With more inclusive samples, the higher proportion of measurement errors can greatly affect regression parameters when those errors are in taxa with close relatives. In more restrictive samples, the absence of closely related species or clades removes important information from regression analyses and can result in misleading parameters. The issue of completeness is always a problem, even when considering only Recent fauna, as some species or clades will be so rare or extinct that measurements are unavailable (*e.g.*, sub-fossil lemurs). Results of this study show that a combined approach using a “complete” data set and a “good” data set (full and reduced in this study) can be used to identify consensus results. For example, in very few cases are phylogenetic or independent contrasts slopes negative in the full data set and positive in the reduced data set for the same analysis, or vice-versa. Those cases in which they differ (*e.g.*, recent contrasts for Catarrhini) can be particularly informative because the difference can be attributed to the missing taxa and their phylogenetic relationships.

Modern, Ancient, and Recent Scaling Patterns

Modern scaling patterns of SSD with size (as detected by traditional interspecific regression) are the result of recent evolutionary processes applied to descendants of successful lineages that preserve ancient evolutionary patterns. When attempting to formulate a general model for the evolution of Rensch’s rule, it is important to consider whether the modern pattern primarily reflects recent evolution, ancient patterns, or a combination of the two. Scaling patterns in this study often differ between recent and ancient contrasts, which offers an opportunity to determine the source of modern scaling patterns.

All Primates

Traditional OLS regressions in this study confirm earlier studies demonstrating significant positive scaling of SSD with size in modern primates (Leutenegger, 1978;

Martin *et al.*, 1994; Smith & Cheverud, 2002). However, phylogenetic regressions performed here do not indicate any relationship between size and SSD. Results from ancient contrasts analyses and PGLS ancestral reconstructions all indicate a positive scaling relationship between size and SSD that has a slope as great or greater than slopes observed using OLS regression. Recent contrasts analyses indicate a significantly negative or weakly positive scaling relationship (for full and reduced data sets, respectively). These results indicate that the modern pattern consistent with Rensch's rule that is observed in primates as a whole is driven by a pattern preserved in the deep ancestry of modern primates. However, recent (intra-generic) evolution does not follow that pattern.

Strepsirhini

Previous studies of size and SSD in strepsirhines found no significant relationship between the two variables using traditional interspecific regression (Kappeler, 1990; Weckerly, 1998; Smith & Cheverud, 2002) and independent contrast analyses (Lindenfors & Tullberg, 1998; Smith & Cheverud, 2002), a result confirmed here for modern, ancient, and recent patterns. What is particularly interesting is not simply that there is no significant scaling relationship in this clade, but very little dimorphism at all. The size range of extant strepsirhines in this study extends well over more than two orders of magnitude, a greater proportional range than that of platyrrhines or catarrhines in this study (both of which extend over slightly less than two orders of magnitude). Any explanatory mechanism for the presence of Rensch's rule in primates must also address the lack of substantial SSD in a group of primates with such a large size range.

Haplorhini

Traditional OLS regressions in this study indicate that SSD scales positively with size in modern haplorhines. Phylogenetic regressions using "best branches" branch

lengths do not find any significant relationship; however, slopes generated using equal branch lengths in this study do yield significant slopes. A separate study that used equal branch lengths in independent contrasts analyses of anthropoids also found a positive slope with a similar coefficient of determination (Plavcan & van Schaik, 1997b: $N = 50$, $r^2 = 0.140$, this study reduced sample: $N = 124$, $r^2 = 0.098$). Mitani *et al.* (1996) also found significant positive scaling of SSD and size using equal branch lengths, but the coefficient of determination is not comparable since the independent variable used was $\log [M]$ rather than $\log [M/F]$. As noted above, equal branch lengths in this study do not meet Garland *et al.*'s (1992) diagnostic, and thus the significantly positive slopes are probably an example of Type I error (Diaz-Uriarte & Garland, 1998). However, Abouheif and Fairbairn (1997) as well as Smith and Cheverud (2002) found highly significant positive slopes in Haplorhini using branch lengths that do pass Garland *et al.*'s (1992) diagnostic. The most likely source of difference between those studies and the results reported here are the taxa selected for inclusion.

Slopes for ancient contrasts regressions in Haplorhini are significantly positive, have similar coefficients of determination to OLS regressions, and have steeper slopes than OLS regressions. Recent contrasts slopes are negative or insignificantly positive and considerably shallower than ancient contrasts (depending on data set and whether or not the *Semnopithecus* outlier is included; see [Table 3.3](#)). These results indicate that the modern pattern of positive scaling of SSD with size in Haplorhini is driven by a pattern preserved in their deep ancestry, a pattern that is not present in recent (intra-generic) haplorhine evolution. The ancient haplorhine pattern also produces the positive scaling seen in primates as a whole since there is no relationship between size and dimorphism in strepsirhines.

Platyrrhini

Traditional OLS regressions performed here are in agreement with previous studies which found that SSD scales positively with size in modern platyrrhines (Ford, 1994; Weckerly, 1998; Smith & Cheverud, 2002). PGLS results are consistent with independent contrasts results of Lindenfors and Tullberg (1998) who found scaling slopes to be shallow and non-significant. Although ancient contrasts slopes in this study are not significantly positive, they are similar in magnitude and correlation strength to OLS slopes found here.

Ancient SSD contrasts are of relatively low magnitude, with the exception of two contrasts. The large positive contrast between Callitrichidae and the *Cebus-Saimiri* clade is likely due to (1) a decrease in body size and dimorphism in the LCA of callitrichids, and (2) an increase in dimorphism in the LCA of the *Cebus-Saimiri* clade relative to the LCA of both clades; both changes are consistent with Rensch's rule. The negative ancient contrast between Atelinae and *Alouatta* is a result of the large size and near absence of dimorphism in atelines, and it is a notable exception to Rensch's rule in platyrrhines. Aside from these two contrasts, ancient contrasts preserve a shallow positive scaling pattern of size and dimorphism in Platyrrhini.

Recent contrasts within platyrrhines are significantly negative, quite steep, and have relatively high coefficients of determination, indicating a strong negative scaling of size and SSD in recent new world monkey evolution. Ancient and recent scaling patterns clearly differ in the platyrrhines, and the apparent positive scaling of size and dimorphism in modern taxa primarily reflects deep ancestral scaling patterns.

Catarrhini

Catarrhines in this study present an interesting problem. They have the lowest and least significant slopes of the four non-strepsirhine groups for OLS analyses of full

and reduced data sets, but the highest and most significant slopes of those same groups for PGLS analyses of both data sets. Smith and Cheverud (2002) found in their analysis of 47 catarrhine species that catarrhine phylogenetic slopes were higher than traditional slopes; that same result is found here, particularly so when the base *Semnopithecus* contrast is excluded from phylogenetic regressions. Smith and Cheverud (2002) also point out that the relationship between size and dimorphism is highly variable in catarrhines, and report that of all groups, the correlation between size and SSD is lowest in catarrhines and the standard error for regressions is highest in catarrhines. That same result is found here.

What is particularly noteworthy about the scaling of size and dimorphism in catarrhines is that ancient contrasts slopes are extremely steep and well correlated; slopes and coefficients of determination are higher for catarrhine ancient contrasts than for any other regression analysis in this entire study. Recent contrasts slopes are also less negative than in platyrrhines, and are positive for the reduced data set when the base *Semnopithecus* contrast is removed.

The sensitivity of phylogenetic analyses to sampling effects is highlighted by the catarrhine results presented here. The exclusion of one contrast dramatically changes slopes, coefficients of determination, and significance of those slopes. Despite all of the differences generated by these sampling issues, a consistent pattern emerges for catarrhines: Rensch's rule is stronger in the deep evolutionary history of catarrhines (in terms of the steepness and correlation strength of the trend) than in platyrrhines or strepsirhines, but the high variability in this relationship in recent evolution obscures its expression in modern catarrhines. Depending on the data set, intra-generic evolution in the catarrhines may be characterized by positive or negative scaling of SSD with size, but

all results are less positive than ancient catarrhine slopes and more positive than recent platyrrhine slopes.

Mechanisms Underlying Rensch's Rule

The positive scaling of SSD with size observed in modern primates is shown here to be a product of positive scaling in ancestral relationships above the genus level in Haplorhini (with some notable exceptions such as the evolution of the Atelinae) which has been obscured by more varied recent evolutionary trends.

The lack of scaling in Strepsirhini provides a strong argument against an obligatory functional constraint requiring SSD to increase as size increases. The large range of body size observed in living strepsirhines coupled with the absence of significant strepsirhine dimorphism indicates that if any obligatory causation link exists between size and dimorphism, it must be changes in dimorphism that produce changes in size, not the reverse. This argument is even more compelling when sub-fossil lemurs are considered: the largest sub-fossil lemurs are nearly four orders of magnitude larger than the smallest living strepsirhines, and there is no evidence for any significant dimorphism in sub-fossil lemurs (Godfrey, 1988; Jungers, 1990a; Godfrey *et al.*, 1993; 1995; 1997; Jungers *et al.*, 2002).

At first glance, potential for obligatory changes of size following changes in SSD also appears to be negated due to the lack of consistent pattern in the recent evolution of size and dimorphism in haplorhines. However, quantitative genetic models can accommodate difference in patterns. As Smith and Chevrud (2002) point out, Lande's (1980) model predicts that with a genetic correlation of 0.9 between the sexes and selection acting only on males, a slope of 0.11 would be expected for $\log [M/F]$ against $\log [F]$ regardless of selection intensity and whether selection is for increased or decreased size. However, Lande's model also predicts that with the same genetic

correlation but selection acting only on female size, a slope of -0.10 would be expected. Thus when male body size is the target of selection, SSD will scale positively with body size, and when female body size is the target of selection, SSD will scale negatively with body size.

Sexual selection theory predicts that body size dimorphism in mammals with polygynous mating systems should be the product of selection primarily acting on male body size (Brown, 1975; Ralls, 1977; Andersson, 1994). If males compete to gain access to mating opportunities or to exclude other males from mating, then large body size is actively selected for in males. Females may also use male size as an indicator of mate quality and choose to mate with large males. Therefore sexual selection for larger males should increase male body size and dimorphism; the genetic correlation between males and females will cause females to get larger by a smaller proportion than males, so positive scaling of size and SSD will result, consistent with Rensch's rule.

However, sexual selection does not always target male size. When male investment in offspring is high, male mate choice is expected to operate (Petrie, 1983; Cunningham & Birkhead, 1998). In those cases, males tend to prefer large females because female fecundity is often correlated with body size (*e.g.*, Ralls, 1976; Gwynne & Simmons, 1990). Also, females may compete for males to help in parental care, in which case body size may play a role in female competitions (Gwynne, 1991; Parker & Simmons, 1996). In such cases, female body size is the primary target of body size (Andersson, 1994); under Lande's (1980) quantitative genetics model, negative scaling of SSD and size is expected as a result. Although sexual selection is expected to target male body size in most haplorhines, some platyrrhines fit the opposite pattern described here (*e.g.*, polyandrous Callitrichidae: Dixson, 1998; Dunbar, 2000; Heymann, 2000; 2003).

Also, sexual selection is not the only mechanism through which different selection pressures can be applied to males and females. Sexual niche separation is one possibility, in which females and males exploit different ecological niches with different optimal body sizes. A more likely possibility in Primates is differential natural selection due to resource limitation. A recent review of primate community structure and resource availability concluded that many primates encounter food shortages (Janson & Chapman, 1999). Due to the energetic costs of reproduction, females should be more responsive to resource pressures than males (Ralls, 1976; Emlen & Oring, 1977; Wrangham, 1980; van Schaik, 1989; Isbell, 1991; Mitchell *et al.*, 1991; van Hooff & van Schaik, 1992; Isbell & Pruettz, 1998; Boinski *et al.*, 2002).

When resources are scarce, a threshold may be crossed at which larger females cannot meet the energetic requirements to maintain their own metabolic needs plus those of a fetus, while smaller females (with absolutely lower energy requirements) are still able to produce offspring (Downhower, 1976). Work on human dimorphism in Native Americans suggests that small body size is advantageous for mothers when resources are scarce during lactation (Hamilton, 1975 cited in Ralls, 1977). It has also been shown that smaller females breed more often than larger females in variable environments (Downhower, 1976), which may lead to greater lifetime reproductive success and thus select for small size in females. In such a case, selection pressure for smaller size in females would result in decreased body size and increased dimorphism. Regardless of the direction of size change, resource limitation should result in a negative scaling of size and SSD.

Lande's (1980) quantitative genetics model predicts that size and SSD should scale positively when selection targets male size (*e.g.*, sexual selection in polygynous groups), and scale negatively when selection targets female size (*e.g.*, resource limitation

or sexual selection in polyandrous groups). Recent patterns of evolution in Haplorhini are consistent with a combination of both of these trends, resulting in non-significant slopes of $\log [M/F]$ against $\log [F]$. However, older patterns of evolution primarily record positive scaling patterns. How can this difference be explained?

It is unlikely that dramatically different evolutionary processes operated in the deep past than in the more recent past. Although human influence has accelerated habitat loss, primates have existed long enough to experience other periods of dramatic climate change. Because phylogenies only preserve the ancestors of living species, ancient patterns in phylogenetic analyses are not representative of all species that lived at a particular time in the past, but only those species that survived to leave modern descendants. The upshot of this recognition is that patterns in ancient (super-generic) relationships will often only represent a subset of patterns present among extinct taxa. Thus the most likely reason for discrepancies between recent and ancient evolutionary patterns is that certain patterns were preferentially preserved and passed on to descendant taxa.

It is not necessary to invoke group selection in order for positive scaling to be preferentially preserved. Consider the following model. There are three ways in which species body size can change: (1) equal selection on body size in males and females, resulting in size change but no change in SSD (and thus no scaling pattern); (2) more intense selection on males than females, resulting in changes in size and SSD with a positive scaling pattern; and (3) more intense selection on females than males, resulting in changes in size and SSD with a negative scaling pattern. In some clades (*e.g.*, Strepsirhini), nearly all changes in size will follow pattern 1, and thus an absence of scaling results. In other clades (*e.g.*, Haplorhini), patterns 2 and 3 will also play large roles in generating size change at any particular point in time, resulting in recent

evolutionary scaling relationships that are more positive or negative depending on the relative frequency of the two patterns. However, when pattern 3 is a product of long term resource limitation, it is more likely to lead to extinction than pattern 2; in the long run, pattern 2 (positive scaling) is more likely to be preserved in ancient phylogenies. Put another way, because resource limited populations are more likely to die out than sexually-selected populations, most living species will be descended from lineages that contain more sexually-selected populations than resource-limited populations. Because polyandrous populations are rare in haplorhines, most sexual selection targets male size in haplorhines, and thus the preserved ancient pattern reflects the greater frequency of positive scaling relationships.

Under this model, Rensch's rule is not obligatory, merely the most likely outcome when different sex-specific selection pressures are applied to populations. It also allows for clades in which scaling patterns of size and dimorphism are completely absent. Scaling patterns in each of the major primate radiations can be explained in the context of this model.

Strepsirhini

The lack of substantial dimorphism in strepsirhines may seem puzzling at first. Although there is no obligatory relationship of SSD with size under the model described here, sexual selection theory predicts that male reproductive skew should occur in polygynous mating systems (Andersson, 1994), and there are a number of strepsirhine species in which males have access to multiple reproductive females (Kappeler, 1997a; Dixson, 1998). However, strepsirhine mating systems may favor female choice over male-male competition. For example, many strepsirhines have dispersed social systems (see Dixson, 1998) in which female ranges may overlap with multiple male ranges, in

which case males have difficulty in monopolizing access to reproductive females and females can exercise choice among several potential mates (Müller & Thalmann, 2000).

Within strepsirhines, competitive exclusion does not appear to occur even in group-living taxa where males would be expected to have the best opportunity to prevent other males from mating. For example, *Lemur catta* has a well-defined breeding season of one to three weeks (Jolly, 1966; Sauther, 1991) during which it is rare for more than one female to be in estrus at any particular time (Pereira, 1991), a situation in which mate-guarding should be expected to occur. However, females typically mate with more than one male (Jolly, 1966; Koyama, 1988; Pereira & Weiss, 1991; Sauther, 1991). In these types of situations, male-male competition is expected to manifest itself in indirect ways such as sperm competition rather than in direct aggressive contests that favor large body size. There is a growing body of evidence that sperm competition is prevalent in strepsirhines (Glander, 1994; 1997c; Kappeler, 1997b; Kraus *et al.*, 1999; Parga, 2003; Johnson *et al.*, in review). Therefore, female mate choice appears to be more important than direct male-male competition in determining mating success (and ultimately, reproductive success) in strepsirhines.

If females preferentially choose large males as mates, SSD should result from female mate choice. However, if females target other characters, dimorphism should not be expected as a necessary consequence of sexual selection. Body size in many strepsirhine species is tremendously variable over the course of the year: even in taxa that do not enter a torpor state, body mass can vary by as much as 19% or more of mean mass over the course of the year in wild adults (Glander, 1994). Because of this large degree of intra-individual variation in body size, male body mass may be a particularly poor indicator of mate quality. As a result, females may base mate choices on other factors. Although not all strepsirhines are so dramatically variable in size, the last common

ancestors of living strepsirhines may have been highly variable, and thus the pattern of selecting mates based on factors other than size could have been set early in strepsirhine evolution. Another explanation may be that male body mass can not respond to sexual selection for size, and thus females target other characters. Leigh and Terranova (1998) point out the relatively short and fast growth of lemur body size as compared to anthropoids, and suggest that natural selection constrains these parameters such that male lemurs cannot grow larger than females.

Characters other than body mass that females may be targeting include scents, coloration, and agility. For example, an investigation into animal communication signals suggested that chemical signals indicate individual quality (Endler, 1993), indicating that scents may function as honest signals targeted by sexual selection (Heymann, 2003). Males have been reported to scent-mark with greater frequency during mating seasons in *Lemur catta* and *Eulemur fulvus rufus* (Gould & Overdorff, 2002), and brain centers associated with olfaction (relative accessory olfactory bulb) are larger in the brains of polygamous strepsirhine species than in monogamous or polygynous species (Alport & Overdorff, 2002). Although these data have previously been interpreted in the context of male olfactory competition and females' use of olfactory cues to incite males into engaging in precopulatory competition, they are also consistent with a greater emphasis on olfaction in species in which females base mate choices on hormonal signals from males. The presence of sexual dichromatism in some strepsirhine species suggests that male coloration may also be a target of female choice (Gerald, 2003); this hypothesis has received experimental support in the *Eulemur fulvus* species group (Cooper & Hosey, 2003). Also, Kappeler (1991) suggests that male agility may be a target of female mate choice. In any of these cases, sexual selection acts to reinforce those characters that

females find desirable. If large male body size is not one of those characters, significant size dimorphism is not expected to evolve.

Under the model for the evolution of body size described earlier, size changes in Strepsirhini must be the result of equal selection intensities applied to both sexes. There is very little variation in the phylogenetic relationship between size and dimorphism in this clade: although coefficients of correlation are quite low due to the near-zero slope in the PGLS regression, standard errors of the regression are lower for Strepsirhini than for any other group even though Strepsirhini has the smallest sample size. This tight fit can be confirmed visually by comparing the variability of both recent and ancient contrasts around the zero line in [Figure 3.4b](#) to the variability in the figures for the other clades. Thus selection intensities for changes in size appear to be equal for both sexes in strepsirhines, allowing for a large range in body size without any appreciable scaling of dimorphism.

Platyrrhini

Scaling of SSD and size is strongly negative in recent platyrrhine evolution. This is due in large part to the high percentage of negative intra-generic contrasts within the Callitrichidae in this study (*Callithrix*, *Saguinus*, and *Leontopithecus*). These taxa are known to be facultatively polyandrous with relatively high paternal care (Dixson, 1998; Dunbar, 2000; Heymann, 2000). Therefore female body size should be the target of male mate choice, leading to negative scaling patterns of size and SSD under Lande's (1980) model. Resource limitation in the recent evolutionary history of other platyrrhine species may reinforce negative scaling patterns in callitrichids, producing the relatively tight negative correlation between size and dimorphism in recent contrasts.

Platyrrhine ancient contrasts reflect a higher proportion of positive scaling contrasts as well as an overall shallowly positive trend, indicating that most differences in

sex-specific selection intensities preserved in super-generic relationships are due to weak sexual selection on male size. There are two noticeable exceptions to this trend.

The first exception is the strong positive scaling of size and dimorphism in the divergence between the callitrichid and *Cebus-Saimiri* lineages. The relatively small body size of callitrichid species is due to substantial decrease in size at the base of the clade that resulted in small, monomorphic species; lineages later increased in size (*e.g.*, *Leontopithecus*, Rosenberger & Coimbra-Filho, 1984; Rosenberger, 1992) or decreased further in size (Garber *et al.*, 1996). The sister clade to the Callitrichidae is composed of two genera, one of which is probably not much different in size than the LCA of both clades (*Saimiri*), and one which is probably substantially larger (*Cebus*); both genera are more dimorphic than the reconstructed last common ancestor of Platyrrhini in this study, and much more dimorphic than the extant callitrichids. Thus the strongly positive ancient contrast probably represents separate major evolutionary events along both descendant lineages that reinforce the same pattern to produce a large contrast.

The second exception is the strong *negative* scaling of size and dimorphism in the divergence between the atelines and the howler monkeys (*Alouatta*), a divergence which produced a clade with the largest body size in New World monkeys, yet an almost complete lack of dimorphism. This example of a strongly negative relationship between changes in size and dimorphism highlights the point that positive scaling in super-generic relationships is not obligatory.

Overall, super-generic patterns in the platyrrhines record a preferential survival of populations subject to equal sex-specific selection or male-targeted sexual selection. Intra-generic relationships of non-callitrichid taxa are slightly more negative than positive, most likely indicating a mix of equal sex-specific selection pressures, male and female targeted sexual selection, and resource limitation. Negative patterns of scaling are

considerably more prevalent in intra-generic relationships within Callitrichidae. The dwarfing of the ancestral callitrichid lineage may have been produced by or resulted in the facultative polyandry observed in living Callitrichidae; either way, the contemporary social grouping serves to promote sexual selection on female size and thus strong negative scaling.

Catarrhini

Scaling patterns of size and dimorphism among recent catarrhine contrasts are highly variable and thus highly dependent on the taxa included in contrast analyses. What can be said is that recent contrasts tend to be evenly split among negative and positive contrasts. Because polyandry is unknown among the catarrhines, it is unlikely that negative scaling patterns are the result of sexual selection acting primarily on female body size. Therefore the combination of positive and negative recent contrasts is most likely a result of sexual selection targeting male size and resource limitation acting primarily on female size, respectively, as well as some changes in size in which equal selection pressures are applied to both sexes.

The strong positive scaling of size and SSD seen in ancient catarrhine contrasts reflects the greater likelihood of extinction for resource limited populations, preserving a higher proportion of male targeted sexually-selected populations and populations for which equal sex-specific selection pressures were applied.

Dimorphism in the Fossil Record

The findings of this study raise concerns regarding the interpretation of dimorphism in the fossil record. Regardless of whether or not the model described here for the evolution of Rensch's rule in primates is correct, the finding of different scaling patterns between ancient and recent contrasts highlights the point that patterns preserved in a phylogeny are not necessarily representative of all taxa that were alive at any

particularly point in time. Because there is no way to definitively identify a particular fossil taxon as ancestral to any living taxa, it is incorrect to assume that fossils will necessarily follow patterns preserved in super-generic or modern relationships. The absence of significant scaling patterns of size and SSD among recent contrasts in platyrrhines and catarrhines demonstrates that recent changes in dimorphism for any taxon, living or extinct, can be the product of (1) sexual selection, or (2) natural selection acting more strongly on one sex, usually females. It is also important to remember that evolutionary changes operate on a prior state. Thus monogamous species recently descended from a highly dimorphic ancestor may be considerably more dimorphic than polygynous species recently descended from a monomorphic ancestor. Therefore it is inappropriate to assume that a high level of dimorphism necessarily indicates a polygynous mating system, or that low dimorphism indicates monogamy. Other comparative studies have confirmed the poor predictive power of dimorphism for identifying mating systems (Plavcan, 2000a; 2002).

Despite these findings, identifying dimorphism in the fossil record is still useful for reconstructions of selection pressures that acted on extinct primates. Although dimorphism may not be a strong indicator of mating system for the particular fossil taxon in which it appears, it is a good indicator of the overall pattern of sex-specific selection pressures in extinct taxa when considered in conjunction with size and dimorphism in other related taxa, fossil and living.

For example, *Australopithecus afarensis* is generally thought to be relatively small in size and highly dimorphic as compared to later hominids and living African apes (McHenry, 1992; Richmond & Jungers, 1995; Kappelman, 1996; Mathers & Henneberg, 1996; Plavcan, 2001; 2003; however, see Reno *et al.*, 2003). Although the record of late Miocene Africa is not one of geographically uniform, monotonic increase in aridity

(Kingston *et al.*, 1994; Griffin, 2002; Jacobs, 2002), it is characterized by an increase open habitat mammals (Janis, 1993; Vrba *et al.*, 1995) and an increase in C₄ plants, most of which are subtropical grasses and sedges (Cerling *et al.*, 1993; Morgan *et al.*, 1994; 1997; 1998; Kingston *et al.*, 2002). Plio-Pleistocene East African habitats reflect these influences by preserving a diversity of open and closed habitats (Kappelman *et al.*, 1997). Thus the late Miocene in Africa likely saw forest fragmentation and habitat loss at forest edges. Early hominid habitats in the Middle Awash and Lukeino are suggested to have been relatively wet and wooded as compared to surrounding regions (WoldeGabriel *et al.*, 2001). Taken altogether, these observations suggest that arboreal proto-hominids may have been restricted to isolated forest fragments resulting in decreases in female body size in response to resource limitation, which would generate significant size dimorphism because of less intense selection on male body size. Selection pressures derived from resource limitation would later be alleviated when more efficient bipedalism allowed the descendants of proto-hominids to travel between isolated food patches.

This explanation for the evolution of SSD in hominid ancestors offers a potential resolution to a conundrum in the analysis of hominid dimorphism. Plavcan and van Schaik (1997a) found high SSD but low canine size dimorphism in *A. afarensis* and *A. boisei*, a pattern they were not able to explain to their own satisfaction using sexual selection theory alone. However, the scenario proposed here is consistent with observed levels of SSD and canine size dimorphism in these hominids. Because SSD in this scenario is primarily a result of natural selection, there is no need to posit intense male competition to account for high SSD, and thus there is no expectation of significant canine dimorphism. This scenario is also consistent with McHenry's (1992) observation that lower levels of SSD in later hominids are probably the result of increases in female

size rather than decreases in male size, since later hominids would not be subject to the same intense selection pressure on female body size. In considering the role of natural selection in addition to sexual selection when analyzing relationships of size and dimorphism in groups of related species and their environments, a more complete picture of social and environmental pressures acting on fossil primates can emerge.

SUMMARY

Previous work has found positive scaling of size and dimorphism in the Primates, also known as Rensch's rule. This pattern is present in Haplorhini, but absent in Strepsirhini. The present study demonstrates that positive scaling patterns in haplorhines are driven by evolutionary relationships between size and SSD above the generic level, while more recent relationships do not follow Rensch's rule. The difference in ancient and recent phylogenetic patterns is consistent with predictions based on Lande's (1980) quantitative genetics model. Positive scaling relationships will usually be the product of sexual selection acting primarily on male body size, while negative relationships will result from sexual selection acting primarily on female body size or natural selection acting primarily on female body size in the form of resource limitation.

Phylogenies are a record of success: only those extinct species that have living descendants are represented in phylogenetic analyses of extant taxa. Because resource limited populations are more likely to go extinct than non-resource limited populations, ancestral lineages preserved in phylogenies will contain a higher proportion of sexually-selected populations than were actually living at any particular point in time. When sexual selection targets male body size (as it does in most polygynous haplorhines), positive scaling patterns of size and dimorphism will preferentially be preserved. When sexual selection targets female body size (as happens in polyandrous callitrichids),

negative patterns will dominate. When sexual selection does not act on body size, no appreciable scaling of size and SSD will emerge (as seen in strepsirhines).

This work has implications for the interpretation of fossil size dimorphism: changes in dimorphism may be the product of sexual selection *or* natural selection, and thus social or mating systems cannot be inferred with a great degree of confidence for any individual fossil taxon. However, by considering the patterns of size and dimorphism among closely related fossil and living forms we may be able to accurately reconstruct the selective forces that were active in extinct lineages.

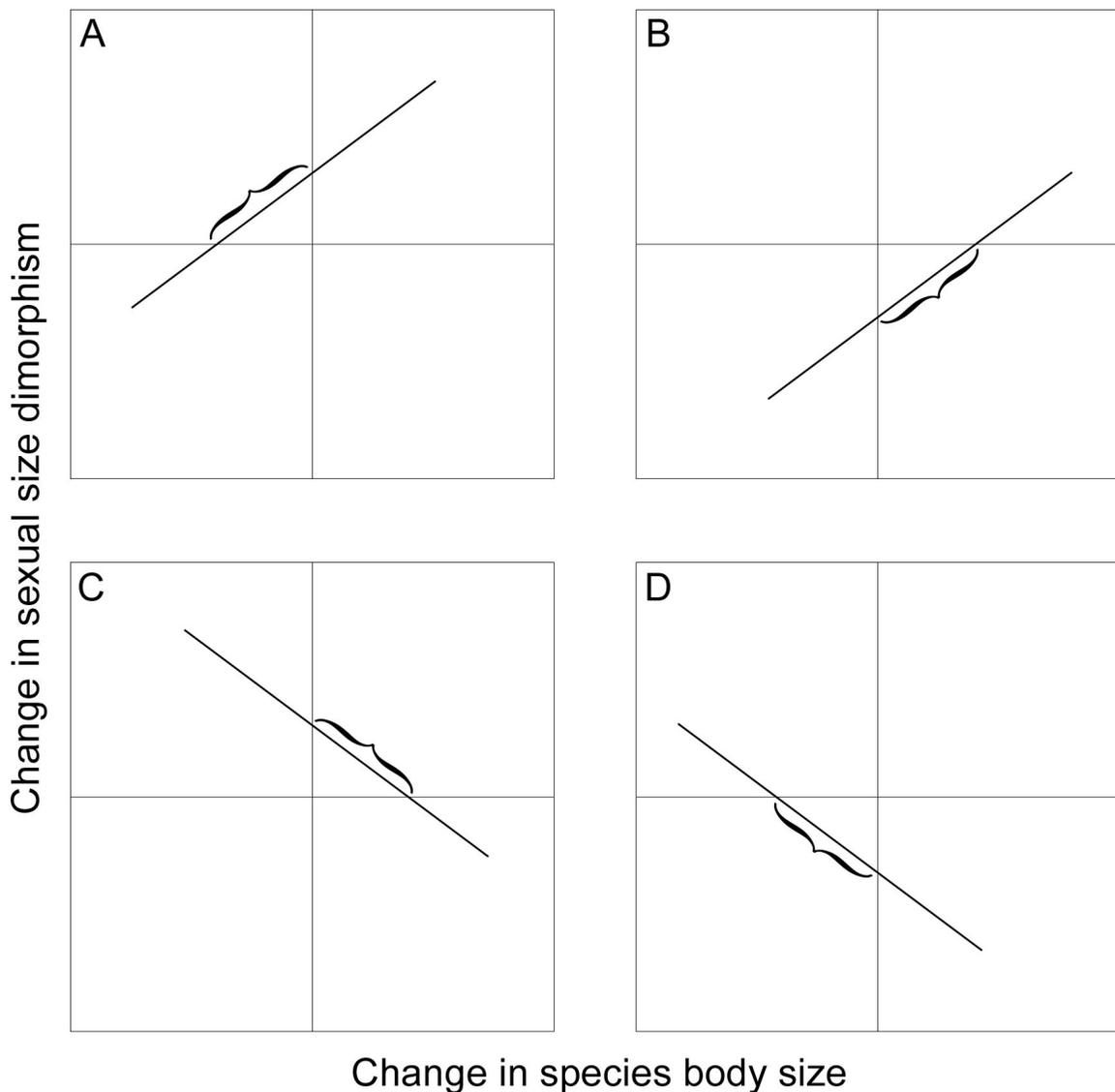


Figure 3.1. Hypothetical regressions of change in SSD against change in species body size in which intercept is not constrained to zero.

In each of the four diagrams, the bracketed portion of the regression line identifies a range of size change for which the overall pattern between change in size and change in dimorphism is reversed. For example, in plot **A** all increases in size (the portion of the line to the right of the y-axis) result in dimorphism increases; however, while most decreases in size (to the left of the bracketed range) are accompanied by dimorphism decreases, decreases in size in the bracketed range are accompanied by dimorphism *increases*. See text for description of other plots.

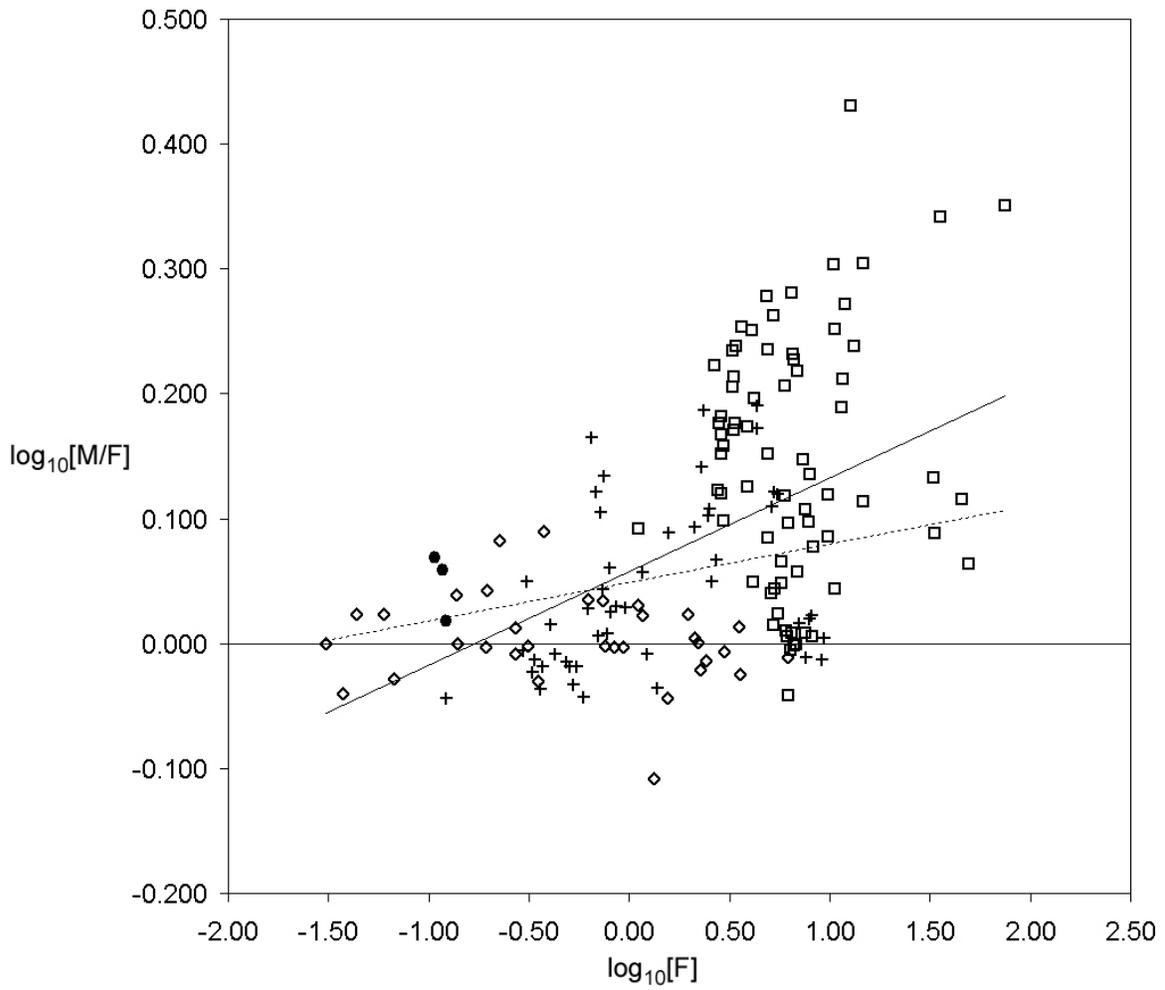


Figure 3.2a. Interspecific regressions of $\log_{10}[M/F]$ against $\log_{10}[F]$ in Primates (reduced data set).

Symbols are as follows: \diamond , Strepsirhini; \bullet , Tarsiidae; $+$, Platyrrhini; \square , Catarrhini. Solid line is OLS regression; dotted line is PGLS regression. OLS slope is significantly positive. PGLS slope is not significantly different from zero.

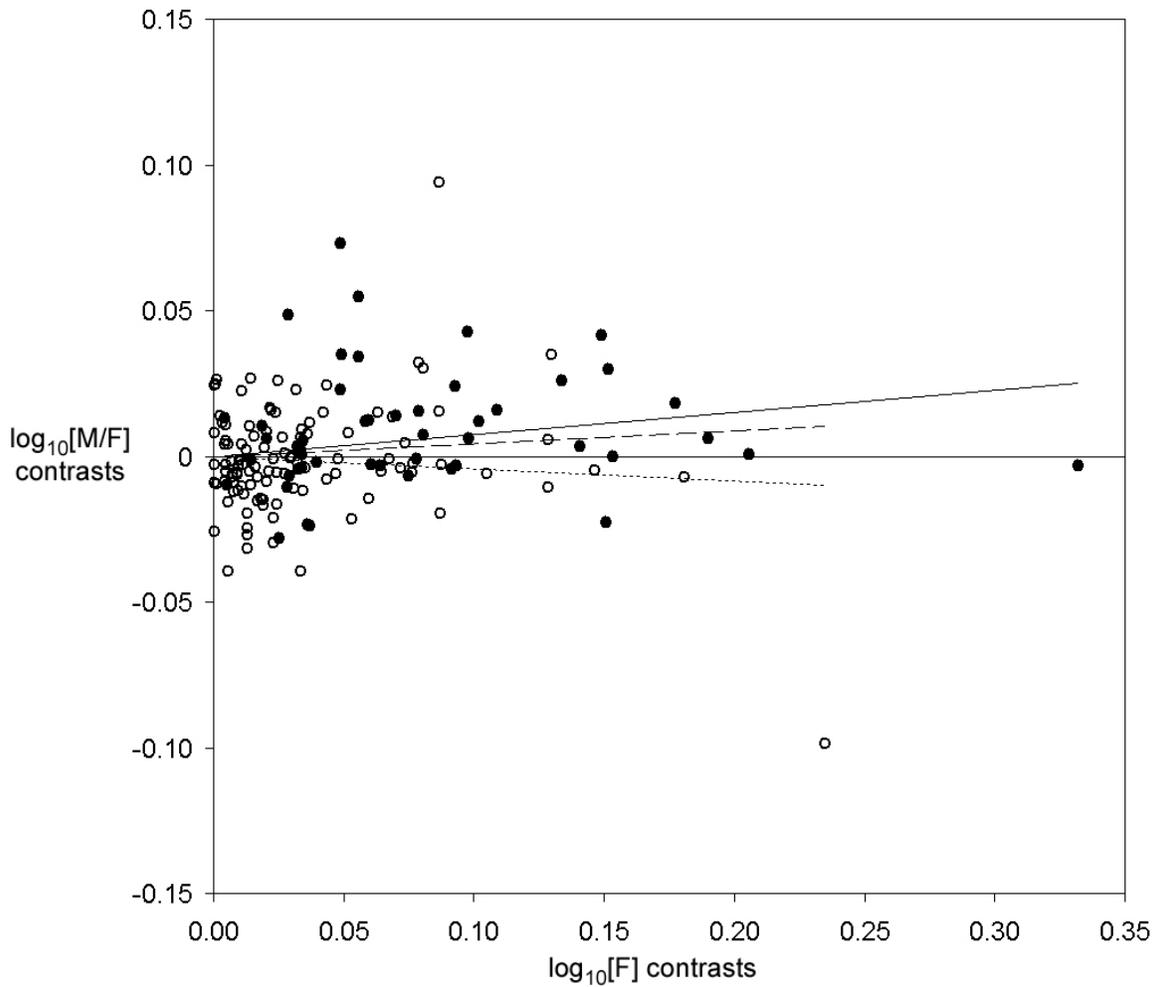


Figure 3.2b. Regressions of ancient and recent contrasts of $\log_{10}[M/F]$ against $\log_{10}[F]$ in Primates (reduced data set).

Closed circles are ancient contrasts; open circles are recent. Solid line is regression for ancient contrasts, dotted line is regression for all recent contrasts, dashed line is regression for recent contrasts with low outlier removed (see text). Ancient contrasts slope is significantly positive. Neither recent contrasts slope is significantly different from zero.

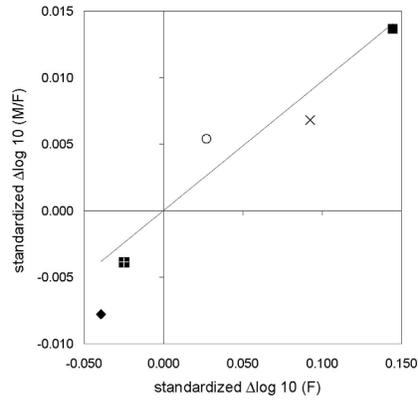


Figure 3.3a. Regression of change in $\log_{10}[M/F]$ against change in $\log_{10}[F]$ using GMM reconstructions of ancestral primate body size (reduced data set).

Symbols are as follows: \blacklozenge , change to LCA Strepsirhini; \circ , change to LCA Haplorhini; \times , change to LCA Anthropoidea; \boxplus , change to LCA Platyrrhini; \blacksquare , change to LCA Catarrhini.

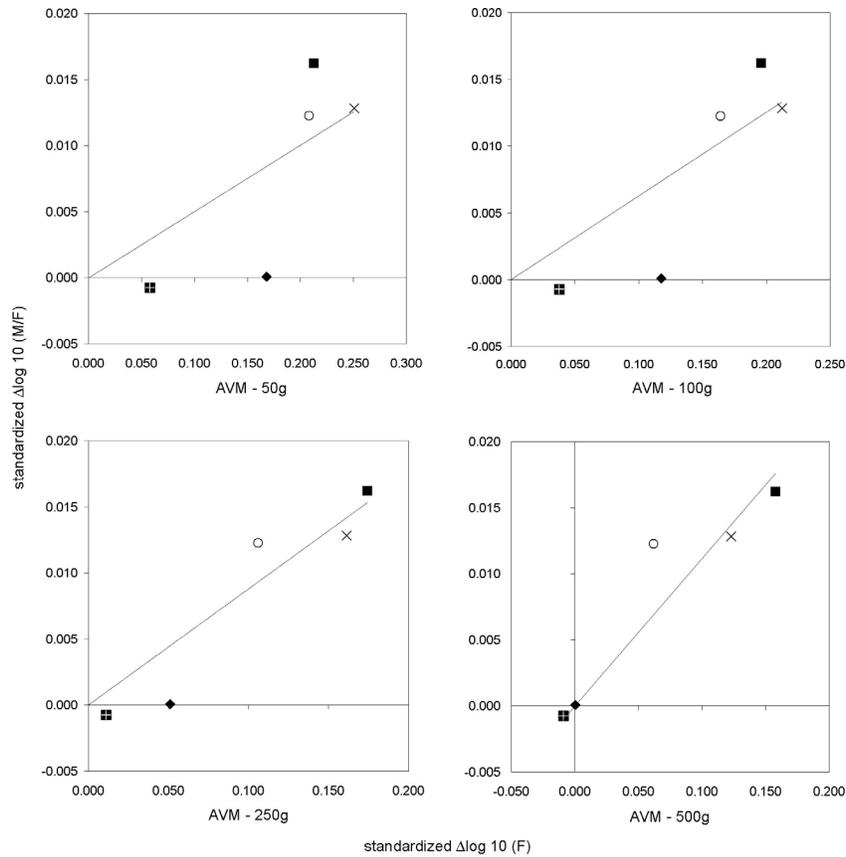


Figure 3.3b. Regression of change in $\log_{10}[M/F]$ against change in $\log_{10}[F]$ using AVM reconstructions of ancestral primate body size (reduced data set).

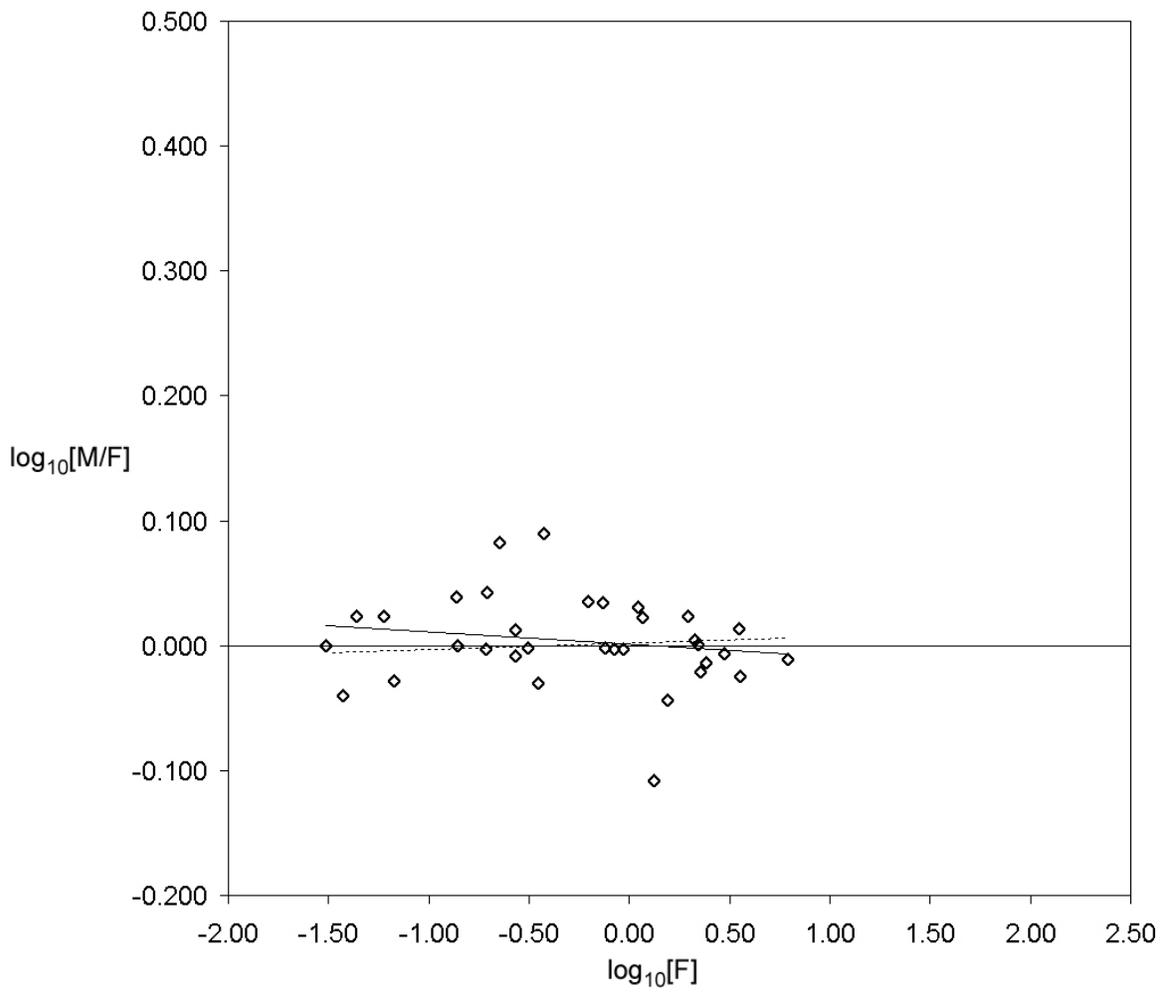


Figure 3.4a. Interspecific regressions of $\log_{10}[M/F]$ against $\log_{10}[F]$ in Strepsirhini (reduced data set).

Symbols and lines are as in Figure 3.2a. Neither regression slope differs significantly from zero.

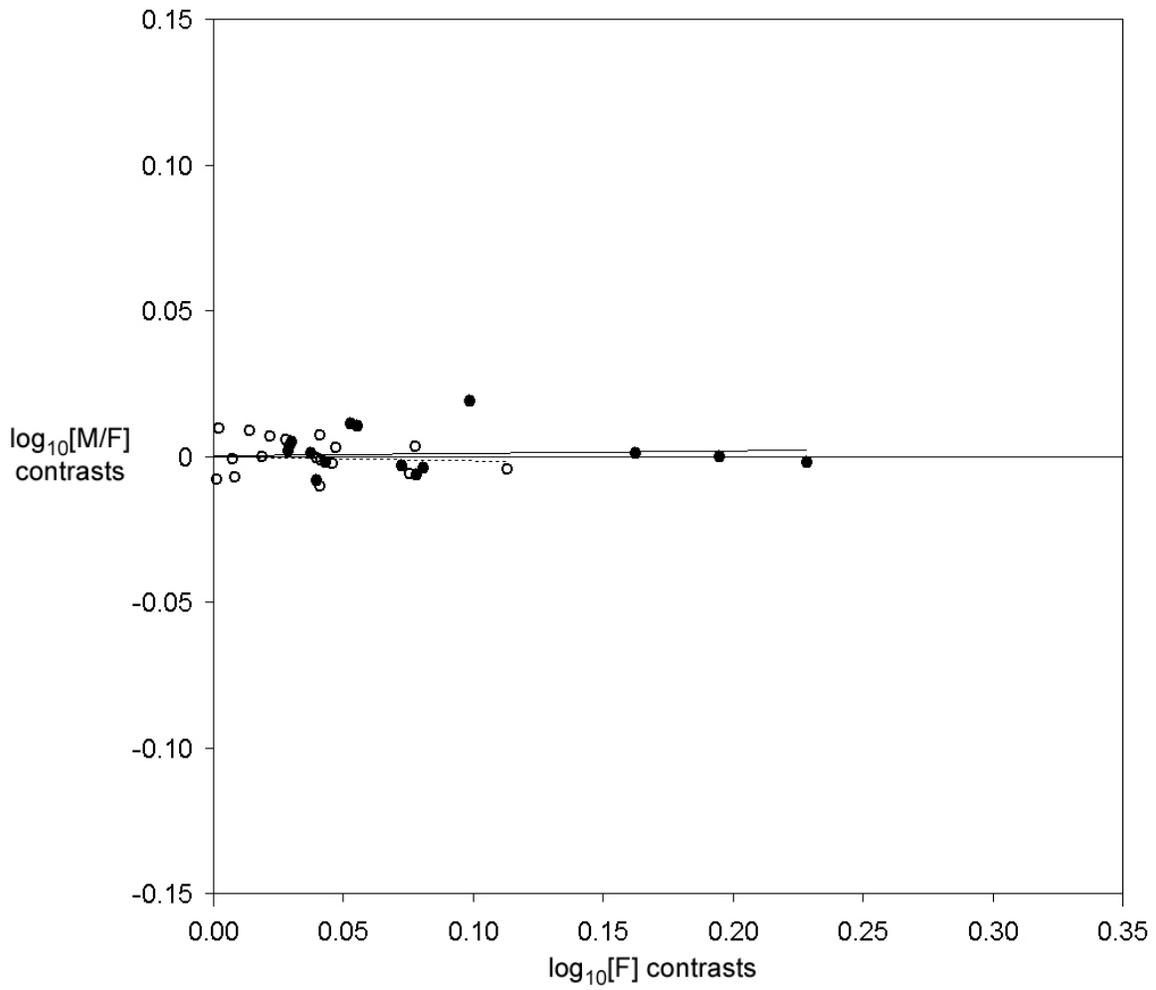


Figure 3.4b. Regressions of ancient and recent contrasts of $\log_{10}[M/F]$ against $\log_{10}[F]$ in Strepsirhini (reduced data set).

Symbols are as in Figure 3.2b. Solid line is regression for ancient contrasts, dotted line is regression for all recent contrasts. Neither regression slope differs significantly from zero.

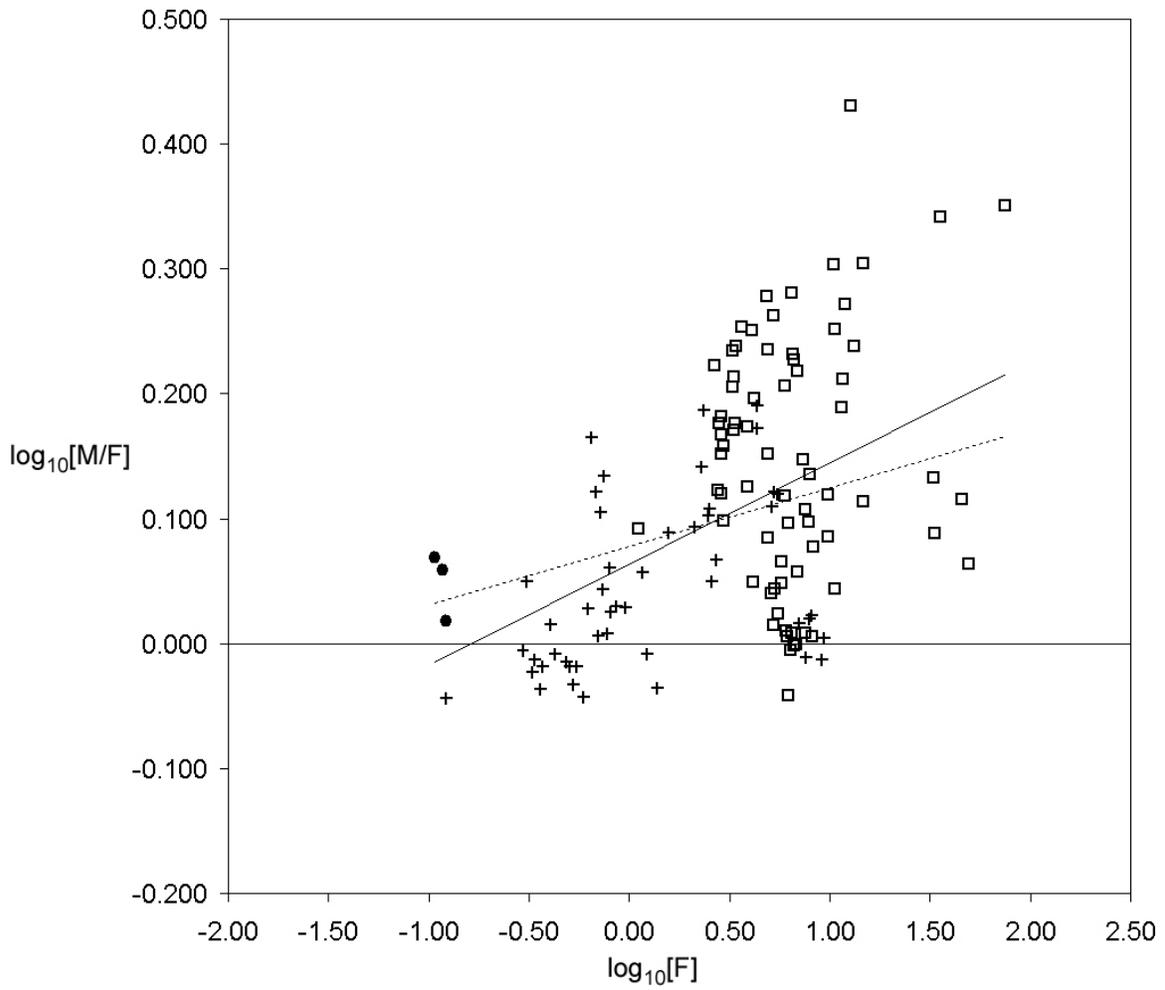


Figure 3.5a. Interspecific regressions of $\log_{10}[M/F]$ against $\log_{10}[F]$ in Haplorhini (reduced data set).

Symbols and lines are as in Figure 3.2a. OLS slope is significantly positive. PGLS slope is not significantly different from zero.

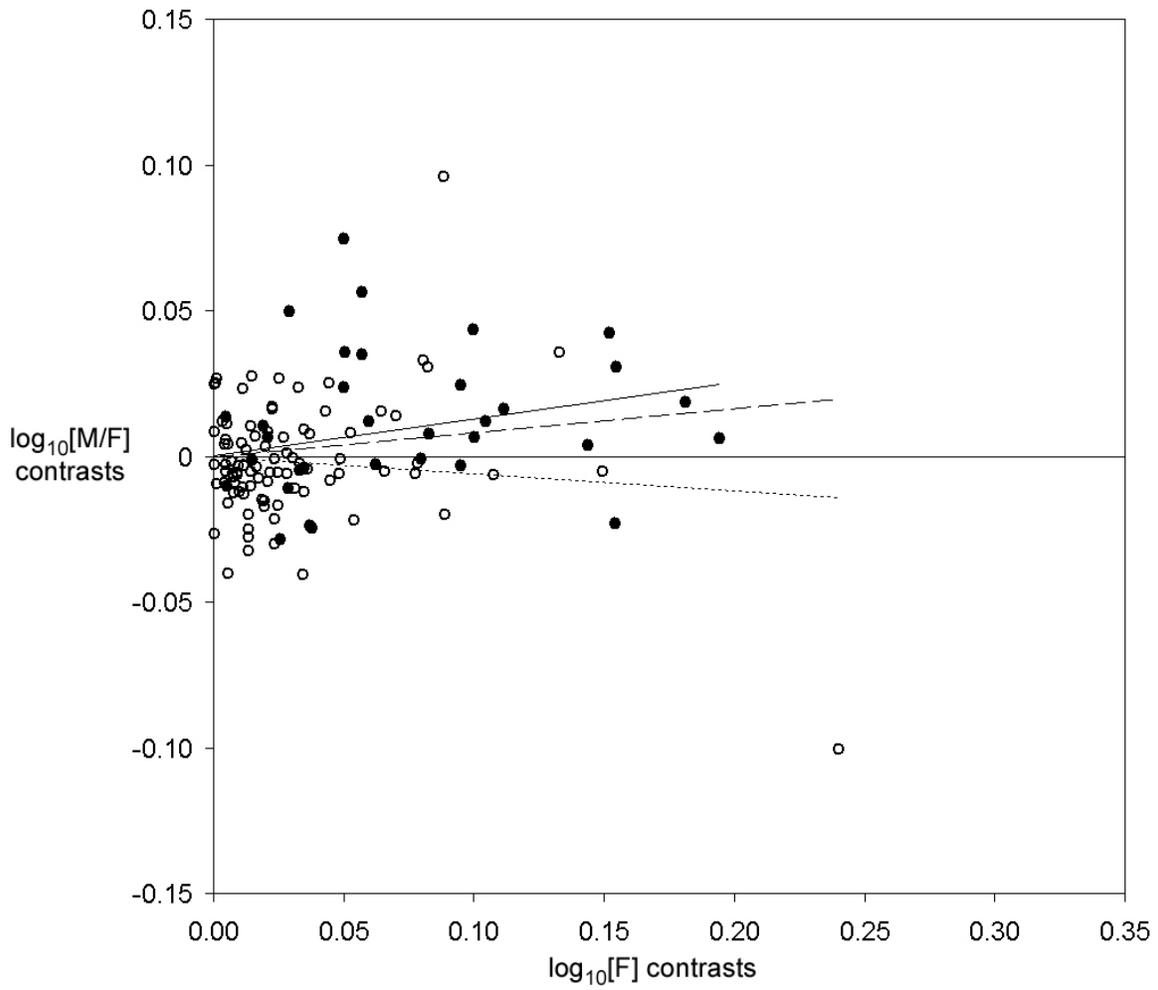


Figure 3.5b. Regressions of ancient and recent contrasts of $\log_{10}[M/F]$ against $\log_{10}[F]$ in Haplorhini (reduced data set).

Symbols and lines are as in Figure 3.2b. Dashed line is regression for recent contrasts with low outlier removed (see text). Ancient contrasts slope is significantly positive. Neither recent contrasts slope is significantly different from zero.

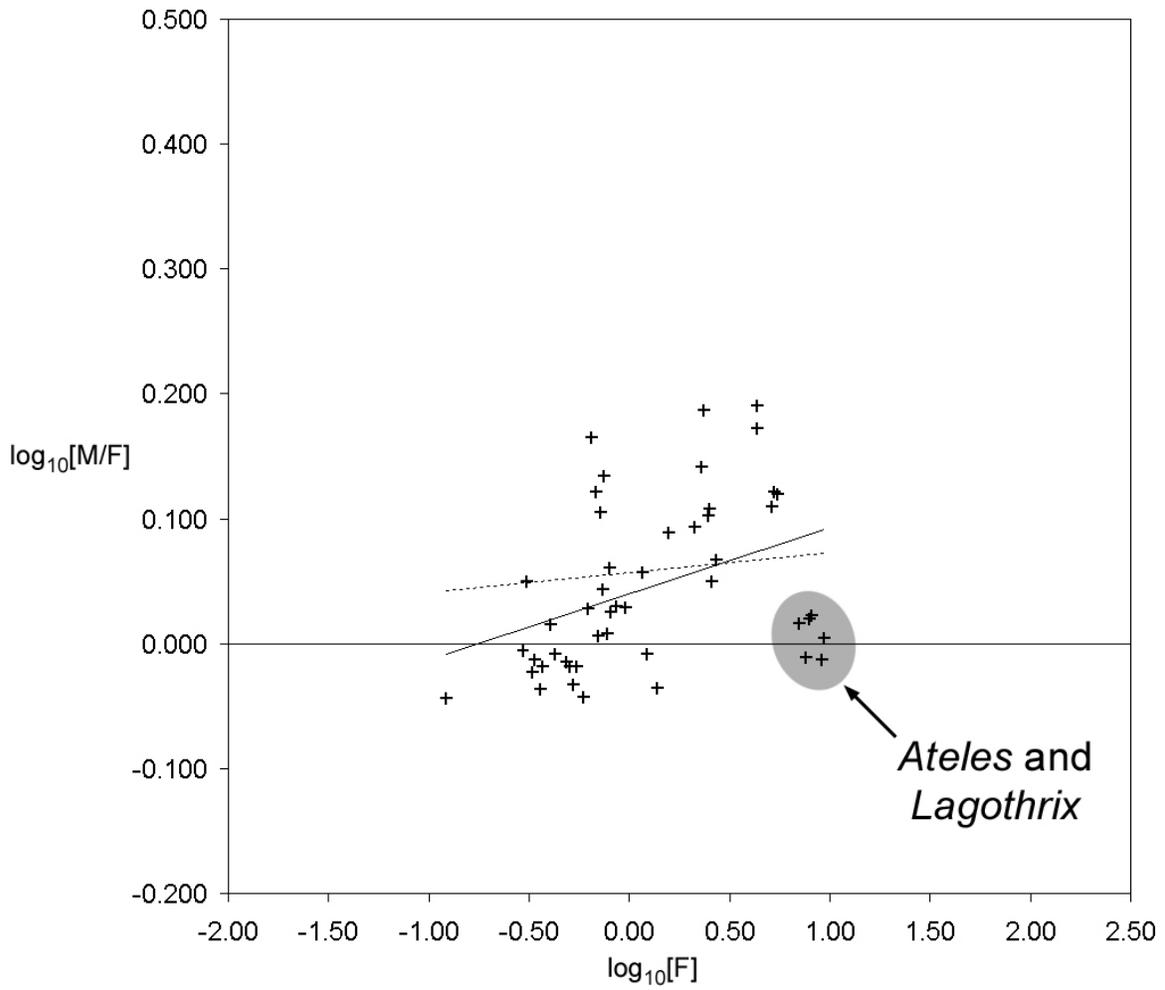


Figure 3.6a. Interspecific regressions of $\log_{10}[M/F]$ against $\log_{10}[F]$ in Platyrrhini (reduced data set).

Symbols and lines are as in Figure 3.2a. OLS slope is significantly positive. PGLS slope is not significantly different from zero. Intercepts are significantly greater than zero in both regressions. Note the largest taxa in this analysis are essentially monomorphic (*Ateles* and *Lagothrix*).

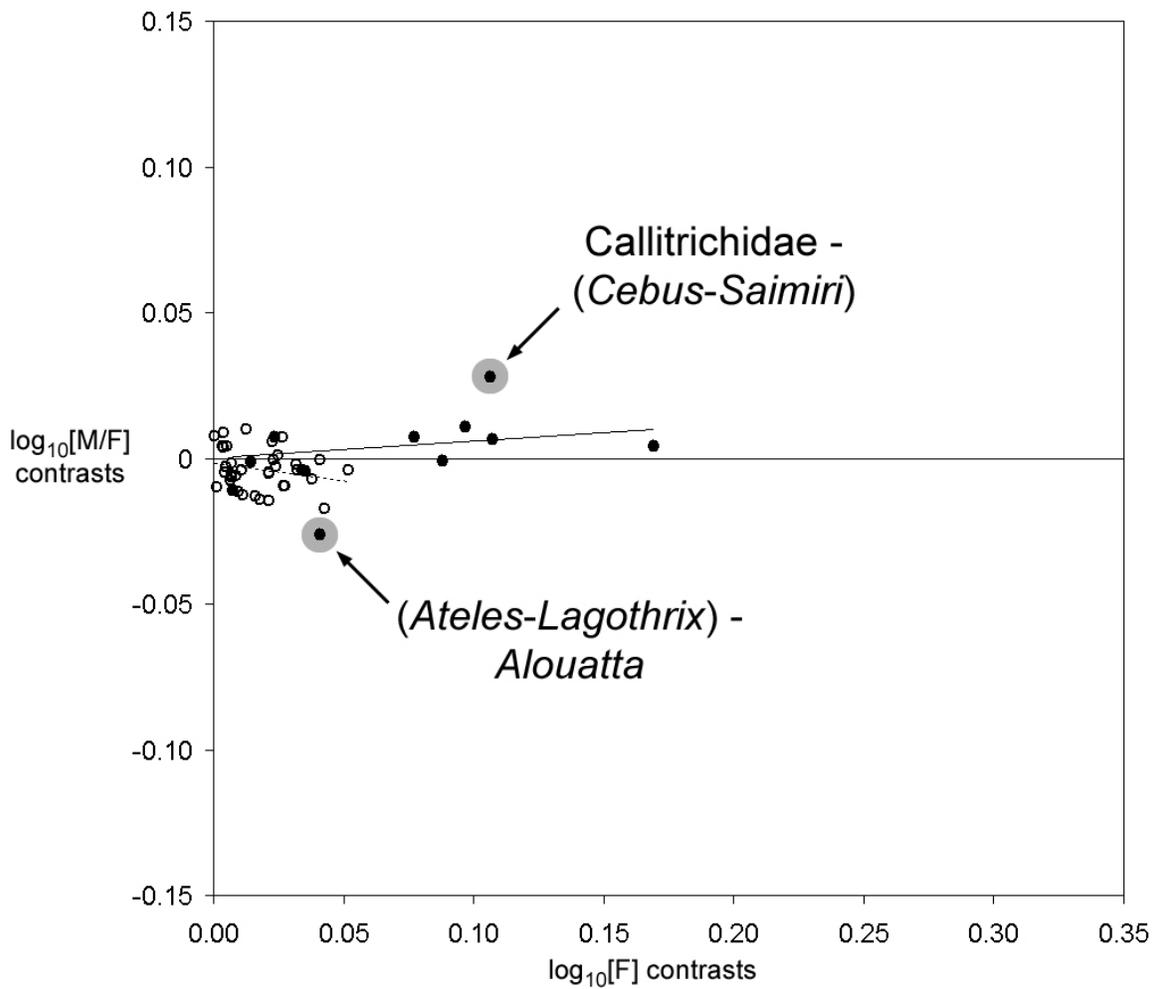


Figure 3.6b. Regressions of ancient and recent contrasts of $\log_{10}[M/F]$ against $\log_{10}[F]$ in Platyrrhini (reduced data set).

Symbols and lines are as in Figure 3.4b. Ancient contrasts slope is not significantly different from zero. Recent contrasts slope is significantly negative. Note the two ancient contrasts that deviate considerably from the regression line.

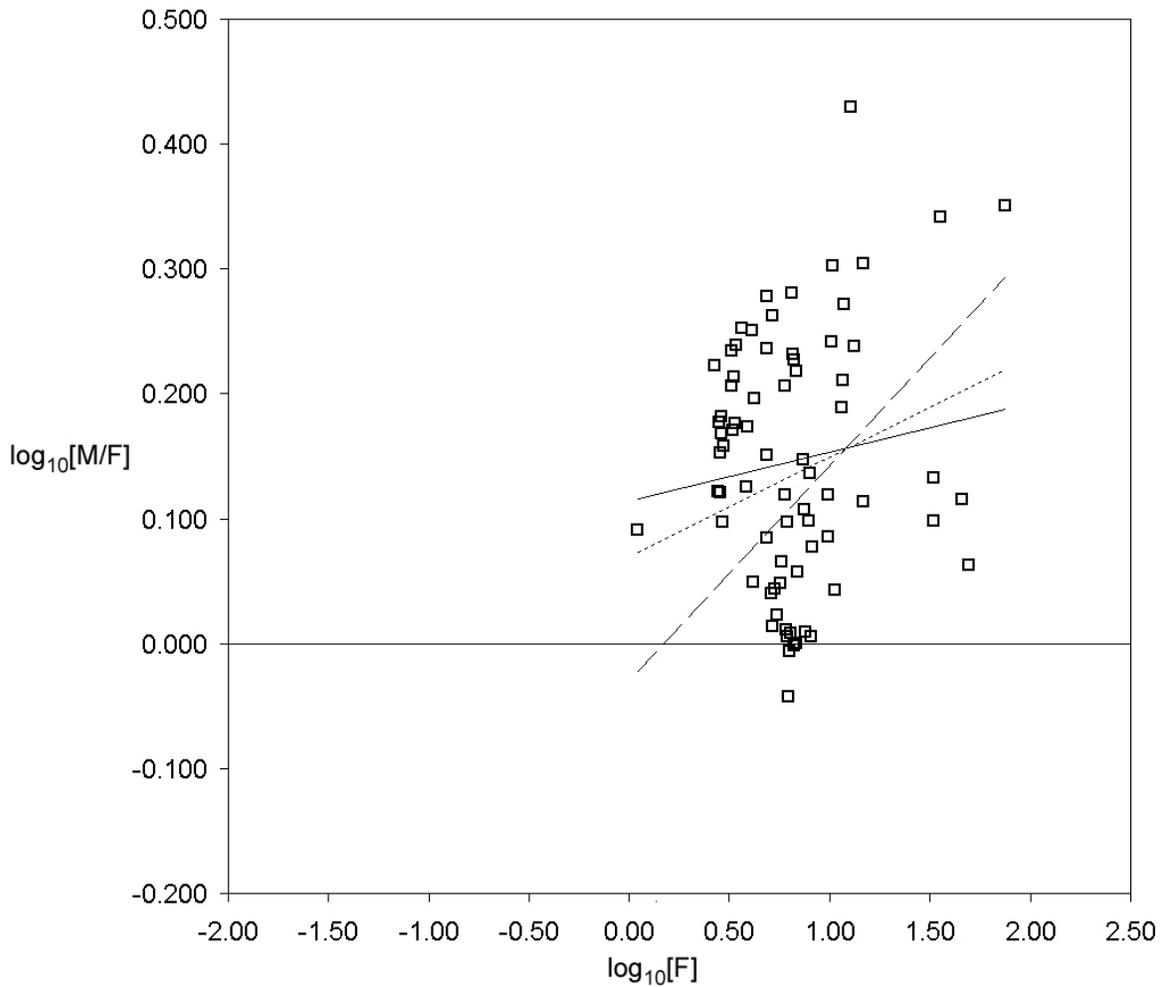


Figure 3.7a. Interspecific regressions of $\log_{10}[M/F]$ against $\log_{10}[F]$ in Catarrhini (reduced data set).

Symbols and lines are as in Figure 3.2a, with the addition of a dashed line for the phylogenetic regression with the *Semnopithecus* contrast removed. Only the dashed regression line has a significantly positive slope (although the OLS slope for the full data set is also significantly positive). Note that both phylogenetic slopes are higher than the OLS slope.

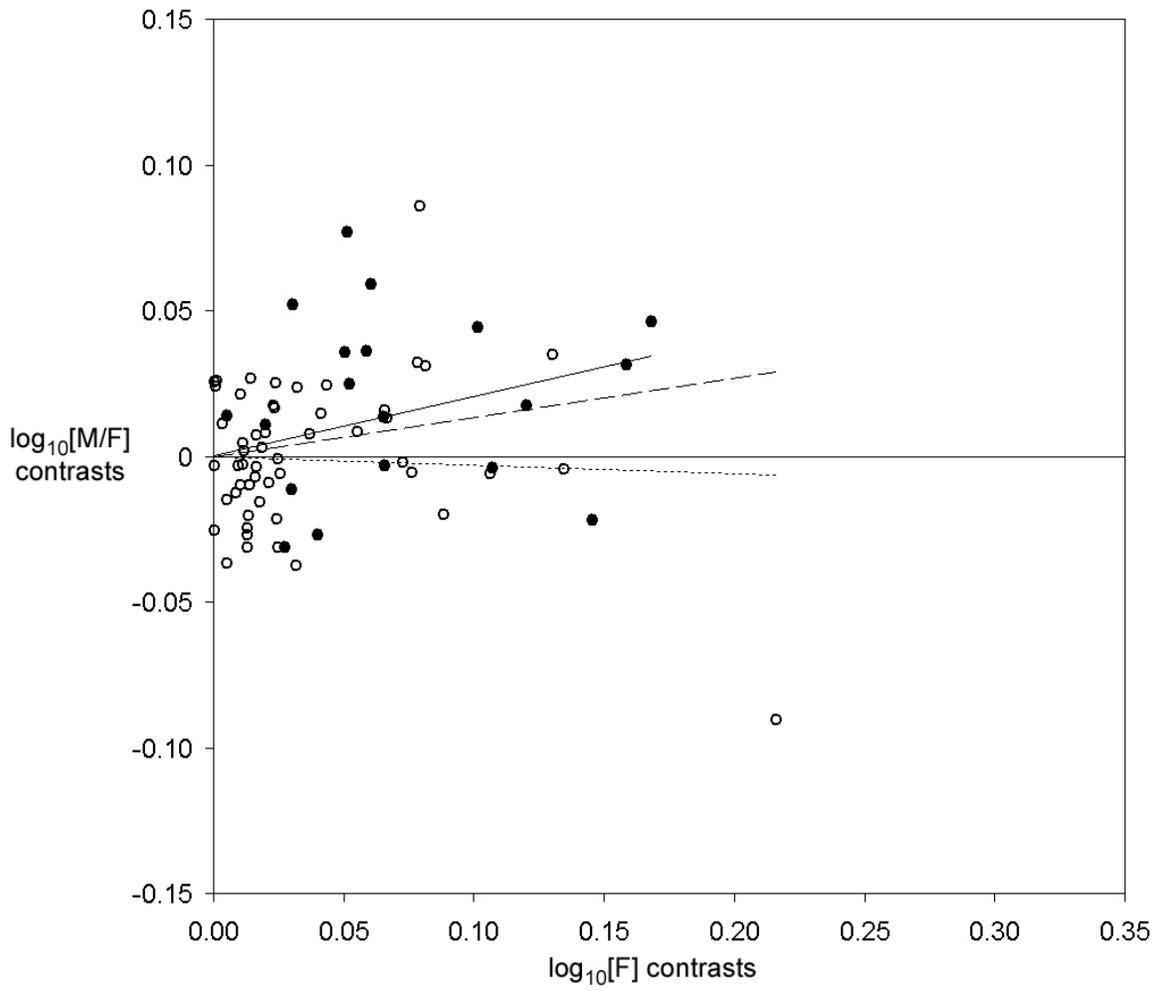


Figure 3.7b. Regressions of ancient and recent contrasts of $\log_{10}[M/F]$ against $\log_{10}[F]$ in Catarrhini (reduced data set).

Symbols and lines are as in Figure 3.2b. Ancient contrasts slope is significantly positive. Slope for all recent contrasts is not significantly different from zero; however, the slope for recent contrasts with outlier removed is significantly positive (see text).

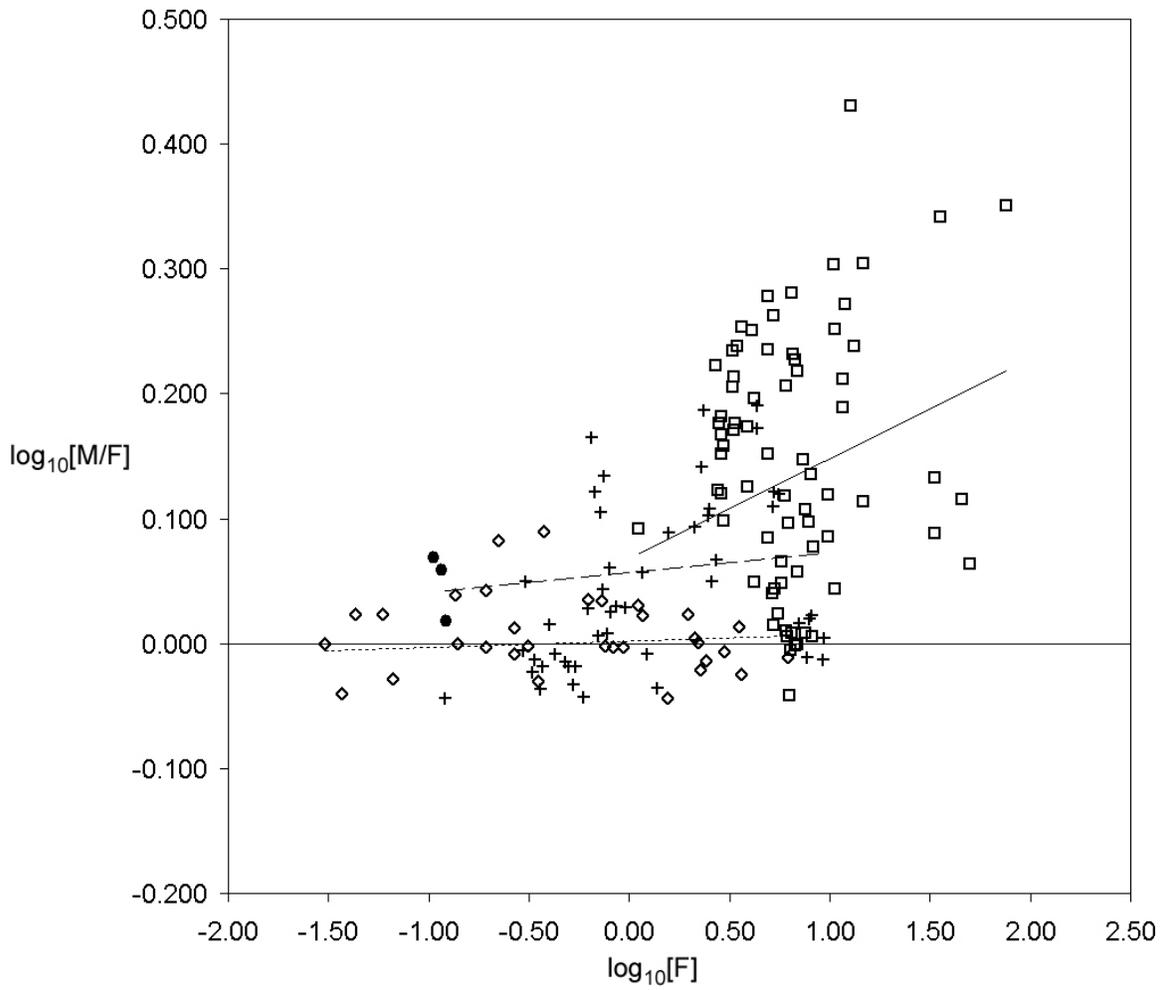


Figure 3.8. PGLS regressions of $\log_{10}[M/F]$ against $\log_{10}[F]$ for Strepsirhini, Platyrrhini, and Catarrhini superimposed over raw data for Primates (reduced data set).

Symbols are as in Figure 3.2a. Regression lines are as follows: dotted, Strepsirhini; dashed, Platyrrhini; solid, Catarrhini.

| Taxon | Sample | Male <i>N</i> | Female <i>N</i> | Male mean (kg) | Female mean (kg) | Reference |
|------------------------------------|--------|------------------|--------------------|----------------------|------------------------|--------------------------------------|
| Cheirogaleidae | | | | | | |
| <i>Allocebus trichotis</i> | F | 2 | 2 | 0.092 | 0.084 | Smith & Jungers (1997) |
| <i>Cheirogaleus major</i> | F | 3 | 6 | 0.438 | 0.362 | Smith & Jungers (1997) |
| <i>Cheirogaleus medius</i> | F, R | W | W | 0.140 | 0.139 | |
| | | 7 | 6 | 0.188 | 0.172 | Smith & Jungers (1997) |
| | | 36 | 43 | 0.128 | 0.134 | Kathrin Dausmann, pc |
| | | 4 | 3 | 0.159 | 0.150 | Alexandra Mueller, pc |
| <i>Microcebus berthae</i> | F, R | 10 | 10 | 0.0341 | 0.0373 | Manfred Eberle, pc |
| <i>Microcebus murinus</i> | F, R | 127 | 120 | 0.0630 | 0.0672 | Manfred Eberle, pc |
| <i>Microcebus myoxinus</i> | F, R | 81 | 48 | 0.0307 | 0.0307 | Schwab (2000) |
| <i>Microcebus rufus</i> | F, R | 17 | 15 | 0.0458 | 0.0435 | Atsalis (1999) |
| <i>Mirza coquereli</i> | F, R | P | P | 0.311 | 0.312 | |
| | | 68 | 77 | 0.309 | 0.299 | Peter Kappler, pc |
| | | 10 | 13 | 0.312 | 0.325 | Stanger <i>et al.</i> (1995) |
| <i>Phaner furcifer</i> | F, R | 8 | 6 | 0.328 | 0.351 | Oliver Schuelke, pc |
| Megaladapidae | | | | | | |
| <i>Lepilemur edwardsi</i> | F, R | 10 | 10 | 0.928 | 0.934 | Rasoloharijaona <i>et al.</i> (2003) |
| <i>Lepilemur leucopus</i> | F | 2 | 5 | 0.617 | 0.594 | Smith & Jungers (1997) |
| <i>Lepilemur ruficaudatus</i> | F, R | P | P | 0.753 | 0.755 | |
| | | 28 | 19 | 0.800 | 0.827 | R. Hilgartner & D. Zinner, pc |
| | | 8 | 8 | 0.705 | 0.682 | Schmid & Ganzhorn (1996) |
| Lemuridae | | | | | | |
| <i>Eulemur coronatus</i> | F | 2 | 2 | 1.28 | 1.08 | Smith & Jungers (1997) |
| <i>Eulemur fulvus albocollaris</i> | F, R | P | P | 2.15 | 2.13 | |
| | | 15 | 9 | 2.20 | 2.16 | Johnson <i>et al.</i> , in review |
| | | 7 | 5 | 2.10 | 2.10 | Bradley <i>et al.</i> (1997) |
| <i>Eulemur fulvus rufus</i> | F, R | P | P | 2.17 | 2.27 | |
| | | 20 | 13 | 2.18 | 2.25 | Smith & Jungers (1997) |
| | | 23 | 15 | 2.15 | 2.29 | Johnson <i>et al.</i> , in review |
| <i>Eulemur fulvus sanfordi</i> | F | 2 | 2 | 1.87 | 1.83 | Smith & Jungers (1997) |
| <i>Eulemur macaco</i> | F, R | W | W | 2.35 | 2.43 | |
| | | 46 | 41 | 2.37 | 2.51 | Smith & Jungers (1997) |
| | | 2 | 5 | 1.88 | 1.76 | Smith & Jungers (1997) |
| <i>Eulemur mongoz</i> | F, R | 4 | 4 | 1.41 | 1.56 | Smith & Jungers (1997) |
| <i>Eulemur rubriventer</i> | F, R | 9 | 13 | 2.07 | 1.96 | Glander <i>et al.</i> (1992) |
| <i>Hapalemur aureus</i> | F | 2 | 1 | 1.60 | 1.50 | Glander <i>et al.</i> (1992) |
| <i>Hapalemur griseus</i> | F | 2 | 2 | 0.748 | 0.670 | Smith & Jungers (1997) |
| <i>Hapalemur simus</i> | F | 2 | 1 | 2.15 | 1.3 | Smith & Jungers (1997) |
| <i>Lemur catta</i> | F, R | 41 | 24 | 2.21 | 2.21 | Smith & Jungers (1997) |
| <i>Varecia variegata</i> | F, R | 13 | 5 | 3.63 | 3.52 | Smith & Jungers (1997) |

| Taxon | Sample | Male <i>N</i> | Female <i>N</i> | Male mean (kg) | Female mean (kg) | Reference |
|--|--------|------------------|--------------------|----------------------|------------------------|------------------------------|
| Indriidae | | | | | | |
| <i>Avahi laniger</i> | F, R | 4 | 4 | 1.03 | 1.32 | Smith & Jungers (1997) |
| <i>Avahi occidentalis</i> | F | 6 | 3 | 0.814 | 0.777 | Smith & Jungers (1997) |
| <i>Indri indri</i> | F | 2 | 2 | 5.83 | 7.14 | Powzyk (1996) |
| <i>Propithecus diadema</i> | F, R | P | P | 6.05 | 6.21 | |
| | | 8 | 6 | 5.59 | 5.90 | Glander <i>et al.</i> (1992) |
| | | 5 | 6 | 6.50 | 6.51 | Powzyk (1996) |
| <i>Propithecus tattersalli</i> | F, R | 10 | 8 | 3.39 | 3.59 | Smith & Jungers (1997) |
| <i>Propithecus verreauxi</i> | F, R | P | P | 2.93 | 2.98 | |
| | | 46 | 27 | 3.02 | 3.20 | Lewis & Kappeler, in review |
| | | 119 | 105 | 2.84 | 2.76 | Richard <i>et al.</i> (2000) |
| Daubentoniidae | | | | | | |
| <i>Daubentonia madagascariensis</i> | F | 3 | 4 | 2.63 | 2.30 | Glander (1994) |
| Lorisidae | | | | | | |
| <i>Arctocebus calabarensis</i> | F | 2 | 8 | 0.324 | 0.301 | Smith & Jungers (1997) |
| <i>Euoticus elegantulus</i> | F | 5 | 3 | 0.287 | 0.261 | Smith & Jungers (1997) |
| <i>Euoticus matschiei</i> | F | 2 | 4 | 0.207 | 0.212 | Smith & Jungers (1997) |
| <i>Galago moholi</i> | F, R | P | P | 0.214 | 0.194 | |
| | | 13 | 13 | 0.217 | 0.200 | Bearder & Martin (1980) |
| | | 53 | 47 | 0.211 | 0.188 | Harcourt & Bearder (1989) |
| <i>Galago senegalensis</i> | F, R | P | P | 0.271 | 0.225 | |
| | | 80 | 67 | 0.227 | 0.199 | Smith & Jungers (1997) |
| | | 8 | 9 | 0.315 | 0.250 | Smith & Jungers (1997) |
| <i>Galagoides alleni</i> | F, R | 9 | 30 | 0.277 | 0.269 | Smith & Jungers (1997) |
| <i>Galagoides demidoff</i> | F, R | 19 | 9 | 0.0628 | 0.0596 | Charles-Dominique (1972) |
| <i>Galagoides thomasi</i> | F | 2 | 1 | 0.103 | 0.130 | Smith & Jungers (1997) |
| <i>Galagoides zanzibaricus</i> | F, R | 35 | 38 | 0.150 | 0.137 | Harcourt & Nash (1986) |
| <i>Loris tardigradus lydekkerianus</i> | F, R | 7 | 4 | 0.264 | 0.269 | Smith & Jungers (1997) |
| <i>Loris tardigradus malabaricus</i> | F, R | 10 | 8 | 0.192 | 0.193 | Smith & Jungers (1997) |
| <i>Nycticebus coucang bengalensis</i> | F | W | W | 1.10 | 1.02 | |
| | | 2 | 1 | 0.890 | 0.900 | Fooden (1971) |
| | | 2 | 1 | 1.31 | 1.14 | Smith & Jungers (1997) |
| <i>Nycticebus coucang coucang</i> | F, R | 56 | 44 | 0.679 | 0.626 | Smith & Jungers (1997) |
| <i>Nycticebus pygmaeus</i> | F, R | 7 | 5 | 0.462 | 0.376 | Smith & Jungers (1997) |
| <i>Otolemur crassicaudatus</i> | F, R | 66 | 35 | 1.19 | 1.11 | Smith & Jungers (1997) |
| <i>Otolemur garnettii</i> | F, R | 120 | 134 | 0.794 | 0.734 | Smith & Jungers (1997) |
| <i>Perodicticus potto potto</i> | F, R | 17 | 15 | 0.830 | 0.836 | Smith & Jungers (1997) |
| <i>Perodicticus potto edwardsi</i> | F, R | 4 | 4 | 1.22 | 1.16 | Smith & Jungers (1997) |

| Taxon | Sample | Male <i>N</i> | Female <i>N</i> | Male mean (kg) | Female mean (kg) | Reference |
|---|--------|------------------|--------------------|-----------------------------|------------------------|-----------------------------|
| Tarsiidae | | | | | | |
| <i>Tarsius bancanus</i> | F, R | P | P | 0.128 | 0.123 | |
| | | 21 | 16 | 0.128 | 0.117 | Smith & Jungers (1997) |
| | | 6 | 6 | 0.128 | 0.128 | Wright <i>et al.</i> (2003) |
| <i>Tarsius diana</i> | F | 1 | 2 | 0.104 | 0.107 | Smith & Jungers (1997) |
| <i>Tarsius spectrum</i> | F, R | 5 | 8 | 0.125 | 0.107 | Gursky (1998) |
| <i>Tarsius syrichta</i> | F, R | 10 | 17 | 0.134 | 0.117 | Smith & Jungers (1997) |
| Callitrichidae | | | | | | |
| <i>Callithrix argentata</i> | F, R | 8 | 10 | 0.330 | 0.360 | Smith & Jungers (1997) |
| <i>Callithrix emiliae</i> | F, R | 12 | 5 | 0.313 | 0.330 | Smith & Jungers (1997) |
| <i>Callithrix humeralifer</i> | F, R | P | P | 0.418 | 0.426 | |
| | | 4 | 5 | 0.360 | 0.380 | Smith & Jungers (1997) |
| | | 15 | 13 | 0.475 | 0.472 | Smith & Jungers (1997) |
| <i>Callithrix jacchus</i> | F | 3 | 2 | 0.362 | 0.381 | Smith & Jungers (1997) |
| <i>Callithrix mauesi</i> | F | 2 | 2 | 0.345 | 0.398 | Smith & Jungers (1997) |
| <i>Callithrix nigriceps</i> | F | 3 | 1 | 0.370 | 0.390 | Smith & Jungers (1997) |
| <i>Callithrix penicillata</i> | F, R | 8 | 8 | 0.344 | 0.307 | Smith & Jungers (1997) |
| <i>Cebuella pygmaea</i> | F, R | 36 | 27 | 0.110 | 0.122 | Smith & Jungers (1997) |
| <i>Leontopithecus chrysomelas</i> | F | 2 | 6 | 0.620 | 0.535 | Smith & Jungers (1997) |
| <i>Leontopithecus rosalia</i> | F, R | 9 | 9 | 0.663 | 0.622 | Dietz <i>et al.</i> (1994) |
| <i>Saguinus bicolor</i> | F | 3 | 4 | 0.431 | 0.430 | Smith & Jungers (1997) |
| <i>Saguinus fuscicollis fuscicollis</i> | F, R | 9 | 10 | 0.328 | 0.338 | Soini (1990) |
| <i>Saguinus fuscicollis illigeri</i> | F, R | 9 | 4 | 0.292 | 0.296 | Soini (1990) |
| <i>Saguinus fuscicollis nigrifons</i> | F, R | P | P | 0.354 | 0.369 | |
| | | 9 | 7 | 0.350 | 0.376 | Soini (1990) |
| | | 17 | 19 | 0.352 | 0.366 | Soini (1990) |
| | | 25 | 15 | 0.359 | 0.366 | Soini (1990) |
| <i>Saguinus geoffroyi</i> | F, R | 55 | 40 | 0.482 | 0.503 | Dawson & Dukelow (1976) |
| <i>Saguinus labiatus</i> | F, R | 136 | 77 | 0.490 | 0.529 | Smith & Jungers (1997) |
| <i>Saguinus leucopus</i> | F | 2 | 2 | 0.494 | 0.490 | Smith & Jungers (1997) |
| <i>Saguinus midas</i> | F, R | P | P | 0.535 | 0.591 | |
| | | 8 | 6 | 0.544 | 0.601 | Smith & Jungers (1997) |
| | | 11 | 7 | 0.526 | 0.580 | Smith & Jungers (1997) |
| <i>Saguinus mystax</i> | F, R | P | P | 0.522 | 0.545 | |
| | | 18 | 10 | 0.568 | 0.585 | Garber <i>et al.</i> (1993) |
| | | 95 | 80 | 0.491 | 0.511 | Moya, <i>et al.</i> (1990) |
| | | 79 | 48 | 0.525 | 0.561 | Soini & Soini (1990) |
| | | 48 | 30 | 0.472 | 0.490 | Soini & Soini (1990) |
| | | 34 | 26 | 0.505 | 0.540 | Soini & Soini (1990) |
| | | 6 | 13 | 0.550 | 0.561 | Garber <i>et al.</i> (1993) |
| 6 | 6 | 0.545 | 0.564 | Garber <i>et al.</i> (1993) | | |

| Taxon | Sample | Male <i>N</i> | Female <i>N</i> | Male mean (kg) | Female mean (kg) | Reference |
|--------------------------------|--------|------------------|--------------------|----------------------|------------------------|-----------------------------------|
| <i>Saguinus nigricollis</i> | F, R | 8 | 6 | 0.468 | 0.484 | Smith & Jungers (1997) |
| <i>Saguinus oedipus</i> | F, R | 37 | 29 | 0.418 | 0.404 | Smith & Jungers (1997) |
| Cebidae | | | | | | |
| <i>Alouatta belzebul</i> | F, R | 27 | 26 | 7.27 | 5.52 | Smith & Jungers (1997) |
| <i>Alouatta caraya</i> | F, R | 58 | 117 | 6.42 | 4.33 | Smith & Jungers (1997) |
| <i>Alouatta fusca</i> | F, R | 4 | 5 | 6.73 | 4.35 | Smith & Jungers (1997) |
| <i>Alouatta palliata</i> | F, R | P | P | 6.96 | 5.28 | |
| | | 14 | 18 | 6.53 | 4.02 | Smith & Jungers (1997) |
| | | 15 | 15 | 7.80 | 6.60 | Smith & Jungers (1997) |
| | | 8 | 10 | 8.35 | 6.17 | Scott <i>et al.</i> (1976) |
| | | 4 | 17 | 4.95 | 4.25 | Scott <i>et al.</i> (1976) |
| | | 110+ | 177+ | 7.17 | 5.35 | Smith & Jungers (1997) |
| <i>Alouatta pigra</i> | F | 2 | 4 | 11.4 | 6.43 | Smith & Jungers (1997) |
| <i>Alouatta seniculus</i> | F, R | P | P | 6.66 | 5.18 | |
| | | 28 | 34 | 7.62 | 6.02 | Smith & Jungers (1997) |
| | | 31 | 29 | 5.62 | 4.03 | Braza <i>et al.</i> (1983) |
| | | 8 | 9 | 7.54 | 6.30 | Hernandez-Camacho & Defler (1985) |
| | | 14 | 4 | 6.70 | 4.50 | Rudran (1979) |
| | | 10 | 4 | 6.50 | 4.50 | Thorington <i>et al.</i> (1979) |
| | | 7 | 4 | 6.00 | 5.70 | Rodriguez & Boher (1988) |
| <i>Aotus azarai</i> | F, R | 5 | 5 | 1.23 | 1.22 | AMNH (this study) |
| <i>Aotus infulatus</i> | F | 1 | 1 | 1.19 | 1.24 | Smith & Jungers (1997) |
| <i>Aotus lemurinus</i> | F, R | 7 | 6 | 0.921 | 0.859 | Hernandez-Camacho & Defler (1985) |
| <i>Aotus nancymaae</i> | F, R | 32 | 24 | 0.795 | 0.78 | Smith & Jungers (1997) |
| <i>Aotus trivirgatus</i> | F, R | 20 | 17 | 0.813 | 0.736 | Smith & Jungers (1997) |
| <i>Aotus vociferans</i> | F, R | 20 | 20 | 0.708 | 0.698 | Smith & Jungers (1997) |
| <i>Ateles belzebuth</i> | F, R | 10 | 16 | 8.26 | 7.88 | Smith & Jungers (1997) |
| <i>Ateles chamek</i> | F, R | 4 | 8 | 9.41 | 9.33 | Smith & Jungers (1997) |
| <i>Ateles fusciceps</i> | F, R | 6 | 11 | 8.89 | 9.16 | Smith & Jungers (1997) |
| <i>Ateles geoffroyi</i> | F, R | 20 | 32 | 7.45 | 7.64 | Schultz (1941) |
| <i>Ateles paniscus</i> | F, R | P | P | 8.49 | 8.07 | |
| | | 20 | 42 | 9.11 | 8.44 | Smith & Jungers (1997) |
| | | 5 | 7 | 7.86 | 7.69 | Fleagle & Mittermeier (1980) |
| <i>Brachyteles arachnoides</i> | F | 3 | 3 | 9.42 | 8.33 | Lemos de Sa & Glander (1993) |
| <i>Cacajao calvus</i> | F | 1 | 2 | 3.45 | 2.88 | Smith & Jungers (1997) |
| <i>Cacajao melanocephalus</i> | F, R | 5 | 6 | 3.16 | 2.71 | Smith & Jungers (1997) |
| <i>Callicebus brunneus</i> | F, R | 6 | 4 | 0.854 | 0.805 | Smith & Jungers (1997) |
| <i>Callicebus cupreus</i> | F | 10 | 2 | 1.02 | 1.12 | Smith & Jungers (1997) |
| <i>Callicebus donacophilus</i> | F | 5 | 2 | 0.991 | 0.909 | Smith & Jungers (1997) |
| <i>Callicebus hoffmannsi</i> | F | 1 | 3 | 1.09 | 1.07 | Smith & Jungers (1997) |
| <i>Callicebus moloch</i> | F, R | 10 | 19 | 1.02 | 0.956 | Smith & Jungers (1997) |

| Taxon | Sample | Sex | | Male | Female | Reference |
|--------------------------------------|--------|----------|----------|--------------|--------------|-----------------------------------|
| | | <i>N</i> | <i>N</i> | mean (kg) | mean (kg) | |
| <i>Callicebus personatus</i> | F, R | 5 | 7 | 1.27 | 1.38 | Smith & Jungers (1997) |
| <i>Callicebus torquatus</i> | F, R | P | P | 1.32 | 1.16 | |
| | | 5 | 9 | 1.49 | 1.27 | Hernandez-Camacho & Defler (1985) |
| | | 8 | 6 | 1.15 | 1.05 | Smith & Jungers (1997) |
| <i>Cebus albifrons</i> | F, R | W | W | 3.18 | 2.29 | |
| | | 8 | 3 | 3.42 | 2.86 | Hernandez-Camacho & Defler (1985) |
| | | 18 | 15 | 3.07 | 2.18 | Smith & Jungers (1997) |
| <i>Cebus apella</i> | F, R | P | P | 3.64 | 2.39 | |
| | | 9 | 5 | 3.74 | 2.33 | Hernandez-Camacho & Defler (1985) |
| | | 6 | 11 | 3.30 | 2.08 | AMNH (this study) |
| | | 13 | 10 | 3.84 | 2.66 | Smith & Jungers (1997) |
| <i>Cebus capucinus</i> | F | 3 | 2 | 3.66 | 2.50 | Hernandez-Camacho & Defler (1985) |
| <i>Cebus olivaceus</i> | F, R | W | W | 3.24 | 2.52 | |
| | | 15 | 3 | 3.10 | 1.90 | Rodriguez & Boher (1988) |
| | | 14 | 7 | 3.38 | 2.79 | Smith & Jungers (1997) |
| <i>Chiropotes albinasus</i> | F, R | 7 | 7 | 3.15 | 2.49 | Smith & Jungers (1997) |
| <i>Chiropotes satanus satanus</i> | F | 4 | 3 | 3.25 | 3.11 | Smith & Jungers (1997) |
| <i>Chiropotes satanus chiropotes</i> | F, R | 20 | 19 | 2.90 | 2.58 | Smith & Jungers (1997) |
| <i>Lagothrix lagotricha</i> | F, R | 16 | 9 | 7.28 | 7.02 | Smith & Jungers (1997) |
| <i>Pithecia irrorata</i> | F | 2 | 2 | 2.25 | 2.07 | Smith & Jungers (1997) |
| <i>Pithecia monachus</i> | F, R | 16 | 10 | 2.61 | 2.11 | Smith & Jungers (1997) |
| <i>Pithecia pithecia</i> | F, R | 10 | 4 | 1.94 | 1.58 | Smith & Jungers (1997) |
| <i>Saimiri boliviensis</i> | F, R | 14 | 13 | 1.02 | 0.75 | AMNH (this study) |
| <i>Saimiri oerstedii</i> | F, R | W | W | 0.897 | 0.680 | |
| | | 3 | 3 | 0.907 | 0.603 | Crile & Quiring (1940) |
| | | 8 | 4 | 0.893 | 0.737 | Schultz (1941) |
| <i>Saimiri sciureus</i> | F, R | P | P | 0.920 | 0.723 | |
| | | 8 | 5 | 0.740 | 0.635 | Fleagle & Mittermeier (1980) |
| | | 17 | 58 | 1.02 | 0.699 | Smith & Jungers (1997) |
| | | 9 | 5 | 1.08 | 0.859 | Hernandez-Camacho & Defler (1985) |
| | | 29 | 34 | 0.840 | 0.698 | Ique (1990) |
| <i>Saimiri ustus</i> | F, R | 11 | 6 | 0.921 | 0.799 | Smith & Jungers (1997) |
| <i>Saimiri vanzolinii</i> | F, R | 9 | 4 | 0.950 | 0.650 | Smith & Jungers (1997) |
| Cercopithecinae | | | | | | |
| <i>Allenopithecus nigroviridis</i> | F | 5 | 1 | 6.13 | 3.18 | Smith & Jungers (1997) |
| <i>Cercocebus agilis</i> | F | 2 | 2 | 9.50 | 5.66 | Smith & Jungers (1997) |
| <i>Cercocebus atys</i> | F | 3 | 4 | 11.0 | 6.20 | Smith & Jungers (1997) |
| <i>Cercocebus galeritus</i> | F, R | W | W | 9.61 | 5.26 | |
| | | 3 | 3 | 10.19 | 5.47 | Gautier-Hion & Gautier (1976) |
| | | 3 | 4 | 9.03 | 5.10 | Smith & Jungers (1997) |
| <i>Cercocebus torquatus</i> | F | 3 | 1 | 8.01 | 5.50 | Sanders & Bodenbender (1994) |

| Taxon | Sample | Male <i>N</i> | Female <i>N</i> | Male mean (kg) | Female mean (kg) | Reference |
|---|--------|------------------|--------------------|----------------------|------------------------|-------------------------------|
| <i>Cercopithecus ascanius schmidti</i> | F, R | 37 | 55 | 3.69 | 2.79 | Colyn (1994) |
| <i>Cercopithecus ascanius katangae</i> | F, R | 32 | 187 | 3.71 | 2.97 | Colyn (1994) |
| <i>Cercopithecus campbelli</i> | F, R | 10 | 9 | 4.50 | 2.70 | Smith & Jungers (1997) |
| <i>Cercopithecus cephus</i> | F, R | 8 | 10 | 4.09 | 2.88 | Gautier-Hion & Gautier (1976) |
| <i>Cercopithecus denti</i> | F, R | 4 | 36 | 4.25 | 2.83 | Colyn (1994) |
| <i>Cercopithecus diana</i> | F, R | 4 | 11 | 5.20 | 3.90 | Smith & Jungers (1997) |
| <i>Cercopithecus hamlyni</i> | F, R | 11 | 9 | 5.49 | 3.36 | Smith & Jungers (1997) |
| <i>Cercopithecus lhoesti</i> | F, R | 19 | 50 | 5.97 | 3.45 | Smith & Jungers (1997) |
| <i>Cercopithecus mitis stuhlmanni</i> | F, R | 41 | 94 | 5.85 | 3.93 | Smith & Jungers (1997) |
| <i>Cercopithecus mitis erythrarchus</i> | F, R | 6 | 6 | 9.31 | 4.91 | Smith & Jungers (1997) |
| <i>Cercopithecus neglectus</i> | F, R | W | W | 7.35 | 4.13 | |
| | | 4 | 4 | 7.00 | 3.96 | Gautier-Hion & Gautier (1976) |
| | | 2 | 2 | 8.05 | 4.46 | Napier (1981) |
| <i>Cercopithecus nictitans</i> | F, R | P | P | 6.67 | 4.25 | |
| | | 16 | 9 | 6.61 | 4.22 | Gautier-Hion & Gautier (1976) |
| | | 17 | 21 | 6.73 | 4.28 | Colyn (1994) |
| <i>Cercopithecus petaurista</i> | F, R | 13 | 7 | 4.40 | 2.90 | Smith & Jungers (1997) |
| <i>Cercopithecus pogonias</i> | F, R | W | W | 4.26 | 2.90 | |
| | | 4 | 6 | 4.50 | 3.03 | Gautier-Hion & Gautier (1976) |
| | | 1 | 4 | 3.30 | 2.70 | Colyn (1994) |
| <i>Cercopithecus wolffi</i> | F, R | 13 | 84 | 3.80 | 2.88 | Colyn (1994) |
| <i>Chlorocebus aethiops</i> | F, R | P | P | 4.94 | 3.34 | |
| | | 109 combined | | 4.21 | 2.74 | Anapol <i>et al.</i> (1995) |
| | | 21 | 15 | 5.77 | 3.53 | Bolter & Zihlman (2003) |
| | | 29 | 30 | 5.51 | 4.09 | Smith & Jungers (1997) |
| | | 60 | 90 | 4.26 | 2.98 | Smith & Jungers (1997) |
| <i>Chlorocebus pygerythrus</i> | F, R | P | P | 4.28 | 2.98 | |
| | | 26 | 36 | 4.13 | 2.57 | Turner <i>et al.</i> (1997) |
| | | 12 | 31 | 4.43 | 3.44 | Turner <i>et al.</i> (1997) |
| | | 18 | 15 | 4.33 | 3.15 | Turner <i>et al.</i> (1997) |
| | | 4 | 10 | 4.24 | 2.75 | Turner <i>et al.</i> (1997) |
| <i>Chlorocebus sabaesus</i> | F, R | 61 | 71 | 5.30 | 3.30 | Horrocks (1986) |
| <i>Erythrocebus patas</i> | F, R | 9 | 14 | 12.40 | 6.50 | Smith & Jungers (1997) |
| <i>Lophocebus albigena</i> | F, R | W | W | 7.89 | 6.01 | |
| | | 5 | 6 | 8.98 | 6.40 | Gautier-Hion & Gautier (1976) |
| | | 4 | 6 | 7.65 | 6.50 | Colyn (1994) |
| | | 4 | 4 | 7.34 | 4.93 | Colyn (1994) |
| | | 4 | 3 | 7.31 | 5.67 | Napier (1981) |
| <i>Lophocebus aterrimus</i> | F | 1 | 4 | 7.90 | 5.64 | Colyn (1994) |

| Taxon | Sample | Male Female | | Male | Female | Reference |
|-------------------------------------|--------|-------------|----------|--------------|--------------|--------------------------------|
| | | <i>N</i> | <i>N</i> | mean (kg) | mean (kg) | |
| <i>Macaca arctoides</i> | F | 7 | 3 | 12.20 | 8.40 | Smith & Jungers (1997) |
| <i>Macaca assamensis assamensis</i> | F, R | 16 | 12 | 11.30 | 6.70 | Fooden (1988) |
| <i>Macaca assamensis pelops</i> | F | 5 | 3 | 11.50 | 7.80 | Fooden (1988) |
| <i>Macaca cyclopis</i> | F, R | 7 | 4 | 6.00 | 4.94 | Smith & Jungers (1997) |
| <i>Macaca fascicularis</i> | F, R | P | P | 5.11 | 3.41 | |
| | | 69 | 46 | 5.36 | 3.59 | Smith & Jungers (1997) |
| | | 13 | 14 | 4.85 | 3.22 | MCZ (this study) |
| <i>Macaca fuscata</i> | F, R | 10 | 23 | 10.97 | 8.03 | Smith & Jungers (1997) |
| <i>Macaca maura</i> | F, R | 17 | 4 | 9.72 | 6.05 | Smith & Jungers (1997) |
| <i>Macaca mulatta</i> | F, R | 5 | 6 | 6.99 | 4.94 | Napier (1981) |
| <i>Macaca nemestrina nemestrina</i> | F, R | W | W | 11.2 | 6.59 | |
| | | 3 | 5 | 10.6 | 6.14 | Fooden (1975) |
| | | 5 | 4 | 11.6 | 7.15 | Fooden (1975) |
| <i>Macaca nemestrina leonina</i> | F, R | 4 | 7 | 8.48 | 4.93 | Fooden (1975) |
| <i>Macaca nigra</i> | F | 11 | 3 | 9.89 | 5.47 | Smith & Jungers (1997) |
| <i>Macaca radiata</i> | F, R | 8 | 8 | 6.6 | 3.69 | Hartman (1938) |
| <i>Macaca sinica</i> | F, R | 14 | 26 | 5.66 | 3.3 | Cheverud <i>et al.</i> (1992) |
| <i>Macaca tonkeana</i> | F | 6 | 3 | 14.9 | 9 | Smith & Jungers (1997) |
| <i>Mandrillus sphinx</i> | F, R | 5 | 7 | 34.4 | 12.8 | Setchell <i>et al.</i> (2001) |
| <i>Miopithecus talapoin</i> | F, R | 7 | 9 | 1.38 | 1.12 | Smith & Jungers (1997) |
| <i>Papio anubis</i> | F, R | P | P | 23.0 | 13.3 | |
| | | 177 | 237 | 21.1 | 12.2 | Berger (1972) |
| | | 10 | 39 | 22.79 | 12.26 | Popp (1983) |
| | | 39 | 35 | 21.2 | 11.7 | Phillips-Conroy & Jolly (1981) |
| | | 43 | 26 | 21.46 | 12.54 | Popp (1983) |
| | | 54 | 23 | 27.1 | 14.0 | Popp (1983) |
| | | 18 | 18 | 21.9 | 12.7 | Gest & Siegel (1983) |
| | | 5 | 10 | 22.72 | 15.16 | Eley <i>et al.</i> (1989) |
| | | 9 | 17 | 23.88 | 13.01 | Eley <i>et al.</i> (1989) |
| | | 4 | 9 | 24.80 | 16.07 | Eley <i>et al.</i> (1989) |
| <i>Papio cynocephalus</i> | F, R | P | P | 22.3 | 12.0 | |
| | | 37 | 21 | 21.8 | 12.3 | Smith & Jungers (1997) |
| | | 12 | 11 | 22.32 | 11.65 | UTA (this study) |
| | | 5 | 5 | 22.8 | 11.9 | Popp (1983) |
| <i>Papio hamadryas</i> | F, R | P | P | 18.0 | 10.3 | |
| | | 41 | 39 | 16.9 | 9.9 | Smith & Jungers (1997) |
| | | 15 | 24 | 16.18 | 9.73 | Popp (1983) |
| <i>Papio ursinus</i> | F, R | 7 | 13 | 21.0 | 11.4 | Smith & Jungers (1997) |
| | | 28 | 22 | 29.8 | 14.8 | Smith & Jungers (1997) |
| <i>Theropithecus gelada</i> | F, R | 5 | 8 | 19.0 | 11.7 | Smith & Jungers (1997) |

| Taxon | Sample | Male <i>N</i> | Female <i>N</i> | Male mean (kg) | Female mean (kg) | Reference |
|--|--------|------------------|--------------------|----------------------|------------------------|----------------------------|
| Colobinae | | | | | | |
| <i>Colobus angolensis</i> | F, R | P | P | 9.71 | 7.59 | |
| | | 4 | 6 | 9.8 | 7.4 | Oates <i>et al.</i> (1994) |
| | | 8 | 5 | 9.62 | 7.77 | Colyn (1994) |
| <i>Colobus guereza guereza</i> | F | 3 | 4 | 13.5 | 9.2 | Smith & Jungers (1997) |
| <i>Colobus guereza matschiei</i> | F, R | 13 | 14 | 9.89 | 7.9 | Smith & Jungers (1997) |
| <i>Colobus polykomos</i> | F, R | 5 | 10 | 9.9 | 8.3 | Smith & Jungers (1997) |
| <i>Colobus satanas</i> | F, R | 5 | 5 | 10.4 | 7.42 | Smith & Jungers (1997) |
| <i>Colobus vellerosus</i> | F | 3 | 5 | 8.5 | 6.9 | Smith & Jungers (1997) |
| <i>Nasalis larvatus</i> | F, R | 6 | 10 | 21.02 | 10.48 | MCZ (this study) |
| <i>Ptilocolobus badius badius</i> | F, R | 9 | 14 | 8.3 | 8.2 | Oates <i>et al.</i> (1990) |
| <i>Ptilocolobus badius rufomitratu</i> | F | 3 | 7 | 9.67 | 7.21 | Smith & Jungers (1997) |
| <i>Presbytis comata</i> | F, R | 4 | 6 | 6.68 | 6.71 | Smith & Jungers (1997) |
| <i>Presbytis femoralis</i> | F, R | 23 | 18 | 6.26 | 6.19 | Smith & Jungers (1997) |
| <i>Presbytis hosei</i> | F | 7 | 3 | 6.18 | 5.63 | Smith & Jungers (1997) |
| <i>Presbytis melalophos</i> | F, R | 11 | 12 | 6.59 | 6.47 | Smith & Jungers (1997) |
| <i>Presbytis potenziani</i> | F, R | W | W | 6.31 | 6.40 | |
| | | 7 | 2 | 6.14 | 6.41 | Brandon-Jones (1993) |
| | | 6 | 4 | 6.5 | 6.4 | Tilson & Tenaza (1976) |
| <i>Presbytis rubicunda</i> | F, R | P | P | 6.26 | 6.11 | |
| | | 16 | 14 | 6.22 | 6.04 | MCZ (this study) |
| | | 35 | 38 | 6.29 | 6.17 | Smith & Jungers (1997) |
| <i>Presbytis thomasi</i> | F | 3 | 5 | 6.77 | 6.69 | Smith & Jungers (1997) |
| <i>Procolobus verus</i> | F, R | 20 | 14 | 4.7 | 4.2 | Smith & Jungers (1997) |
| <i>Pygathrix nemaus</i> | F | 2 | 1 | 11.0 | 8.18 | Smith & Jungers (1997) |
| <i>Rhinopithecus roxellana</i> | F, R | 7 | 4 | 17.9 | 11.6 | Smith & Jungers (1997) |
| <i>Semnopithecus entellus entellus</i> | F, R | 9 | 11 | 13.0 | 9.89 | Smith & Jungers (1997) |
| <i>Semnopithecus entellus schistacea</i> | F, R | 5 | 9 | 19.2 | 14.8 | Smith & Jungers (1997) |
| <i>Semnopithecus entellus thersites</i> | F, R | 14 | 11 | 11.4 | 6.91 | Smith & Jungers (1997) |
| <i>Simias concolor</i> | F | 3 | 3 | 9.15 | 6.80 | Napier (1985) |
| <i>Trachypithecus cristatus</i> | F, R | 11 | 19 | 6.72 | 5.78 | MCZ (this study) |
| <i>Trachypithecus francoisi</i> | F | 3 | 2 | 7.70 | 7.35 | Smith & Jungers (1997) |
| <i>Trachypithecus geei</i> | F | 4 | 1 | 10.8 | 9.5 | Smith & Jungers (1997) |
| <i>Trachypithecus johnii</i> | F | 7 | 3 | 12.0 | 11.2 | Smith & Jungers (1997) |
| <i>Trachypithecus obscurus</i> | F, R | 7 | 8 | 7.77 | 6.22 | Fooden (1971) |
| <i>Trachypithecus phayrei</i> | F, R | 8 | 5 | 7.93 | 6.95 | Napier (1985) |
| <i>Trachypithecus pileatus</i> | F, R | 7 | 5 | 12.0 | 9.86 | Smith & Jungers (1997) |
| <i>Trachypithecus vetulus</i> | F | 3 | 3 | 8.17 | 5.90 | Smith & Jungers (1997) |

| Taxon | Sample | Male <i>N</i> | Female <i>N</i> | Male mean (kg) | Female mean (kg) | Reference |
|--------------------------------------|--------|------------------|--------------------|----------------------|------------------------|-------------------------|
| Hylobatidae | | | | | | |
| <i>Hylobates agilis albibarbis</i> | F, R | 5 | 5 | 5.71 | 6.30 | Geissmann (1993) |
| <i>Hylobates agilis unko</i> | F, R | 12 | 4 | 5.85 | 5.55 | Geissmann (1993) |
| <i>Hylobates concolor</i> | F, R | 7 | 13 | 7.77 | 7.62 | Geissmann (1993) |
| <i>Hylobates hoolock</i> | F, R | 13 | 5 | 6.87 | 6.88 | Smith & Jungers (1997) |
| <i>Hylobates klossii</i> | F | 2 | 4 | 5.67 | 5.89 | Smith & Jungers (1997) |
| <i>Hylobates lar lar</i> | F | 2 | 2 | 5.56 | 4.65 | Geissmann (1993) |
| <i>Hylobates lar carpenteri</i> | F, R | 33 | 24 | 5.92 | 5.36 | MCZ (this study) |
| <i>Hylobates lar entelloides</i> | F, R | P | P | 6.44 | 5.77 | |
| | | 8 | 6 | 5.65 | 4.89 | Geissmann (1993) |
| | | 11 | 3 | 7.23 | 6.65 | Geissmann (1993) |
| <i>Hylobates lar vestitus</i> | F | 5 | 3 | 5.01 | 5.25 | Geissmann (1993) |
| <i>Hylobates leucogenys</i> | F | 6 | 2 | 7.27 | 7.65 | Geissmann (1993) |
| <i>Hylobates moloch</i> | F | 1 | 1 | 6.58 | 6.25 | Smith & Jungers (1997) |
| <i>Hylobates muelleri muelleri</i> | F, R | 5 | 7 | 5.44 | 5.27 | Geissmann (1993) |
| <i>Hylobates muelleri abbotti</i> | F | 5 | 3 | 6.28 | 5.82 | Geissmann (1993) |
| <i>Hylobates muelleri funereus</i> | F, R | W | W | 5.66 | 5.16 | |
| | | 6 | 3 | 5.63 | 5.37 | Geissmann (1993) |
| | | 2 | 4 | 5.75 | 5.01 | Geissmann (1993) |
| <i>Hylobates pileatus</i> | F | 1 | 1 | 5.50 | 5.44 | Smith & Jungers (1997) |
| <i>Hylobates syndactylus</i> | F, R | P | P | 11.79 | 10.70 | |
| | | 7 | 10 | 11.88 | 10.71 | Smith & Jungers (1997) |
| | | 5 | 7 | 11.70 | 10.68 | Geissmann (1993) |
| Hominidae | | | | | | |
| <i>Gorilla gorilla</i> | R | W | W | 169.3 | 75.7 | |
| <i>Gorilla gorilla gorilla</i> | F | 10 | 3 | 170.4 | 71.5 | Smith & Jungers (1997) |
| <i>Gorilla gorilla graueri</i> | F | 4 | 2 | 175.2 | 71.0 | Smith & Jungers (1997) |
| <i>Gorilla gorilla beringei</i> | F | 5 | 1 | 162.5 | 97.5 | Smith & Jungers (1997) |
| <i>Homo sapiens</i> | F, R | P | P | 57.4 | 49.7 | |
| | | 49 | 49 | 53.9 | 45.8 | Smith & Jungers (1997) |
| | | 121 | 162 | 60.2 | 53.6 | Smith & Jungers (1997) |
| | | 194 | 193 | 58.1 | 49.7 | Smith & Jungers (1997) |
| <i>Pan paniscus</i> | F, R | 7 | 6 | 45.0 | 33.2 | Smith & Jungers (1997) |
| <i>Pan troglodytes schweinfurthi</i> | F, R | W | W | 41.4 | 33.1 | |
| | | 9 | 6 | 39.5 | 29.8 | Wrangham & Smuts (1980) |
| | | 6 | 8 | 42.0 | 35.2 | Uehara & Nishida (1987) |
| | | 3 | 9 | 42.8 | 34.3 | Uehara & Nishida (1987) |
| <i>Pan troglodytes troglodytes</i> | F, R | W | W | 59.7 | 45.8 | |
| | | 3 | 3 | 60.0 | 47.4 | Jungers & Susman (1984) |
| | | 2 | 1 | 59.3 | 41.0 | Smith & Jungers (1997) |
| <i>Pan troglodytes verus</i> | F | 1 | 3 | 46.3 | 41.6 | Smith & Jungers (1997) |

| Taxon | Sample | Male <i>N</i> | Female <i>N</i> | Male mean (kg) | Female mean (kg) | Reference |
|--------------------------------|--------|------------------|--------------------|----------------------|------------------------|------------------------|
| <i>Pongo pygmaeus abelli</i> | F | 3 | 4 | 77.9 | 35.6 | Smith & Jungers (1997) |
| <i>Pongo pygmaeus pygmaeus</i> | F, R | 7 | 13 | 78.5 | 35.8 | Smith & Jungers (1997) |

Table 3.1. Male and female mean body mass data used in this study.

Abbreviations: F, full data sample; R, reduced data sample; W, weighted mean of sex-specific population values; P, unweighted mean of sex-specific population values; AMNH, American Museum of Natural History; MCZ, Museum of Comparative Zoology (Harvard University); UTA, University of Texas at Austin.

| Full Sample | Traditional OLS | | | | PGLS Best Branches | | | | PGLS Divergence Dates | | | | PGLS Equal Bra | | | | |
|--------------|-----------------|-----------|--------|--------|--------------------|--------|--------|-----------|-----------------------|---------|-----------|--------|----------------|-----------|-------|--------|----------------|
| | N | Slope | p | SE | r ² | Slope | p | SE | r ² | Slope | p | SE | r ² | Slope | p | SE | r ² |
| Primates | 221 | 0.078* | <0.001 | 0.0088 | 0.262 | 0.001 | 0.984 | 0.0245 | 0.000 | -0.048 | 0.110 | 0.0301 | 0.012 | 0.033 | 0.102 | 0.0199 | 0.012 |
| Strepsirhini | 49 | -0.004 | 0.737 | 0.0125 | 0.002 | -0.006 | 0.793 | 0.0222 | 0.001 | -0.025 | 0.350 | 0.0260 | 0.019 | -0.020 | 0.434 | 0.0259 | 0.013 |
| Haplorhini | 172 | 0.087* | <0.001 | 0.0119 | 0.241 | 0.011 | 0.754 | 0.0354 | 0.001 | -0.063 | 0.135 | 0.0418 | 0.013 | 0.072* | 0.009 | 0.0270 | 0.040 |
| Platyrrhini | 64 | 0.067* | <0.001 | 0.0165 | 0.209 | 0.013 | 0.684 | 0.0321 | 0.003 | -0.079* | 0.050 | 0.0396 | 0.060 | 0.027 | 0.462 | 0.0366 | 0.009 |
| Catarrhini | 104 | 0.062* | 0.042 | 0.0303 | 0.040 | 0.028 | 0.582 | 0.0510 | 0.003 | -0.066 | 0.251 | 0.0569 | 0.013 | 0.096* | 0.041 | 0.0463 | 0.040 |
| Group | N | Intercept | p | SE | Intercept | p | SE | Intercept | p | SE | Intercept | p | SE | Intercept | p | SE | p |
| Primates | 221 | 0.054* | <0.001 | 0.0066 | 0.052 | 0.476 | 0.0727 | 0.046 | 0.795 | 0.1764 | 0.055 | 0.207 | 0.0432 | 0.016 | 0.667 | 0.0364 | 0.0364 |
| Strepsirhini | 49 | 0.012 | 0.142 | 0.0080 | 0.017 | 0.522 | 0.0268 | 0.012 | 0.891 | 0.0846 | 0.084 | 0.059 | 0.0443 | 0.084 | 0.059 | 0.0443 | 0.0443 |
| Haplorhini | 172 | 0.055* | <0.001 | 0.0093 | 0.076 | 0.376 | 0.0859 | 0.082 | 0.691 | 0.206 | 0.069 | 0.107 | 0.0423 | 0.045 | 0.110 | 0.0279 | 0.0279 |
| Platyrrhini | 64 | 0.036* | <0.001 | 0.0079 | 0.057* | 0.009 | 0.0211 | 0.069 | 0.107 | 0.0423 | 0.045 | 0.110 | 0.0279 | 0.045 | 0.110 | 0.0279 | 0.0279 |
| Catarrhini | 104 | 0.087* | 0.002 | 0.0278 | 0.120 | 0.213 | 0.0962 | 0.226 | 0.303 | 0.218 | 0.069 | 0.318 | 0.0691 | 0.069 | 0.318 | 0.0691 | 0.0691 |

| Reduced Sample | Traditional OLS | | | | PGLS Best Branches | | | | PGLS Divergence Dates | | | | PGLS Equal Bra | | | | |
|----------------|-----------------|-----------|--------|--------|--------------------|-------|--------|-----------|-----------------------|--------|-----------|--------|----------------|-----------|--------|--------|----------------|
| | N | Slope | p | SE | r ² | Slope | p | SE | r ² | Slope | p | SE | r ² | Slope | p | SE | r ² |
| Primates | 157 | 0.075* | <0.001 | 0.0104 | 0.250 | 0.031 | 0.181 | 0.0231 | 0.012 | -0.017 | 0.537 | 0.0277 | 0.002 | 0.061* | 0.002 | 0.0192 | 0.061 |
| Strepsirhini | 33 | -0.010 | 0.315 | 0.0100 | 0.033 | 0.005 | 0.764 | 0.0151 | 0.003 | 0.007 | 0.678 | 0.0177 | 0.006 | 0.001 | 0.978 | 0.0179 | 0.000 |
| Haplorhini | 124 | 0.081* | <0.001 | 0.0141 | 0.212 | 0.047 | 0.162 | 0.0335 | 0.016 | -0.033 | 0.403 | 0.0389 | 0.006 | 0.093* | <0.001 | 0.0256 | 0.098 |
| Platyrrhini | 48 | 0.053* | 0.006 | 0.0185 | 0.153 | 0.018 | 0.553 | 0.0300 | 0.008 | -0.039 | 0.262 | 0.0340 | 0.027 | 0.030 | 0.386 | 0.0343 | 0.016 |
| Catarrhini | 73 | 0.039 | 0.279 | 0.0362 | 0.016 | 0.080 | 0.124 | 0.0513 | 0.033 | -0.037 | 0.503 | 0.0546 | 0.006 | 0.155* | 0.001 | 0.0454 | 0.142 |
| Group | N | Intercept | p | SE | Intercept | p | SE | Intercept | p | SE | Intercept | p | SE | Intercept | p | SE | p |
| Primates | 157 | 0.058* | <0.001 | 0.0077 | 0.049 | 0.421 | 0.0608 | 0.045 | 0.747 | 0.139 | 0.057 | 0.127 | 0.0372 | 0.009 | 0.676 | 0.0207 | 0.0207 |
| Strepsirhini | 33 | 0.001 | 0.868 | 0.0069 | 0.003 | 0.873 | 0.0167 | 0.003 | 0.956 | 0.0505 | 0.086 | 0.598 | 0.163 | 0.094* | 0.019 | 0.0398 | 0.0398 |
| Haplorhini | 124 | 0.064* | <0.001 | 0.0107 | 0.078 | 0.286 | 0.0728 | 0.064 | 0.059 | 0.0331 | 0.051* | 0.049 | 0.0254 | 0.051* | 0.049 | 0.0254 | 0.0254 |
| Platyrrhini | 48 | 0.040* | <0.001 | 0.0091 | 0.057* | 0.004 | 0.0190 | 0.064 | 0.059 | 0.0331 | 0.051* | 0.049 | 0.0254 | 0.051* | 0.049 | 0.0254 | 0.0254 |
| Catarrhini | 73 | 0.113* | <0.001 | 0.0320 | 0.069 | 0.439 | 0.0887 | 0.199 | 0.267 | 0.178 | -0.001 | 0.985 | 0.0652 | -0.001 | 0.985 | 0.0652 | 0.0652 |

Table 3.2. Ordinary least squares (OLS) and phylogenetic least squares (PGLS) regression parameters and standard errors (SE) for interspecific regressions of $\log_{10}[M/F]$ against $\log_{10}[F]$.

Note that PGLS regression parameters are identical to the independent contrast (IC) regression parameters for this analysis when IC slopes are situated in raw data space by passing regression lines through the reconstructed value of the base node. Probabilities correspond to $H_0 = 0$. * indicates significant difference from H_0 at $\alpha = 0.05$.

| Group | Branch Lengths | Age | Full Sample | | | | | Reduced Sample | | | | |
|--------------|----------------|-----|-------------|---------|----------|--------|-----------------------|----------------|---------|----------|--------|-----------------------|
| | | | <i>N</i> | Slope | <i>p</i> | SE | <i>r</i> ² | <i>N</i> | Slope | <i>p</i> | SE | <i>r</i> ² |
| Primates | BB | A | 58 | 0.102* | 0.002 | 0.0312 | 0.159 | 49 | 0.076* | 0.015 | 0.0301 | 0.117 |
| | | R | 162 | -0.121* | 0.001 | 0.0349 | 0.069 | 107 | -0.042 | 0.247 | 0.0361 | 0.013 |
| | DD | A | 58 | 0.154* | < 0.001 | 0.0395 | 0.211 | 49 | 0.063 | 0.051 | 0.0316 | 0.077 |
| | | R | 162 | -0.155* | < 0.001 | 0.0373 | 0.097 | 107 | -0.072 | 0.067 | 0.0389 | 0.031 |
| | EB | A | 58 | 0.083* | 0.003 | 0.0267 | 0.145 | 49 | 0.087* | 0.003 | 0.0280 | 0.168 |
| | | R | 162 | -0.088* | 0.009 | 0.0332 | 0.042 | 107 | -0.035 | 0.303 | 0.0338 | 0.010 |
| Strepsirhini | BB | A | 20 | 0.011 | 0.588 | 0.0195 | 0.016 | 15 | 0.009 | 0.629 | 0.0186 | 0.017 |
| | | R | 28 | -0.056 | 0.277 | 0.0501 | 0.044 | 17 | -0.015 | 0.641 | 0.0314 | 0.014 |
| | DD | A | 20 | 0.018 | 0.313 | 0.0178 | 0.053 | 15 | 0.016 | 0.405 | 0.0190 | 0.050 |
| | | R | 28 | -0.064 | 0.156 | 0.0440 | 0.073 | 17 | -0.004 | 0.902 | 0.0315 | 0.001 |
| | EB | A | 20 | -0.008 | 0.667 | 0.0193 | 0.010 | 15 | 0.006 | 0.796 | 0.0209 | 0.005 |
| | | R | 28 | -0.043 | 0.426 | 0.0534 | 0.024 | 17 | -0.013 | 0.726 | 0.0372 | 0.008 |
| Haplorhini | BB | A | 37 | 0.186* | 0.001 | 0.0499 | 0.279 | 33 | 0.128* | 0.011 | 0.0474 | 0.185 |
| | | R | 134 | -0.154* | 0.001 | 0.0453 | 0.080 | 90 | -0.058 | 0.229 | 0.0477 | 0.016 |
| | DD | A | 37 | 0.301* | < 0.001 | 0.0618 | 0.397 | 33 | 0.116* | 0.038 | 0.0537 | 0.127 |
| | | R | 134 | -0.193* | < 0.001 | 0.0468 | 0.113 | 90 | -0.097* | 0.049 | 0.0488 | 0.043 |
| | EB | A | 37 | 0.142* | 0.001 | 0.0386 | 0.272 | 33 | 0.128* | 0.002 | 0.0389 | 0.255 |
| | | R | 134 | -0.134* | 0.004 | 0.0455 | 0.061 | 90 | -0.049 | 0.283 | 0.0457 | 0.013 |
| Platyrrhini | BB | A | 13 | 0.063 | 0.179 | 0.0445 | 0.145 | 12 | 0.057 | 0.211 | 0.0433 | 0.138 |
| | | R | 50 | -0.178* | 0.004 | 0.0589 | 0.158 | 35 | -0.168* | 0.004 | 0.0537 | 0.224 |
| | DD | A | 13 | 0.067 | 0.149 | 0.0436 | 0.165 | 12 | 0.064 | 0.160 | 0.0423 | 0.171 |
| | | R | 50 | -0.193* | < 0.001 | 0.0506 | 0.229 | 35 | -0.157* | 0.001 | 0.0434 | 0.278 |
| | EB | A | 13 | 0.089 | 0.054 | 0.0417 | 0.275 | 12 | 0.084 | 0.060 | 0.0403 | 0.285 |
| | | R | 50 | -0.207* | 0.005 | 0.0712 | 0.147 | 35 | -0.228* | 0.001 | 0.0657 | 0.261 |
| Catarrhini | BB | A | 22 | 0.286* | 0.002 | 0.0795 | 0.382 | 19 | 0.205* | 0.025 | 0.0836 | 0.251 |
| | | R | 81 | -0.137* | 0.023 | 0.0593 | 0.063 | 53 | -0.030 | 0.647 | 0.0643 | 0.004 |
| | DD | A | 22 | 0.394* | < 0.001 | 0.0864 | 0.498 | 19 | 0.142 | 0.113 | 0.0855 | 0.134 |
| | | R | 81 | -0.193* | 0.002 | 0.0616 | 0.109 | 53 | -0.092 | 0.167 | 0.0657 | 0.036 |
| | EB | A | 22 | 0.260* | 0.002 | 0.0737 | 0.371 | 19 | 0.243* | 0.005 | 0.0768 | 0.356 |
| | | R | 81 | -0.116 | 0.051 | 0.0585 | 0.047 | 53 | 0.002 | 0.972 | 0.0593 | 0.000 |

Table 3.3a. Regressions of $\log_{10}[M/F]$ contrasts against $\log_{10}[F]$ contrasts.

Contrasts are separated into recent (within genera) and ancient (between genera and higher taxonomic groups). Abbreviations are as follows: BB, best branches; DD, divergence dates; EB, equal branch lengths; A, ancient contrasts; R, recent contrasts. Regressions are constrained to intercept the y-axis at zero. Probabilities for slopes correspond to $H_0 = 0$. * indicates significant difference from H_0 at $\alpha = 0.05$.

| Group | Branch Lengths | Age | Full Sample | | | | | Reduced Sample | | | | |
|------------|----------------|-----|-------------|---------|----------|--------|-----------------------|----------------|--------|----------|--------|-----------------------|
| | | | <i>N</i> | Slope | <i>p</i> | SE | <i>r</i> ² | <i>N</i> | Slope | <i>p</i> | SE | <i>r</i> ² |
| Primates | BB | R | 161 | -0.080* | 0.028 | 0.0362 | 0.030 | 106 | 0.043 | 0.224 | 0.0352 | 0.014 |
| | DD | R | 161 | -0.092* | 0.023 | 0.0400 | 0.032 | 106 | 0.072 | 0.064 | 0.0386 | 0.032 |
| | EB | R | 161 | -0.068* | 0.044 | 0.0336 | 0.025 | 106 | 0.008 | 0.813 | 0.0332 | 0.001 |
| Haplorhini | BB | R | 133 | -0.092 | 0.062 | 0.0489 | 0.026 | 89 | 0.084 | 0.090 | 0.0489 | 0.032 |
| | DD | R | 133 | -0.108* | 0.045 | 0.0532 | 0.030 | 89 | 0.120* | 0.024 | 0.0520 | 0.057 |
| | EB | R | 133 | -0.097* | 0.043 | 0.0476 | 0.031 | 89 | 0.025 | 0.596 | 0.0465 | 0.003 |
| Catarrhini | BB | R | 80 | -0.069 | 0.282 | 0.0641 | 0.015 | 52 | 0.132* | 0.047 | 0.0650 | 0.075 |
| | DD | R | 80 | -0.097 | 0.175 | 0.0712 | 0.023 | 52 | 0.163* | 0.024 | 0.0701 | 0.096 |
| | EB | R | 80 | -0.066 | 0.292 | 0.0617 | 0.014 | 52 | 0.116* | 0.050 | 0.0579 | 0.073 |

Table 3.3b. Regressions of $\log_{10}[\text{M}/\text{F}]$ contrasts against $\log_{10}[\text{F}]$ contrasts for recent contrasts with "artificial" *Semnopithecus entellus* contrast removed.

Abbreviations are as in Table 4.2. Regressions are constrained to intercept the y-axis at zero. Probabilities for slopes correspond to $H_0 = 0$. * indicates significant difference from H_0 at $\alpha = 0.05$.

| Full Sample | | PGLS Best Branches | | | | PGLS Divergence Dates | | | | PGLS Equal Branch Lengths | | | |
|----------------|------------------|-------------------------------|-------|-------------------------------|-------|-------------------------------|-------|-------------------------------|-------|-------------------------------|-------|-------------------------------|-------|
| | | log ₁₀ [M] (kg) | SE | log ₁₀ [F] (kg) | SE | log ₁₀ [M] (kg) | SE | log ₁₀ [F] (kg) | SE | log ₁₀ [M] (kg) | SE | log ₁₀ [F] (kg) | SE |
| GMM | Description | | | | | | | | | | | | |
| | LCA Primates | -0.037 | 0.212 | -0.089 | 0.200 | -0.063 | 0.415 | -0.115 | 0.395 | -0.209 | 0.156 | -0.256 | 0.145 |
| | LCA Strepsirhini | -0.204 | 0.252 | -0.238 | 0.237 | -0.236 | 0.506 | -0.268 | 0.481 | -0.257 | 0.175 | -0.291 | 0.163 |
| | LCA Haplorhini | 0.044 | 0.222 | -0.017 | 0.209 | 0.021 | 0.439 | -0.040 | 0.417 | -0.161 | 0.175 | -0.220 | 0.163 |
| | LCA Anthropoidea | 0.321 | 0.259 | 0.244 | 0.244 | 0.338 | 0.521 | 0.258 | 0.496 | 0.271 | 0.213 | 0.187 | 0.198 |
| | LCA Platyrrhini | 0.266 | 0.292 | 0.197 | 0.274 | 0.266 | 0.587 | 0.198 | 0.559 | 0.220 | 0.256 | 0.155 | 0.238 |
| AVM: 50g | LCA Catarrhini | 0.823 | 0.319 | 0.705 | 0.300 | 0.885 | 0.642 | 0.760 | 0.611 | 0.754 | 0.255 | 0.626 | 0.237 |
| | LCA Primates | -1.301 | - | -1.301 | - | -1.301 | - | -1.301 | - | -1.301 | - | -1.301 | - |
| | LCA Strepsirhini | -0.742 | 0.272 | -0.754 | 0.256 | -0.692 | 0.516 | -0.705 | 0.491 | -0.779 | 0.194 | -0.791 | 0.181 |
| | LCA Haplorhini | -0.791 | 0.239 | -0.817 | 0.226 | -0.746 | 0.447 | -0.776 | 0.426 | -0.699 | 0.194 | -0.735 | 0.181 |
| | LCA Anthropoidea | -0.076 | 0.280 | -0.137 | 0.263 | 0.004 | 0.531 | -0.062 | 0.506 | 0.010 | 0.235 | -0.063 | 0.220 |
| | LCA Platyrrhini | 0.056 | 0.314 | -0.004 | 0.296 | 0.106 | 0.599 | 0.044 | 0.570 | 0.099 | 0.283 | 0.039 | 0.264 |
| AVM: 100g | LCA Catarrhini | 0.646 | 0.344 | 0.535 | 0.324 | 0.755 | 0.655 | 0.635 | 0.623 | 0.629 | 0.282 | 0.507 | 0.263 |
| | LCA Primates | -1.000 | - | -1.000 | - | -1.000 | - | -1.000 | - | -1.000 | - | -1.000 | - |
| | LCA Strepsirhini | -0.614 | 0.264 | -0.626 | 0.248 | -0.581 | 0.512 | -0.594 | 0.487 | -0.635 | 0.185 | -0.647 | 0.173 |
| | LCA Haplorhini | -0.592 | 0.232 | -0.619 | 0.218 | -0.560 | 0.444 | -0.589 | 0.422 | -0.551 | 0.185 | -0.587 | 0.173 |
| | LCA Anthropoidea | 0.018 | 0.271 | -0.042 | 0.255 | 0.085 | 0.527 | 0.020 | 0.501 | 0.082 | 0.225 | 0.009 | 0.209 |
| | LCA Platyrrhini | 0.106 | 0.305 | 0.046 | 0.287 | 0.145 | 0.594 | 0.083 | 0.565 | 0.132 | 0.270 | 0.072 | 0.252 |
| AVM: 250g | LCA Catarrhini | 0.688 | 0.334 | 0.577 | 0.314 | 0.787 | 0.649 | 0.667 | 0.618 | 0.663 | 0.269 | 0.541 | 0.251 |
| | LCA Primates | -0.602 | - | -0.602 | - | -0.602 | - | -0.602 | - | -0.602 | - | -0.602 | - |
| | LCA Strepsirhini | -0.445 | 0.256 | -0.456 | 0.240 | -0.434 | 0.508 | -0.447 | 0.483 | -0.445 | 0.178 | -0.457 | 0.165 |
| | LCA Haplorhini | -0.330 | 0.226 | -0.356 | 0.212 | -0.313 | 0.440 | -0.342 | 0.419 | -0.355 | 0.178 | -0.391 | 0.165 |
| | LCA Anthropoidea | 0.144 | 0.264 | 0.083 | 0.247 | 0.193 | 0.523 | 0.127 | 0.497 | 0.177 | 0.216 | 0.104 | 0.200 |
| | LCA Platyrrhini | 0.172 | 0.296 | 0.112 | 0.278 | 0.196 | 0.590 | 0.135 | 0.561 | 0.176 | 0.259 | 0.116 | 0.241 |
| AVM: 500g | LCA Catarrhini | 0.744 | 0.325 | 0.633 | 0.305 | 0.829 | 0.644 | 0.709 | 0.613 | 0.709 | 0.258 | 0.587 | 0.240 |
| | LCA Primates | -0.301 | - | -0.301 | - | -0.301 | - | -0.301 | - | -0.301 | - | -0.301 | - |
| | LCA Strepsirhini | -0.317 | 0.253 | -0.328 | 0.237 | -0.323 | 0.506 | -0.336 | 0.482 | -0.301 | 0.175 | -0.313 | 0.163 |
| | LCA Haplorhini | -0.131 | 0.223 | -0.157 | 0.209 | -0.126 | 0.439 | -0.155 | 0.417 | -0.207 | 0.175 | -0.243 | 0.163 |
| | LCA Anthropoidea | 0.238 | 0.260 | 0.177 | 0.244 | 0.274 | 0.521 | 0.208 | 0.496 | 0.249 | 0.213 | 0.176 | 0.198 |
| | LCA Platyrrhini | 0.222 | 0.293 | 0.162 | 0.275 | 0.235 | 0.588 | 0.174 | 0.559 | 0.210 | 0.256 | 0.150 | 0.238 |
| LCA Catarrhini | 0.786 | 0.321 | 0.675 | 0.301 | 0.860 | 0.642 | 0.740 | 0.611 | 0.744 | 0.255 | 0.621 | 0.237 | |

Table 3.4a. Reconstructed values for primate ancestral nodes: Full sample.

Abbreviations are as follows: GMM, grand mean method; AVM, assigned value method; LCA, last common ancestor. Values after AVM indicate the constraint for the size of the last common ancestor of all primates in the analysis. Note that the "reconstructed" value of the basal primate does not have a standard error under the AVM method.

| Reduced Sample | | PGLS Best Branches | | | PGLS Divergence Dates | | | PGLS Equal Branch Lengths | | | | | |
|-----------------------|------------------|-------------------------------|-------|-------------------------------|-----------------------|-------------------------------|-------|-------------------------------|-------|-------------------------------|-------|--------|-------|
| Method | Description | log ₁₀ [M] (kg) | SE | log ₁₀ [F] (kg) | SE | log ₁₀ [M] (kg) | SE | log ₁₀ [F] (kg) | SE | log ₁₀ [F] (kg) | SE | | |
| GMM | LCA Primates | -0.018 | 0.226 | -0.065 | 0.211 | -0.046 | 0.417 | -0.092 | 0.401 | -0.186 | 0.167 | -0.229 | 0.153 |
| | LCA Strepsirhini | -0.175 | 0.266 | -0.196 | 0.249 | -0.208 | 0.508 | -0.226 | 0.487 | -0.231 | 0.187 | -0.256 | 0.172 |
| | LCA Haplorhini | 0.057 | 0.236 | -0.002 | 0.220 | 0.033 | 0.441 | -0.027 | 0.423 | -0.141 | 0.187 | -0.201 | 0.172 |
| | LCA Anthropoidea | 0.325 | 0.274 | 0.247 | 0.256 | 0.341 | 0.523 | 0.260 | 0.502 | 0.279 | 0.226 | 0.195 | 0.208 |
| | LCA Platyrrhini | 0.261 | 0.308 | 0.192 | 0.288 | 0.261 | 0.589 | 0.192 | 0.565 | 0.227 | 0.271 | 0.158 | 0.249 |
| | LCA Catarrhini | 0.828 | 0.337 | 0.707 | 0.315 | 0.891 | 0.644 | 0.763 | 0.618 | 0.751 | 0.271 | 0.628 | 0.249 |
| AVM: 50g | LCA Primates | -1.301 | - | -1.301 | - | -1.301 | - | -1.301 | - | -1.301 | - | -1.301 | - |
| | LCA Strepsirhini | -0.740 | 0.293 | -0.740 | 0.275 | -0.683 | 0.522 | -0.683 | 0.501 | -0.776 | 0.212 | -0.780 | 0.197 |
| | LCA Haplorhini | -0.792 | 0.259 | -0.820 | 0.243 | -0.746 | 0.454 | -0.777 | 0.435 | -0.696 | 0.212 | -0.735 | 0.197 |
| | LCA Anthropoidea | -0.082 | 0.301 | -0.144 | 0.283 | 0.001 | 0.538 | -0.067 | 0.516 | 0.006 | 0.257 | -0.068 | 0.238 |
| | LCA Platyrrhini | 0.045 | 0.338 | -0.017 | 0.318 | 0.097 | 0.606 | 0.034 | 0.582 | 0.095 | 0.307 | 0.031 | 0.285 |
| | LCA Catarrhini | 0.646 | 0.370 | 0.532 | 0.348 | 0.758 | 0.662 | 0.635 | 0.636 | 0.618 | 0.307 | 0.500 | 0.285 |
| AVM: 100g | LCA Primates | -1.000 | - | -1.000 | - | -1.000 | - | -1.000 | - | -1.000 | - | -1.000 | - |
| | LCA Strepsirhini | -0.607 | 0.282 | -0.607 | 0.264 | -0.569 | 0.516 | -0.569 | 0.495 | -0.629 | 0.201 | -0.633 | 0.185 |
| | LCA Haplorhini | -0.592 | 0.250 | -0.621 | 0.234 | -0.559 | 0.448 | -0.591 | 0.430 | -0.546 | 0.201 | -0.585 | 0.185 |
| | LCA Anthropoidea | 0.014 | 0.290 | -0.049 | 0.272 | 0.082 | 0.532 | 0.015 | 0.510 | 0.080 | 0.243 | 0.006 | 0.224 |
| | LCA Platyrrhini | 0.095 | 0.326 | 0.034 | 0.305 | 0.137 | 0.599 | 0.073 | 0.575 | 0.131 | 0.291 | 0.067 | 0.268 |
| | LCA Catarrhini | 0.689 | 0.357 | 0.574 | 0.334 | 0.790 | 0.654 | 0.667 | 0.628 | 0.654 | 0.290 | 0.536 | 0.268 |
| AVM: 250g | LCA Primates | -0.602 | - | -0.602 | - | -0.602 | - | -0.602 | - | -0.602 | - | -0.602 | - |
| | LCA Strepsirhini | -0.432 | 0.272 | -0.432 | 0.254 | -0.418 | 0.511 | -0.418 | 0.490 | -0.434 | 0.191 | -0.439 | 0.175 |
| | LCA Haplorhini | -0.329 | 0.241 | -0.357 | 0.225 | -0.312 | 0.443 | -0.343 | 0.425 | -0.348 | 0.191 | -0.387 | 0.175 |
| | LCA Anthropoidea | 0.140 | 0.280 | 0.077 | 0.262 | 0.190 | 0.526 | 0.122 | 0.505 | 0.177 | 0.231 | 0.103 | 0.212 |
| | LCA Platyrrhini | 0.163 | 0.314 | 0.101 | 0.294 | 0.189 | 0.592 | 0.126 | 0.568 | 0.178 | 0.276 | 0.114 | 0.254 |
| | LCA Catarrhini | 0.745 | 0.344 | 0.631 | 0.321 | 0.832 | 0.647 | 0.709 | 0.621 | 0.701 | 0.276 | 0.583 | 0.253 |
| AVM: 500g | LCA Primates | -0.301 | - | -0.301 | - | -0.301 | - | -0.301 | - | -0.301 | - | -0.301 | - |
| | LCA Strepsirhini | -0.299 | 0.268 | -0.300 | 0.250 | -0.305 | 0.508 | -0.305 | 0.488 | -0.287 | 0.187 | -0.292 | 0.172 |
| | LCA Haplorhini | -0.130 | 0.237 | -0.158 | 0.221 | -0.125 | 0.441 | -0.156 | 0.424 | -0.198 | 0.187 | -0.237 | 0.172 |
| | LCA Anthropoidea | 0.235 | 0.276 | 0.172 | 0.257 | 0.272 | 0.523 | 0.204 | 0.502 | 0.251 | 0.227 | 0.177 | 0.208 |
| | LCA Platyrrhini | 0.214 | 0.309 | 0.152 | 0.289 | 0.228 | 0.590 | 0.165 | 0.566 | 0.213 | 0.271 | 0.149 | 0.249 |
| | LCA Catarrhini | 0.788 | 0.339 | 0.673 | 0.316 | 0.864 | 0.644 | 0.741 | 0.618 | 0.737 | 0.271 | 0.619 | 0.249 |

Table 3.4b. Reconstructed values for primate ancestral nodes: Reduced sample.

Abbreviations are as in Table 3.4a.

| Method | Branch Lengths | Full Sample | | | Reduced Sample | | |
|-----------|----------------|-------------|-------|---------|----------------|-------|---------|
| | | Slope | SE | p-value | Slope | SE | p-value |
| GMM | BB | 0.086 | 0.010 | 0.001 | 0.100 | 0.015 | 0.003 |
| | DD | 0.087 | 0.012 | 0.002 | 0.096 | 0.016 | 0.004 |
| | EB | 0.086 | 0.020 | 0.012 | 0.080 | 0.023 | 0.024 |
| AVM: 50g | BB | 0.052 | 0.009 | 0.005 | 0.050 | 0.013 | 0.017 |
| | DD | 0.054 | 0.010 | 0.007 | 0.051 | 0.014 | 0.020 |
| | EB | 0.057 | 0.013 | 0.012 | 0.052 | 0.014 | 0.020 |
| AVM: 100g | BB | 0.064 | 0.009 | 0.002 | 0.062 | 0.013 | 0.008 |
| | DD | 0.066 | 0.010 | 0.002 | 0.064 | 0.014 | 0.010 |
| | EB | 0.071 | 0.014 | 0.006 | 0.065 | 0.015 | 0.012 |
| AVM: 250g | BB | 0.088 | 0.005 | < 0.001 | 0.087 | 0.011 | 0.001 |
| | DD | 0.090 | 0.008 | < 0.001 | 0.090 | 0.011 | 0.001 |
| | EB | 0.095 | 0.016 | 0.004 | 0.087 | 0.018 | 0.008 |
| AVM: 500g | BB | 0.109 | 0.014 | 0.002 | 0.111 | 0.013 | 0.001 |
| | DD | 0.107 | 0.017 | 0.003 | 0.112 | 0.013 | 0.001 |
| | EB | 0.106 | 0.029 | 0.020 | 0.099 | 0.028 | 0.024 |

Table 3.5. Regressions of change in $\log_{10}[M/F]$ against $\log_{10}[F]$ for six reconstructed ancestral primate nodes.

Method abbreviations follow Table 2.4. Branch length abbreviations follow Table 2.3. Regressions are constrained to intercept the y-axis at zero. Probabilities for slopes correspond to $H_0 = 0$. Note that all regression slopes are significantly greater than one at $\alpha = 0.05$.

Chapter 4: Relative Influence of Body Size and Sexual Selection Proxies on Sexual Size Dimorphism in Primates

INTRODUCTION

Primates exhibit a large range of body size and sexual size dimorphism (SSD). Body size dimorphism in primates is generally thought to be the product of sexual selection (*e.g.*, Clutton-Brock *et al.*, 1977; Gaulin & Sailer, 1984; Clutton-Brock, 1985; Rodman & Mitani, 1987; Ford, 1994; Martin *et al.*, 1994; Mitani *et al.*, 1996; Plavcan & van Schaik, 1997b; Lindenfors & Tullberg, 1998; Plavcan, 1999; Barton, 2000; 2001). The relationship between SSD and sexual selection is of particular interest to anthropologists because of the potential to infer social and/or mating behaviors of extinct primates based on body size dimorphism in the fossil record (*e.g.*, Wolpoff, 1976; Schroder, 1993; McHenry, 1994a; Kappelman, 1996; Plavcan & van Schaik, 1997a; Plavcan, 2002; Reno *et al.*, 2003). However, a number of studies have also shown that SSD scales positively with body size in primates, particularly within haplorhines (Clutton-Brock *et al.*, 1977; Leutenegger, 1978; Leutenegger & Cheverud, 1982; Gaulin & Sailer, 1984; Kappeler, 1990; Ford, 1994; Martin *et al.*, 1994; Abouheif & Fairbairn, 1997; Plavcan & van Schaik, 1997b; Smith & Cheverud, 2002).

A persistent question for studies of primate dimorphism is whether or not it is appropriate to correct for the effects of body size on SSD before investigating the relationship between SSD and other variables. Several studies of primate dimorphism have applied size corrections to SSD (Ford, 1994; Martin *et al.*, 1994; Mitani *et al.*, 1996; Plavcan & van Schaik, 1997b). Some researchers have noted that there is no compelling theoretical reason to expect that SSD should scale with size (Reiss, 1986; Fairbairn, 1997; Smith & Cheverud, 2002) and point out that size and dimorphism might both

increase in response to some third factor, in which case “correcting” for body size actually removes important variation in SSD (Smith & Cheverud, 2002; Plavcan, in press).

Body size correction is only called for if SSD changes as a direct consequence of change in body size. To determine whether or not this occurs we may consider the relationship between size and SSD once sexual selection is taken into account. Consider four hypothetical relationships shown in [Figure 4.1](#). Each species is assigned to one of three groups in which the intensity of sexual selection is low, intermediate, or high. In agreement with previous findings regarding SSD in primates, in all four cases SSD scales positively with body size when sexual selection is ignored, and mean SSD increases with intensity of sexual selection when body size is ignored. However, the three variables have distinctly different relationships in these four hypothetical cases.

In the first three cases, positive scaling of SSD with size persists when analyzed within taxa experiencing similar levels of sexual selection. The relationship between size and SSD may exhibit positive scaling unmodified by selection levels (*e.g.*, case **A**), positive scaling modified by the intensity of sexual selection (*e.g.*, case **B**), or scaling patterns that vary by selection intensity (*e.g.*, case **C**). Scaling relationships in any of the three cases may represent (1) effect of body size on SSD, in which case a size correction is appropriate; (2) effect of SSD on body size, in which case a size correction is *not* appropriate; or (3) effect of some third variable on body size and SSD, in which case a size correction is also *not* appropriate. Therefore size correction may or may not be appropriate for cases **A**, **B**, and **C**. However, in case **D** there is no relationship between size and dimorphism once sexual selection has been taken into account, and thus size is shown not to have a direct effect on SSD. In such a case it is not appropriate to “correct” for size, as any such correction will inevitably remove relevant variation from the SSD

variable. If SSD does not scale with size in primates once sexual selection intensity has been taken into account then size corrections should not be applied to measures of dimorphism, although it is not necessarily true that a correction should be applied if scaling persists.

The best way to identify groups that have similar levels of selection intensity remains an open question. A simple categorical variable that is available for most primate species and which should be correlated with male reproductive skew distinguishes between monogamous and polygynous taxa, then further divides polygynous taxa into multi-male and uni-male species (Harvey *et al.*, 1978; Lindenfors, 2002). This variable has been used to represent male-male competition levels in previous primate studies (*e.g.*, Harvey *et al.*, 1978; Barton, 2000; Plavcan, 2001; Lindenfors, 2002). If mating system is a good proxy for sexual selection then it is particularly useful because mating system data is available for most primate species.

However, mating system has several drawbacks as a proxy for sexual selection. For example, many strepsirhines social systems fall along a continuum from pair-bonded to dispersed, which may not match neatly with haplorhine categories (Kappeler, 1997a; Dixson, 1998). Also, a significant proportion of populations within the same species can use different mating systems (*e.g.*, lemurs, Kappeler, 2000a; red colobus monkeys, Struhsaker, 2000; mountain gorillas, Robbins, 1999). Mating systems also fail to distinguish between groups in which males are highly competitive for access to reproductive females and groups where they are not; incorporating this extra information into categorical analyses has shown male competition levels to be associated with dimorphism in primates (Plavcan & van Schaik, 1992; 1997b; Plavcan, 1999; 2002). Although competition data is available for many primate species, it is not as widely available as mating system data.

Continuous variables have also been suggested as proxies for sexual selection. Mitani *et al.*'s (1996) restatement of Emlen and Oring's (1977) operational sex ratio accounts for many factors that influence male reproductive skew: average number of males and females in groups, mating season duration, female estrous cycle duration, number of estrous cycles females have before conceiving, and length of interbirth intervals. Unfortunately, much of this information is not available for most primate species. Operational sex ratios also fail to take into account whether females cycle together or separately, which affects males' ability to monopolize reproductive encounters and thus affects selection pressures on male size. The information required for Clutton-Brock *et al.*'s (1977) socionomic sex ratio (average number of males and females in groups) is more readily available, but it fails to distinguish between groups in which one male monopolizes access to reproductive females and groups where multiple males have such access.

All of the variables proposed above act primarily as proxies for the effects of male competition and neglect the effects of female choice. Although male competition is thought to be a more significant force than female choice in mammals in general (Brown, 1975) and haplorhines in particular (Plavcan, 2001), testing that assertion requires some measure of female choice. Plavcan (in press) has suggested a binary variable in which female choice is determined to either reinforce or counteract the effects of male competition; however, comparative studies of SSD that incorporate such a variable (or any other measure of female choice) have yet to be published.

In addition to social variables that are more or less directly related to male competition, ecological variables have been proposed to influence SSD in primates. For example, terrestrial primates have been shown to be more dimorphic on average than arboreal ones (Clutton-Brock *et al.*, 1977; Leutenegger & Kelly, 1977; Plavcan & van

Schaik, 1997b). Thus dimorphism may be facilitated by terrestriality, inhibited by arboreality, or some combination thereof; the effect of substrate on dimorphism is usually thought to exist because of a relationship between substrate and body size or substrate and predation pressure, which has been suggested to select for large males to defend against predators (Clutton-Brock *et al.*, 1977; Leutenegger & Kelly, 1977; Andersson, 1994). Predation pressure is difficult to incorporate into large comparative analyses as a separate variable because it is highly variable in space and time and thus not usually available for the same populations that published size data are drawn from. In addition, it is unclear why females would not also benefit from large body size if it confers an advantage against predation.

The present study has two primary goals. The first goal is to determine whether a size correction for SSD is appropriate in comparative studies of primate dimorphism. The second goal is to identify the most important variables in accounting for the variance in primate body size dimorphism.

SAMPLE AND METHODS

Sample

When building samples for broad comparative studies, there are two competing objectives: represent as many taxa as possible, and restrict sample inclusion to reliable data. While exclusionary data sets may be more reliable in terms of the accuracy of mass measurements, they often have built in biases. For example, body mass measurements for a large number of wild primates are much less likely to be available for small solitary cryptic nocturnal species than for larger-bodied, group living diurnal species. Because phylogenetic comparative analyses are particularly sensitive to differences in sample membership ([Chapter 2](#)), I analyze two data sets in this study: a full data set in which

taxonomic inclusion is maximized, and a reduced data set which includes only taxa with body mass measurements from at least 4 individuals of each sex (Table 4.1).

In most cases species are the basic taxonomic unit of consideration (*i.e.*, one mean is calculated for all populations of a species), although subspecies are treated as separate taxa when sample sizes meet the reduced data set criteria and sex-specific means differ considerably between subspecies. The full sample is composed of 221 taxa representing 194 species in the Order Primates, including 29 Lemuroidea, 15 Lorisioidea, 4 Tarsioidea, 61 Ceboidea, 70 Cercopithecoidea, and 15 Hominoidea. The reduced sample is made up of 157 taxa representing 143 species in the Order Primates, including 19 Lemuroidea, 10 Lorisioidea, 3 Tarsioidea, 47 Ceboidea, 53 Cercopithecoidea, and 11 Hominoidea.

Methods

Measuring Size, Dimorphism, Sexual Selection, and Substrates

SSD in this study is measured as $\log_{10}[M/F]$, where M is mean male mass and F is mean female mass. Body size is measured as $\log_{10}[F]$. Published and unpublished sex-specific body mass means were gathered for 221 primate taxa (Table 4.1). Because mean body size varies between populations, species means are calculated as the mean of population averages when all constituent populations have at least 4 members of each sex (denoted by the letter P in Table 4.1). When all populations do not meet that criterion, species means are calculated as a weighted mean of each population average with the number of individuals as weights (denoted by the letter W in Table 4.1).

Smith and Jungers' (1997) compilation of primate body mass data serves as the source for much of the mass data in Table 4.1. I also draw mass data from other published sources as well as unpublished data generously shared with me by field workers in Madagascar. Eric Delson supplied museum numbers and body mass data from a recent review of size in extant and extinct cercopithecoids (Delson *et al.*, 2000)

that are used to calculate sex-specific means for geographically distinct populations identified in the *Catalogue of Primates in the British Museum (Natural History) and Elsewhere in the British Isles* (Napier, 1981; 1985). In general, mass data from wild populations and large populations are preferred over data from captive and small populations, but means from captive and/or small groups are included if no other data are available for a particular primate species. Because I prefer to give equal weight to populations rather than individuals, population means are reported separately within [Table 4.1](#) whenever possible.

Three mating systems are used to approximate sexual selection intensities in this study: monogamous (*Mon*); multi-male, multi-female (*MM*); and uni-male, multi-female (*UM*). Taxa in these categories are expected to have low, medium, and high levels of sexual selection, respectively. I also note taxa in which polyandry is reported to occur ([Table 4.1](#)). Polyandrous taxa are included with *Mon* taxa in categorical analyses. There are also several species in [Table 4.1](#) for which both *UM* and *MM* groups are known. In those cases a decision must be made as to which category they belong to for categorical analyses. Any taxon that has some uni-male populations is placed in the *UM* category for two reasons. First, the presence of even a few uni-male groups in a taxon should provide more opportunities for pronounced male reproductive skew than are present in taxa with exclusively multi-male groups. Second, number of taxa in each category tends to be more equal in each of the data sets in this study when mixed mating system taxa are placed in *UM* rather than *MM*.

Mating system data is drawn from a variety of sources, particularly Kappeler's (2000b) edited volume on primate group composition, Lindenfors and Tullberg's (1998) analysis of sexual selection in Primates, and Dixson's (1998) book on primate sexuality.

I note in [Table 4.1](#) if taxa have populations that fall into more than one of these categories, and also those taxa where polyandry is reported to occur.

Data on substrate use is taken from *Walker's Primates of the World* (Nowak, 1999) as well as Nunn and van Schaik's (2002) comparative study of primate socioecology. Previous studies have classified primate substrate use in one variable with three categories: completely arboreal, mixed use arboreal/terrestrial, and primarily terrestrial (Plavcan & van Schaik, 1992; Plavcan *et al.*, 1995; 1997b). Because dimorphism may be related to arboreality or terrestriality, I instead use two substrate variables: one in which species that spend substantial amounts of time in the trees are designated as arboreal, and another in which species that spend substantial amounts of time on the ground are designated as terrestrial. Thus some species may be designated as arboreal for the first variable but terrestrial for the second, and so the relative influence of each substrate can be tested. These two variables are referred to as arboreality and terrestriality, respectively.

Traditional Linear Models: ANCOVA, ANOVA, and Regression

Linear models allow researchers to distinguish between the different types of relationships between size, dimorphism, and sexual selection present in [Figure 4.1](#). An analysis of covariance (ANCOVA) tests three null hypotheses: (1) that regression slopes are not significantly different between categories (H_0^1), (2) that the common slope for all categories is not different from zero (H_0^2), and (3) that the intercepts are not significantly different between categories (H_0^3). In this study, ANCOVA are performed with SSD as the dependent variable, body size as a continuous independent variable, and mating system as a categorical independent variable. If slopes differ significantly between categories or differ significantly from zero, a separate ordinary least squares (OLS) regression of SSD against female body size is performed for each mating system and

results are compared. In addition, an analysis of variance (ANOVA) is performed to determine whether mean SSD differs between mating systems.

Linear models are also used to evaluate the relative significance of mating system, body size, and substrate in accounting for variance in SSD. Residual sums of squares are calculated for a series of linear models containing all possible combinations of these independent variables so that F-tests can be used to determine the relative importance of each independent variable.

Phylogeny

In studying the relationship between body size, dimorphism, and mating system, one must recognize the importance of phylogeny. Evolutionary relationships between species affect comparative analyses in two main ways. First, scaling patterns may differ between major clades. For example, many researchers believe that there are basic differences in the relationship between social interactions and size dimorphism in strepsirhines and haplorhines (*e.g.*, Kappeler, 1990; Godfrey *et al.*, 1993; van Schaik & Kappeler, 1996; Leigh & Terranova, 1998; Plavcan, 2001; Smith & Cheverud, 2002). Second, closely related taxa may share similar values for dependent and independent variables because of shared evolutionary history rather than due to a functional relationship between variables.

In order to address the first phylogenetic concern, I follow Smith and Cheverud (2002) in analyzing major primate clades separately. I first consider relationships within Primates as a whole, then analyze Strepsirhini and Haplorhini separately, and finally analyze Platyrrhini and Catarrhini individually. To address the second phylogenetic concern I supplement traditional linear models with analyses of phylogenetic linear models, discussed further below.

The various phylogenetic analyses of this study are conducted using a branching sequence and divergence dates based on Purvis' (1995; 1999) composite primate phylogeny, which is a “supertree” compiled from many published phylogenies for various primate taxa. The Purvis supertree is modified through a series of stages to produce the set of trees used in this study ([Appendix D](#)). NEXUS code is available for the complete supertree ([Appendix E](#)).

Although it is hoped that the phylogenetic branching sequence used here is an accurate representation of the ancestral-descendant relationships within primates, there are likely to be some errors in the topology. A number of studies have shown that results of phylogenetic methods are not compromised by some inaccuracies in branching sequence and branch length (Martins & Garland, 1991; Martins, 1996b; Diaz-Uriarte & Garland, 1998; Martins & Housworth, 2002). It has been suggested that in absence of knowledge of the true phylogeny, analyses should be performed on a large number of random trees (Martins, 1996a), and that partial knowledge of phylogenies can be used to constrain random trees so that random branching sequences are generated only for the unknown portion of the phylogeny (Housworth & Martins, 2001). However, Symonds (2002) found that random trees do a particularly poor job of estimating the actual evolutionary correlation between characters. Recently it has been suggested that correlation parameters can be calculated by weighting random trees by the probability that they are correct using Bayesian inference to determine tree weights (Huelsenback & Rannala, 2003). Theoretical concerns aside, a recent study of the relationship between competition levels and SSD in primates found that results were not significantly altered when branches were swapped (Plavcan, in press). The tree for the present study is well resolved, and what few inaccuracies in branching sequence exist are unlikely to affect the results of phylogenetic analyses.

Three methods are used to set branch lengths for the primate tree. They are as follows.

Divergence Dates. Under a gradualistic model of character evolution, the amount of evolutionary change within a lineage is expected to be correlated with time (as a proxy for number of generations). Purvis (1995) provides estimates of divergence dates for various nodes in his supertree using arithmetic means and medians of divergence dates gathered from the various trees he samples to construct the composite phylogeny. When available, Purvis' mean dates are used to assign dates to divergences in the tree used for the present study. However, many divergences are not dated or are resolved differently here than in Purvis' original supertree (Purvis, 1995).

Divergences between subspecies in this study are arbitrarily assigned branch lengths of 0.25 myr unless otherwise noted. In the case of polytomies in the original Purvis (1995) supertree that are resolved, here the first divergence and last divergence of taxa included within the Purvis polytomy are arbitrarily separated by 2 million years (myr) for divergences occurring between 10 and 20 million years ago (mya), 1 myr for divergences between 5 and 10 mya, and 0.5 myr for divergences between 1 and 5 mya. Previously resolved relationships that are now polytomies are dated using a weighted mean of the divergence dates given for the original divergences in Purvis (1995). Weights are the number of trees used to calculate the mean dates for the Purvis supertree. When a divergence date is unavailable for a particular group of species and those species are considered one species by some authorities, an arbitrary divergence date of 1 mya is imposed. When dates are unavailable for other divergences, one of two methods is used. Grafen's (1989) method based on species diversity can be used to scale branch lengths between nodes of known age and tips. In some cases the resulting dates will disagree with younger divergence dates reported in Purvis (1995), or with information from the

fossil record. In those cases divergence dates for the undated nodes will be assigned as occurring at half the time from the last dated divergence to the present.

Equal Branch Lengths. Several previous studies of sexual size dimorphism (SSD) in primates have set all branch lengths equal to one (*e.g.*, Mitani *et al.*, 1996; Plavcan & van Schaik, 1997b; Lindenfors & Tullberg, 1998; Smith & Cheverud, 2002). This procedure has been argued to represent a punctuated equilibrium model of character evolution because each speciation event is expected to produce an equal amount of change (Mitani *et al.*, 1996; Lindenfors & Tullberg, 1998). However, Smith and Cheverud (2002) point out that a true punctuated equilibrium model would only allow change along one branch of a divergence. Equal branch length models allow change to occur along both branches, and thus do not accurately represent punctuated equilibrium (Smith & Cheverud, 2002). Equal branch lengths are used here so that results may be compared between this study and other studies that have used equal branch lengths. Divergences between subspecies are arbitrarily assigned branch lengths of one-half.

Best Branches. Garland *et al.* (1992) state that independent contrast analyses should only be performed with trees in which the absolute value of standardized contrasts are not significantly correlated with their standard deviations. Correlations are significant at $\alpha = 0.05$ for all trees in this analysis with the exception of the reduced Platyrrhini tree based on divergence dates. I use Grafen's (1989) ρ transform to modify branch lengths such that absolute values of standardized contrasts and their standard deviations are uncorrelated. This method scales the height of the entire tree to one, then transforms the height of each node (*i.e.*, the distance between the node and terminal taxa) by raising it to the user-selected positive exponent ρ . Values for ρ are as follows (values are the same for full and reduced data sets): Primates, 0.69; Strepsirhini, 0.38; Haplorhini, 0.69; Platyrrhini, 0.50; Catarrhini, 0.62.

Phylogenetic Generalized Linear Model (PGLM)

In addition to traditional linear models, this study also employs phylogenetic linear models. Taxa may be similar in size, mating system, and/or dimorphism because of a functional relationship between variables or because of shared evolutionary history; *e.g.*, two closely-related species that are similarly large and dimorphic may be recently descended from a large, dimorphic ancestor. Changes in sexual selection pressures may affect the degree of dimorphism in a species, but they must do so by modifying an existing amount of dimorphism. Consider a highly dimorphic species that undergoes a change from high intensity sexual selection to low intensity sexual selection: even if dimorphism decreases as expected, descendant species may still be more dimorphic than other taxa of similar mating systems that are descended from less dimorphic ancestors. Phylogenetic ANCOVA procedures essentially estimate the change in size, dimorphism, and mating system from the last common ancestors of sister taxa.

The way in which I implement phylogenetic categorical analyses is by extension of Martins and Hansen's (1997) phylogenetic generalized least squares (PGLS) method into a full phylogenetic generalized linear model (PGLM). PGLS analyses work by specifying the covariance matrix for a data set, which is a function of the branching sequence and branch lengths of the sample phylogeny. Here I use the most common evolutionary model, in which the value of a trait at a particular internal node (hypothetical taxonomic unit, or HTU) or tip (operational taxonomic unit, or OTU) is equal to the value of the node directly ancestral to it, plus an error term. Variance of the error term is proportional to branch length between ancestor and descendant, which determines the structure of the covariance matrix (see Rohlf, 2001 for a detailed description of this process).

Application of PGLM analyses is relatively straightforward. Categorical variables are coded as binary dummy variables, just as they would be in traditional generalized linear models. Residual sums of squares for full and reduced models are calculated following Martins and Hansen (1997) and are used to generate F-statistics. For a PGLM ANCOVA, differences between category slopes are tested with the addition and removal of an interaction variable between category and female body size. Difference between the common slope and zero is tested by calculating a t-statistic based on the standard error of the slope (*i.e.*, the standard PGLS procedure). Differences between intercepts are tested by removing the categorical variables from the full model. A PGLM ANOVA simply tests the difference between means using the categorical variables. All PGLM analyses are performed using code written in the programming language *R* (Ihaka & Gentleman, 1996) ([Appendix F](#)). This code performs traditional analyses at the same time as the PGLM analyses using the same algorithm (except that the scaled variance matrix for traditional analyses is the identity matrix); results for traditional analyses are identical to those generated by SAS version 8.02 (1999).

Interpreting PGLM Results

Slopes, intercepts, means, and confidence intervals for traditional ANCOVA and ANOVA will differ from those for PGLM analyses. In traditional ANCOVA, slopes for each category of the discrete variable (in this case, mating system) are tested for significant difference from each other. This also occurs in the PGLM analysis, although the slopes are phylogenetic slopes. Because PGLS regression parameters for continuous analyses are identical to independent contrasts regressions where the contrast slope is forced to pass through the reconstructed base ancestral state for all characters in an analysis (Garland & Ives, 2000; Rohlf, 2001), the method of independent contrasts can be used to illustrate what a phylogenetic slope is.

Independent contrasts are data points generated by calculating differences in traits ($\log [F]$ and $\log [M/F]$ in this study) between sister taxa – observed taxa in the case of tips, and hypothetical taxa in the case of internal nodes. A bivariate PGLS regression can therefore be thought of as a line passing through reconstructions of the X and Y variables for the last common ancestor of all taxa in the analysis; this line is weighted away from horizontal by the functional relationship between independent and dependent variables in pairs of sister taxa. If size and dimorphism always increase or decrease together, the regression line will take on a significantly positive slope. If one trait always decreases when the other increases, and vice-versa, the line will take on a significantly negative slope. A combination of both patterns will tend to cancel each other out, resulting in a slope that does not significantly differ from zero. In the case of a PGLM ANCOVA, an F-test is performed that tests for significant difference between phylogenetic slopes as calculated for each category. Then the common phylogenetic slope for all mating categories is tested against zero.

When slopes differ significantly between mating categories in a traditional ANCOVA, separate regressions are run for each mating system. In the case of a PGLM analysis, a decision must be made due to the nature of phylogenetic analyses. Separate PGLS regressions can be performed on the complete data set by analyzing each mating system in turn, setting the value of the continuous independent variable to zero for all points not in that mating system, and only using the binary dummy variable for that mating system. This preserves the error structure of the full phylogeny and thus produces slopes that take into account the existence of related taxa in other mating systems. However, confidence intervals and *p*-values are incorrect precisely because the error structure incorporates information from all three mating categories. Reducing degrees of freedom to take into account the number of data points in the mating system under

consideration does not solve the problem, because standard errors that t-tests are based on are a function of the full error structure. The alternative is to remove data points in the other mating systems altogether and perform PGLS regressions on the remaining data. However, this removes important information regarding close relatives who fall into different mating categories, and slopes will vary in ways that are often nonsensical. The approach advocated here is the former, which yields meaningful slopes but unusable p -values. Although a confidence level cannot be applied to these slopes, they are useful for consideration in comparison to traditional OLS slopes.

Interpreting a phylogenetic ANOVA also differs from interpreting a traditional procedure. In traditional ANOVA, standard errors are based on a pooled variance for all categories, but means for each category are independent of the data in other categories. In a PGLM ANOVA, means are not independent among the categories. Just as PGLS regressions consider how two variables change between sister taxa, PGLM ANOVA essentially consider how a continuous variable (log male/female ratio) and a discrete variable (mating system category) change between pairs of taxa.

A PGLM ANOVA procedure can be described as follows. Disregarding categories for the time being, a grand mean and standard error is calculated for the dependent variable (SSD in this case). The grand mean is a mean weighted by the phylogenetic covariance matrix. All categories (in this case, *Mon*, *MM*, and *UM*) begin with the same grand mean and standard error. Next, values for the independent variable are compared for all possible pairs of observed taxa. In some cases both species in a pair will belong to the same category, in which case the difference in the independent variable will affect the standard error for that category. When comparisons are between two taxa of different categories, the difference will affect the means of both categories. For example, if a *Mon* species has lower SSD than a *MM* species, the *Mon* mean will

decrease and the *MM* mean will increase. The amount of change in the means depends on the relatedness of the compared species. Differences between closely related species will affect means more than differences between distantly related taxa because of the expectation of similarity between close relatives. Thus the means produced by phylogenetic ANOVA are phylogenetically weighted means. The important information that PGLM ANOVA provides is the relative ordering of means for all categories involved, as this is an indication of the strength of the relationship between change in continuous variable and change in categorical variable once the phylogeny relating all of the taxa is taken into consideration. Phylogenetically weighted means produced in this way will tend to be similar in overall magnitude to traditional ANOVA means, and 95% confidence intervals will usually include traditional means.

RESULTS

In the reporting of results, all mentions of phylogenetic analyses refer to results using the “best branches” branch lengths unless explicitly noted, although tables report statistics for all three trees. A significance level of $\alpha = 0.05$ is assumed unless otherwise noted. Brief notes regarding degrees of freedom and significant figures in the reporting of results follow below.

Degrees of freedom. In this study, branch lengths are transformed for the “best branches” tree to meet the assumption of no relationship between absolute value of standardized contrasts and standard deviations (Garland *et al.*, 1992; Diaz-Uriarte & Garland, 1996). It has been suggested that the transformation process reduces the degrees of freedom in regression analyses by an additional two (Diaz-Uriarte & Garland, 1996; Diaz-Uriarte & Garland, 1998) or three (Smith & Cheverud, 2002) degrees of freedom. In reporting results of phylogenetic analyses, I choose not to reduce the degrees of freedom for branch transformations so that comparisons of significance between

traditional and phylogenetic analyses are based on the same degrees of freedom. However, I report standard errors for all parameters so that significance tests can be recalculated and new p -values generated with fewer degrees of freedom if so desired. Sample sizes in this study are large enough that a difference of three degrees of freedom will usually not make a difference in significance tests at $\alpha = 0.05$. The smallest sample in this study, the reduced data set for Strepsirhini, has 33 data points. The fewest degrees of freedom for ANCOVA procedures in this study have $N-4$ degrees of freedom. Thus in the analysis with the greatest loss of degrees of freedom in smallest data set, the full degrees of freedom are 29 and the maximally-reduced degrees of freedom are 26, both of which are relatively large values for analyses of this kind.

Significant figures. Because statistics for analyses of female size and dimorphism are more appropriately interpreted in the context of analyses of female size and male size (see [Chapter 2](#)), regression slopes of $\log [M/F]$ against $\log [F]$ should be interpreted as slopes of $\log [M]$ against $\log [F]$ minus one when interpreting how significant figures are used in reporting regression slopes. For example, with three significant figures a slope would be reported as -0.005 rather than -0.00499, since the appropriate slope is actually 0.995 minus 1. For the sake of symmetry, positive slopes are also reported to the third decimal place (*e.g.*, 0.008 rather than 0.01).

Scaling of Body Size, Mating System, and Dimorphism in Primates

Categorical analyses follow in which SSD is dependent on mating system and body size. Categories are as follows: monogamous (*Mon*), multi-male (*MM*), and uni-male (*UM*). Five taxonomic groups are analyzed: Primates, Strepsirhini, Haplorhini, Platyrrhini, and Catarrhini.

All Primates

Slopes for regressions of $\log_{10}[\text{M/F}]$ against $\log_{10}[\text{F}]$ differ significantly between mating categories in primates in full and reduced ANCOVA analyses (Table 4.2). Slopes for *UM* taxa are significantly positive in both data sets; *MM* slope approaches significance in the full data set ($p = 0.095$); *Mon* slopes do not differ significantly from zero in either data set (Table 4.3, Fig. 4.2). ANOVA results show that mean $\log_{10}[\text{M/F}]$ differences are highly significant between mating categories in both data sets; *UM* are highest and *Mon* are lowest in the reduced data set, although the *MM* mean is higher than the *UM* mean in the full data set (Fig. 4.3a, Table 4.4). Thus traditional ANCOVA and ANOVA results support a significant relationship between mating system and size dimorphism in Primates, as well as indicating a positive relationship between size and dimorphism in non-monogamous primates, although not in monogamous taxa.

The PGLM analyses of $\log_{10}[\text{M/F}]$ against $\log_{10}[\text{F}]$ produce mating category slopes that do not differ from each other with a common slope for all mating categories that is not significantly different from zero in either data set (Table 4.2). Mean $\log_{10}[\text{M/F}]$ for *Mon*, *MM*, and *UM* ranks as expected by sexual selection theory for full and reduced data sets (Fig. 4.3b). Differences between means are significant at $\alpha = 0.05$, although not as significant as differences detected by traditional ANOVA (Table 4.4). The PGLM ANOVA results are consistent with a significant relationship between mating system and size dimorphism in primates once phylogeny has been taken into account, although the PGLM ANCOVA does not indicate any relationship between size and dimorphism in non-monogamous primates when phylogeny is considered.

Strepsirhini

Among strepsirhines, slopes for the three mating systems do not differ significantly from each other, and common slopes are extremely close to zero (traditional

ANCOVA analyses for the full and reduced data sets; [Table 4.2](#), [Fig 4.4](#)). A traditional ANOVA of mean $\log_{10}[M/F]$ ranks mating systems as expected by sexual selection theory for the reduced data set, although *Mon* taxa have a higher mean than *MM* taxa in the full data set ([Table 4.4](#)). Differences between means are not significant for the full data set ($p = 0.776$), but are significant for the reduced data set ($p = 0.015$). The mean for *Mon* strepsirhines is particularly low in the reduced data set due to marked reverse dimorphism in *Avahi laniger*. When this species is removed from the analysis, the *Mon* mean for the reduced data set increases to -0.013 and the p -value for difference among the means increases to 0.079 .

Note that the difference in means from the most dimorphic category (*UM*) to the least dimorphic category (*Mon*) in the reduced data set is $0.049 \log_{10}$ units ([Table 4.4](#)). When transformed back to a ratio, the statistically significant difference among means corresponds to uni-male species being 11.9% more dimorphic than monogamous species on average (mean M/F ratios: *Mon* = 0.929, *MM* = 0.991, *UM* = 1.04; see [Fig 4.3a](#)). Despite the statistically significant difference between dimorphism means, the highest mean is not noticeably different from monomorphism (compare the placement of the *UM* mean with respect to the zero line for Strepsirhini in [Figure 4.3a](#) to the position of *UM* and *MM* means for all other taxonomic analyses in that figure). These results indicate a small statistically significant difference between means for mating systems in Strepsirhini, although perhaps not a biologically significant difference.

The PGLM analysis of SSD against size produces mating category slopes that do not differ significantly from each other, and a common slope very close to (and not significantly different from) zero in the full and reduced data sets ([Table 4.2](#)). PGLM analyses of variance show that means for $\log_{10}[M/F]$ rank as expected for full and reduced data sets ([Fig. 4.3b](#)). Differences between means are not significant ([Table 4.4](#)).

The phylogenetic analyses do not provide any support for a relationship between mating system and size dimorphism in Strepsirhini once relatedness between taxa is considered.

Haplorhini

Slopes of $\log_{10}[\text{M}/\text{F}]$ against $\log_{10}[\text{F}]$ differ significantly between the three mating categories in a traditional ANCOVA analysis of the full haplorhine data set, and approach significant difference in the reduced data set ($p = 0.078$) (Table 4.2). In separate regression analyses, slopes for *UM* taxa are significantly positive in both data sets while slopes for *MM* and *Mon* do not differ significantly from zero (Table 4.3, Fig. 4.5). *UM* slopes are leveraged by *Tarsius syrichta* in both data sets; exclusion of this data point yields even higher slopes (full: slope = 0.123, $p = 0.002$, $r^2 = 0.174$; reduced: slope = 0.111, $p = 0.030$, $r^2 = 0.118$). A traditional ANOVA shows that mean dimorphism for mating systems ranks as expected by sexual selection theory, and differences among means are highly significant for both data sets (Fig. 4.3a, Table 4.4). Thus traditional ANOVA and ANCOVA results support a significant relationship between mating system and size dimorphism in Haplorhini, and a positive relationship between size and dimorphism in *UM* taxa.

PGLM slopes of $\log_{10}[\text{M}/\text{F}]$ against $\log_{10}[\text{F}]$ do not differ significantly between mating categories for the full and reduced data set, nor do the common slopes differ significantly from zero (Table 4.2). Means for mating categories rank as expected for full and reduced haplorhine data sets (Fig. 4.3b). Differences between means are significant at $\alpha = 0.05$ in both data sets, but not as significant as differences detected by traditional ANOVA (Table 4.4). PGLM ANOVA results are consistent with a significant relationship between mating system and size dimorphism in Haplorhini once phylogeny has been taken into account, although PGLM ANCOVA does not indicate any

relationship between size and dimorphism in *UM* haplorhines when phylogeny is considered.

Platyrrhini

In Platyrrhini, slopes of $\log_{10}[\text{M}/\text{F}]$ against $\log_{10}[\text{F}]$ do not differ significantly between the three mating categories in traditional ANCOVA analyses of the full and reduced data sets, and the common slope for all mating systems is significantly negative (Table 4.2). Separate regression analyses indicate that in both samples, slopes for *Mon* species are significantly positive, slopes for *MM* species are significantly *negative*, and slopes for *UM* species are positive, but not significantly different from zero (Table 4.3, Fig. 4.6). The positive relationship in monogamous taxa is primarily a product of low dimorphism and small body size in *Cebuella pygmaea*, and relatively high dimorphism and large body size in the two *Pithecia* species. The negative relationship in multi-male taxa is driven by the placement of *Ateles* and *Lagothrix* (and *Brachyteles* in the full data set), which form a clump of *MM* data points in the lower right hand portion of Figure 4.6.

When monogamous platyrrhines are divided into those taxa that exhibit polyandry and those that do not, no regression of SSD against size is significant (full data set: PA slope = 0.048, $p = 0.301$, $r^2 = 0.056$; *Mon* slope = 0.075, $p = 0.270$, $r^2 = 0.086$; reduced data set: PA slope = 0.023, $p = 0.584$, $r^2 = 0.024$; *Mon* slope = 0.111, $p = 0.161$, $r^2 = 0.206$). Regressions for polyandrous taxa have lower slopes and coefficients of determination than regressions for the complete *Mon* sample. Regression slopes are higher for the remaining monogamous platyrrhines, although their coefficients of determination are also lower relative to the complete *Mon* sample. Two-tailed t-tests for full and reduced data sets show that mean $\log_{10}[\text{M}/\text{F}]$ is significantly lower in polyandrous taxa than in other monogamous platyrrhines (full: $p = 0.005$; reduced: $p = 0.002$).

Differences in mean dimorphism between *Mon*, *MM*, and *UM* platyrrhines are highly significant in traditional ANOVA analyses for full and reduced data sets, and means rank as expected by sexual selection theory (Fig. 4.3a, Table 4.4). In Platyrrhini, uni-male species are 33.0% more dimorphic than monogamous species on average (mean M/F ratios for reduced data set: *Mon* = 1.01, *MM* = 1.21, *UM* = 1.35), considerably more different than dimorphism ratios in strepsirhines. These results support a significant relationship between mating system and size dimorphism in platyrrhines.

PGLM analyses of $\log_{10}[M/F]$ against $\log_{10}[F]$ produce mating category slopes that do not differ significantly from each other in either data set; common slope for all mating systems does not differ significantly from zero in the reduced data set, but is significantly negative in the full data set (Table 4.2). Tests for significance of slopes are not appropriate when phylogenetic regressions are partitioned by mating category, but PGLS slopes for *Mon* groups are less positive than traditional slopes (full slope = -0.009, reduced slope = +0.024), *MM* slopes are even more negative than traditional slopes (full slope = -0.150, reduced slope = -0.109), and *UM* slopes are about the same (full slope = +0.287, reduced slope = -0.028). Mating system means for $\log_{10}[M/F]$ rank as expected for full and reduced platyrrhine data sets (Fig. 4.3b). Differences between means are significant at $\alpha = 0.05$ in the full data set, but not as significant as differences detected by traditional ANOVA; differences are not significant in the reduced data set (Table 4.4). Thus the PGLM ANOVA results are generally consistent with a significant relationship between mating system and size dimorphism in Platyrrhini when phylogeny has been taken into account, although weakly so. The phylogenetic analysis also indicates that the positive relationship between size and dimorphism in monomorphic platyrrhines disappears when phylogeny is considered, but the negative relationship

between size and dimorphism in multi-male platyrrhines *increases* with phylogenetic consideration.

Catarrhini

Differences between mating systems for slopes of $\log_{10}[M/F]$ against $\log_{10}[F]$ in Catarrhini approach significance in traditional ANCOVA analyses of the full data set ($p = 0.072$), and the common slope is significantly positive (Table 4.2). The common slope approaches significant difference from zero in the reduced data set ($p = 0.086$). When separate OLS regressions are performed for each mating category, only slopes for *UM* taxa differ significantly from zero; these slopes are significantly positive in both data sets (Table 4.3, Fig. 4.7). However, *UM* slopes are highly leveraged by data from *Gorilla*, *Pongo*, and *Mandrillus*; removal of these data generates negative slopes for *UM* taxa, although not significantly negative (full: slope = -0.086, $p = 0.161$, $r^2 = 0.045$; reduced: slope = -0.051, $p = 0.464$, $r^2 = 0.017$). A traditional ANOVA of $\log_{10}[M/F]$ shows that mating system means do not rank as expected: *MM* species have a higher mean than *UM* species in both data sets, although 95% confidence intervals overlap considerably (Fig. 4.3a). Differences between mating systems are highly significant for both data sets (Table 4.4). Within catarrhines, uni-male species are 40.0% more dimorphic than monogamous species on average, and multi-male species are slightly more dimorphic than uni-male species (mean M/F ratios for reduced data set: *Mon* = 1.04, *MM* = 1.48, *UM* = 1.46). Note that not only is the range of means broader in Catarrhini than in Platyrrhini; means for each mating category are elevated in Catarrhini as compared to Platyrrhini (Fig. 4.3a). These results support a significant relationship between mating system and size dimorphism in catarrhines, although the ordering of *MM* and *UM* means does not follow predictions of sexual selection theory. Also, size dimorphism is shown to scale

positively with body size in *UM* taxa as a result of large body size and high SSD in three genera: *Gorilla*, *Pongo*, and *Mandrillus*.

PGLM analyses of $\log_{10}[\text{M}/\text{F}]$ against $\log_{10}[\text{F}]$ produce mating category slopes for the full and reduced data sets that do not differ significantly from each other, and common slopes that do not differ significantly from zero (Table 4.2). Unlike in traditional analyses, SSD ranks as expected for full and reduced catarrhine data sets in PGLM ANOVA (Fig. 4.3b). Differences between mating systems are significant at $\alpha = 0.05$ in the full data set and approach significance in the reduced data set ($p = 0.068$), but differences are not as significant as those found using traditional ANOVA (Table 4.4). Thus PGLM results are consistent with a significant relationship between mating system and size dimorphism in Catarrhini once phylogeny has been taken into account, and provide a better fit with theoretical expectations regarding the ordering of mean dimorphism among mating systems than do results from traditional analyses. No relationship between size and dimorphism is indicated in *UM* taxa once phylogeny is considered.

Linear Model Generalizations

Residual sums of squares are calculated for all possible linear models in which $\log_{10}[\text{M}/\text{F}]$ is dependent upon one or more of the following variables: $\log_{10}[\text{F}]$, mating system, arboreality, and/or terrestriality (Appendix G). F-tests are performed to determine which independent variables improve model fits better than other independent variables. No correction is made to p -values for the large number of analyses performed because the intention is to evaluate the relative importance of particular variables in linear models and not the significance of particular relationships *per se*. What follows is a generalization of the patterns observed in these comparisons.

For the full primate data set, all variables contribute significantly to traditional linear models, *i.e.*, addition of any independent variable in this study to any linear model yields a significantly better fit for the full Primates data set. In the reduced data set the result is nearly the same, although when arboreality is added to models that already contain terrestriality, the p -value is as high as 0.070. In phylogenetic models for the full data set, the only variable that always significantly improves model fits by its inclusion is mating system. The addition of any variable to body size significantly improves model fits. The addition of terrestriality, while not always improving models significantly, always improves models more than does the addition of arboreality. Results for the reduced data set are much the same, except that p -values are generally slightly higher, and the relative importance of the two substrate variables swaps such that arboreality always improves models more than terrestriality.

For all full strepsirhine linear models, no reduced model is significantly different from any complete model; *i.e.*, no variable or combination of variables in this study contributes significantly more information when added to a linear model for the full Strepsirhini data set. In the reduced data set, only the addition of mating system significantly improves the model, and only for traditional models, not for phylogenetic models.

For the full haplorhine data set, the only cases in which addition of an independent variable does not significantly improve model fits for traditional linear models is when body size is added to a model that already contains mating system and at least one substrate variable. In the reduced data set the same is true; also, the addition of body size to mating system does not produce a significantly better fit than mating system alone. Haplorhine phylogenetic models are quite similar to those for all primates. The only variable that always significantly improves model fits for the full data set is mating

system. The addition of any variable to body size significantly improves model fits. The addition of terrestriality, while not always improving models significantly, always improves models more than does the addition of arboreality. As observed for all primates, results for the reduced Haplorhini data set are much the same as the full data set, except that p -values are generally higher and the relative importance of the two substrate variables swaps such that arboreality always improves models more than terrestriality.

For the full platyrrhine data set, the addition of mating system to any traditional linear model significantly improves the fit, as does the addition of size to terrestriality (which is the only substrate variable for Platyrrhini and contains only one semi-terrestrial platyrrhine, *Lagothrix lagothrica*; the coefficient for this variable is negative rather than positive, counter to the usual observation that SSD increases with terrestriality). In no other case does the model improve by the addition of size or substrate. The same is true for the reduced data set. For phylogenetic linear models of the full data set, the addition of mating system to phylogenetic linear models always significantly improves model fits, but no other variable significantly improves fits when added to phylogenetic models. For the reduced data set, in no case does the addition of any variable significantly improve model fits, although the most significant (or least insignificant) improvements occur with the addition of mating system.

For full and reduced catarrhine data sets, the addition of any variable except size significantly improves model fits for traditional linear models. In no case does the addition of body size significantly improve model fits. Catarrhine phylogenetic models are similar to those for haplorhines and all primates. Mating system is the only variable that always significantly improves phylogenetic model fits for the full data set. The addition of any variable to body size significantly improves model fits. Unlike Primates

and Haplorhini, the two substrate variables have approximately the same influence (usually non-significant) when added to phylogenetic linear models. As observed for haplorhines and all primates, results for the reduced Catarrhini data set are much the same as the full data set, except that p -values are generally higher and the relative importance of the two substrate variables are such that arboreality always improves models more than terrestriality.

In addition, coefficients of determination are calculated for complete linear models for every clade; *i.e.*, models which incorporate all possible independent variables for that clade (Table 4.5). In no case does any traditional model account for more than 56.6% of the variance in SSD. Phylogenetic models are substantially lower, with no model accounting for more than 15.4% of the variance in SSD.

DISCUSSION

The two primary goals of this study are to determine whether a size correction for SSD is appropriate in comparative studies, and to identify the most important variables in accounting for the variance in primate body size dimorphism. The sections below address these two topics in turn.

Size, Mating System, and SSD

Correction for the influence of body size may be appropriate if positive scaling of size and SSD persists within groups of taxa that are expected to have similar levels of dimorphism. However, if no scaling is present within those groups, a correction is unnecessary and would in fact remove important information from consideration in later analyses. Groups subject to similar sexual selection pressures are approximated here by mating systems, and thus the relationship between size and dimorphism within mating systems can address the question of whether or not size correction is appropriate when

analyzing primate dimorphism. In addition, the relationship between mating system and SSD can inform on the role of sexual selection in producing dimorphism in primates.

All Primates

In the Order Primates as a whole there is strong positive scaling of size and dimorphism in *UM* species (as observed using traditional OLS regression), positive scaling approaching significance in *MM* species, and the absence of such scaling in *Mon* species. These patterns result from calculating regressions that essentially run through two large data clusters: Strepsirhini, which are relatively small and low in SSD for all mating systems; and Haplorhini, which are relatively large and more or less dimorphic according to mating system. The marked absence of difference between slopes and similarity of those slopes to zero in phylogenetic ANCOVA for Primates supports this assertion, indicating that size does not scale significantly with dimorphism across Primates once mating system and phylogeny have been taken into account. Although size dimorphism does vary significantly between mating systems in both traditional and phylogenetic analyses, this variable is more appropriately analyzed separately for Strepsirhini and Haplorhini.

Strepsirhini

Very little size dimorphism is present in strepsirhines, and no significant relationship exists between size and SSD in any of the analyses undertaken here. What little relationship there is between mating system and SSD (present only in the traditional ANOVA of the reduced data set) appears to be the product of slight negative dimorphism (females larger than males) in monomorphic species rather than positive dimorphism in polygynous species; this weak relationship disappears once phylogeny is taken into account.

The near-absence of body size dimorphism in Strepsirhini, even in *MM* and *UM* species, indicates that size is probably not a target of sexual selection in these species. Research on strepsirhines suggests that sexual selection may be acting through female mate choice on olfactory cues (Alport & Overdorff, 2002), coloration (Cooper & Hosey, 2003), agility (Kappeler, 1991), or some combination of these characters. Indirect competition between males in the form of sperm competition is also known to be prevalent in strepsirhines (Glander, 1994; 1997c; Kappeler, 1997b; Kraus *et al.*, 1999; Parga, 2003; Johnson *et al.*, in review). When size is not the target of sexual selection, particularly in the form of direct male-male competition, no correlation is expected between mating system and SSD.

Haplorhini

Just as is seen in Primates as a whole, strong positive scaling of size and dimorphism is present in traditional OLS regressions for *UM* Haplorhini. No scaling exists in *Mon* or *MM* species. With regards to positive scaling in *UM* taxa, there are only 4 *UM* platyrrhines in the full data set and 3 in the reduced, all of which plot in the middle of the main cluster of *UM* points in [Figure 4.5](#). The one *UM* tarsier is separated from all other *UM* species by a substantial amount of size and phylogenetic distance. Thus the *UM* pattern is primarily a catarrhine pattern and will be discussed further below. Relationships between size, mating system, and SSD differ considerably between platyrrhines and catarrhines.

Platyrrhini

Platyrrhines exhibit two unexpected patterns in the scaling of size and dimorphism: strong positive scaling in *Mon* species, and strong negative scaling in *MM* species. When *Mon* taxa are divided into those that exhibit polyandry and those that do not, slopes and coefficients of polyandrous taxa drop considerably and are no longer

significant. This result, considered in conjunction with the significant difference in mean dimorphism between polyandrous and non-polyandrous *Mon* taxa, suggest that it is appropriate to include polyandry as a fourth mating system in future analyses. The separation of polyandrous and monogamous species is also consistent with expectations that male choice and female competition may play significant roles in determining selection pressures on female body size for polyandrous taxa (Petrie, 1983; Gwynne, 1991; Parker & Simmons, 1996; Cunninngham & Birkhead, 1998).

Removing polyandrous species leaves remaining *Mon* species with a more positive relationship between size and SSD, although the fit is poorer. This is due to the large size and dimorphism present in *Pithecia* species. Although *Pithecia* has been characterized as monogamous (e.g., Buchanan *et al.*, 1981; Robinson *et al.*, 1987), it is not a typical monogamous primate. For example, social groups containing multiple adults of both sexes are present in *P. pithecia* (Kinzey *et al.*, 1988; Gleason & Norconk, 1995) and *P. hirsuta* (Soini, 1986). Additionally, multiple females may be reproductively active in a single group, and a single male may monopolize all matings even when other males are present (*P. pithecia*, Rosenberger *et al.*, 1996). If *Pithecia* social groups are actually multi-male, multi-female, then saki monkeys are mid-sized, mildly dimorphic *MM* platyrrhines rather than large, highly dimorphic *Mon* platyrrhines (Fig. 4.6), and the strong positive scaling between size and dimorphism in monogamous Platyrrhini disappears. The interpretation of the relationship between size and dimorphism within *Mon* platyrrhines is highly dependent on the uncertain mating system classification of one genus.

The other unexpected pattern in Platyrrhini, the striking negative relationship in *MM* species, is driven by the Atelinae: *Ateles*, *Lagothrix*, and *Brachyteles* (*Brachyteles* appears in the full data set only). This relationship is more negative in phylogenetic

analyses than traditional analyses because the *MM* species most closely related to the atelines are *Alouatta belzebul* and *A. palliate*, both of which are smaller and considerably more dimorphic than all of the Atelinae. Because of this strong negative relationship that persists when phylogeny is considered, it might appear that body size needs to be taken into account when analyzing dimorphism in these platyrrhines. However, mating system is a poor proxy for sexual selection in this case.

Although atelines live in multi-male, multi-female groups, there does not appear to be much competition between males for mating opportunities (*Brachyteles arachnoides* (Milton, 1985b), and females have been observed to mate with several different males over short time periods (*Ateles paniscus*, van Roosmalen & Klein, 1988; *Lagothrix lagotricha*, Nishimura, 1988; *Brachyteles arachnoides*, Milton, 1985a). If body size does not confer an advantage to male reproductive success then SSD is not expected to evolve. In the case of the atelines, mating system almost certainly provides a misleading estimate of reproductive skew. Consideration of competition levels generates predictions more in line with the lack of dimorphism observed in the Atelinae (e.g., Plavcan & van Schaik, 1992; 1997b; Plavcan, 1999; 2002).

Despite the poor job of estimating sexual selection pressures for some taxa, mating systems are generally well correlated with SSD in platyrrhines, highly significantly in traditional analyses of variance but less significantly in phylogenetic categorical analyses. In particular, 95% confidence limits for monogamous platyrrhines include monomorphism in traditional and phylogenetic analyses, while confidence limits for *MM* and *UM* do not (Fig. 4.3 a & b), resulting in a good fit between theoretical expectations and observations regarding the level of dimorphism associated with monogamy and polygyny.

Catarrhini

Catarrhines exhibit pronounced positive scaling of size and SSD in *UM* species. This pattern is responsible for the positive scaling observed in Haplorhini and Primates. However, positive scaling disappears (leaving a non-significantly *negative* slope) if *Mandrillus*, *Pongo*, and *Gorilla* are removed from consideration.

Plavcan (in press) found that SSD is especially large in those taxa where female choice reinforces male-male competition, particularly *Mandrillus*, *Pongo*, *Gorilla*, and *Theropithecus*. When female choice and male competition both select for increased male size, selection pressures on male size should be exceptionally strong. Quantitative genetics models predict that intense selection pressure on male body size should produce not only high dimorphism but also large female body size as a consequence of correlated response (Lande, 1980; Leutenegger & Cheverud, 1982). *Mandrillus*, *Pongo*, and *Gorilla* are not only uncommonly dimorphic, they are also uncommonly large. Thus the significantly positive slope of SSD against body size for *UM* catarrhines results from the inclusion of three genera that have selection intensities on male body size that are expected to be much higher than those of other *UM* catarrhines. In this case, mating system fails to capture the expected increase in SSD and size due to the effect of female choice on selection pressures.

Catarrhine analyses resemble platyrrhine analyses in the following manner: although mating systems are poor estimators of sexual selection pressures for some taxa, mating systems are well correlated with SSD in general. Similarly, 95% confidence limits for *Mon* catarrhines include monomorphism in traditional and phylogenetic analyses, while confidence limits for *MM* and *UM* catarrhines do not (Fig. 4.3 a & b). Although mean dimorphism is lower for *UM* than *MM* species in traditional analyses of variance, the higher value for *UM* species in phylogenetic analyses indicates that *UM*

taxa tend to be more dimorphic than closely related *MM* taxa. Thus there is a good fit between theoretical expectations and observations for SSD in monogamous and polygynous catarrhines.

Summary

Overall, body size is shown to be generally uncorrelated with dimorphism within major radiations when mating system is taken into account. The deviations from this generalization occur when mating system categories do a poor job of estimating the sex-specific differences in selection pressure on body size, either underestimating those pressures (in the case of *Pithecia*, *Mandrillus*, *Pongo*, and *Gorilla*) or overestimating them (as in the case of the Atelinae). These findings indicate that not only is it appropriate to analyze dimorphism without “correcting” for body size, but also that applying such a correction will remove important variation from comparative analyses of SSD.

Within Haplorhini, mating system itself is generally well correlated with dimorphism, and can be considered a reasonable proxy for sexual selection intensity for large comparative studies. In Strepsirhini mating system is poorly associated with SSD. The poor correlation within strepsirhines results from mating system categories being poor estimators of sex-specific selection pressure on body size, probably because body size is not the target of sexual selection in these taxa.

Relative Importance of Independent Variables

Because strepsirhines exhibit such low levels of dimorphism and because linear models in this study generally do not predict strepsirhine dimorphism with any significance, the relative importance of various independent variables in accounting for SSD in Strepsirhini will not be addressed here. Instead, this section will focus on the Haplorhini, which exhibit marked levels of dimorphism.

SSD is slightly higher in polygynous catarrhines than in polygynous platyrrhines, but both clades have similar dimorphism in monogamous species, are similar in the general pattern of significance among the independent variables in this study, and follow the same trends in variable importance as are seen in Haplorhini as a whole. Comparison of traditional and phylogenetic linear models demonstrates that mating system is the most important of the independent variables analyzed in this study when considering SSD in haplorhines. Other variables occasionally improve model fits significantly, but not as much as mating system. Body size is shown to be the weakest predictor of SSD once phylogeny has been taken into account. No clear difference emerges between the two substrate variables, and neither variable contributes much to linear models. The only conclusions that can be drawn regarding substrate variables is that neither terrestriality nor arboreality is particularly important in accounting for variation in SSD, especially once mating system has been taken into account.

Although mating system is the most important variable in this analysis, much of the variance in SSD remains unaccounted for by it. The performance of mating system in this study can be compared to model fits for proxies of sexual selection in other studies. In a traditional analysis of 85 haplorhines, Plavcan (in press) found that male competition levels account for 54.9% of variation in SSD. Mating system only accounts for 39.6% of variation in SSD for the reduced sample of 124 haplorhine species in this study. Clutton-Brock *et al.* (1977) found that socioeconomic sex ratio (SSR) accounted for 37.2% of the variance in SSD for 40 haplorhines and 2 strepsirhines. Using data from Mitani *et al.*'s (1996) study of operational sex ratio (OSR) and SSD in 18 haplorhine species, log OSR accounts for 34.1% of the variance in SSD. The low fits of SSR and OSR data may be due to sampling effects (sample sizes are considerably lower than in the present study and Plavcan's study) or a weaker relationship between sex ratios and SSD. Regardless,

Plavcan's competition levels clearly do a better job than mating system in accounting for variation in haplorhine SSD.

The relatively poor fit of SSR and OSR with SSD when compared to competition levels may be accounted for in part by the failure of either sex ratio to address whether females cycle together or separately, because effectiveness of male competition should be dependent upon males' ability to monopolize reproductive opportunities. Competition levels avoid this problem by simply assessing the degree of male competition rather than attempting to account for the various factors that may influence male competition.

Overall, it is to be expected that of all the variables considered here, male competition levels are the best predictors of SSD in haplorhines. Selection intensity on male body size should be related to the importance of body size in male competitions and female mate selection. If male competition is more important than female choice in determining sexual selection pressures on body size for most haplorhines (Plavcan, 2001), then male competition levels should be better proxies for sexual selection than a mating system variable that does not take male competition into account.

However, even for these best-case predictors (competition levels), nearly half of the variance in haplorhine SSD (45.1%) remains unaccounted for. In this study, the addition of body size, arboreality, and terrestriality as independent variables in traditional analyses only accounted for an additional 15.7% of the variance in haplorhine SSD than mating system alone, and less than half of that amount in phylogenetic analyses. Only 12.6% of the variance in haplorhine SSD is accounted for by all of the variables in the present study when phylogeny is taken into account. By extension, it is likely there is a large portion of the variance of SSD that remains unexplained in haplorhines regardless of whether competition levels, sex ratios, or mating systems are used as proxies for sexual selection, even when body size and substrate use are included as independent

variables. Some of the unexplained variance in mating system and competition level models is likely to be due to differences in sexual selection intensity within categories, and all models will have a certain amount of stochastic variation that will add error. Diet may also influence SSD in haplorhines, although probably only weakly (Plavcan & van Schaik, 1997b). However, there are other likely sources of variation that none of these variables take into account.

Although sexual selection in haplorhines is thought to primarily result from male competition, there are indications that female choice (Small, 1989; van Hooff, 2000; Reeder, 2003) and even female competition and male mate choice (Heymann, 2003) may play a role in some haplorhine taxa. Additionally, a recent investigation into the scaling of size and dimorphism within primates concluded that natural selection in the form of resource limitation probably plays a larger role in producing SSD than previously thought (Chapter 3). Future investigations of the forces producing SSD would benefit from consideration of all possible sources of sex differences in selection intensity on body size. Analyses that incorporate phylogenetic methods into quantitative genetics models have recently been developed (Gordon, 2001). These analyses offer a new way to investigate the effects of differences in sex-specific selection intensity on SSD, regardless of the source of those differences (male competition, female choice, resource limitation, *etc.*). Consideration of such models in conjunction with analyses that distinguish between the various types of differences in selection pressures will allow researchers to better understand the relative importance of different types of sexual selection and natural selection in the generation and maintenance of SSD in primates.

SUMMARY

Positive scaling of size and SSD within Primates as a whole is shown to primarily result from the absence of substantial dimorphism in Strepsirhini and the presence of

marked dimorphism in polygynous Haplorhini. Within haplorhines, scaling patterns between size and dimorphism are the product of phylogenetic similarity and similar degrees of dimorphism within mating system groups; thus few significant scaling patterns for size and dimorphism persist once phylogeny and mating systems are taken into account. The few exceptions to this generalization are due to failures of mating system to approximate the intensity of sexual selection in particular taxa. These findings support the argument that it is unnecessary to “correct” for body size when measuring sexual size dimorphism, and that such corrections are actually inappropriate because they remove variation relevant to studies of SSD and sexual selection.

Mating system is found to be a better predictor of SSD than body size or substrate. Mating system is generally well correlated with size dimorphism, and analyses of mating system and SSD are consistent with sexual selection theoretical predictions. However, mating systems do not always estimate sexual selection pressures well because of variability in male competition levels and female choice within mating system categories. Mating system is a reasonable proxy for sexual selection pressures for broad comparative studies, particularly if polyandrous taxa are distinguished from monogamous taxa, but other variables such as male competition levels are preferable when available. Competition levels are better estimators of SSD because they take into account the degree of competition between males when assigning taxa into groups, and thus are more likely than mating systems to reflect actual levels of sexual selection intensity. However, sex-differences in selection pressures on body size may also be due to female choice and natural selection, and thus new methods that include all potential differences in male and female selection pressures should be considered in conjunction with analyses that use proxies for particular selective forces.

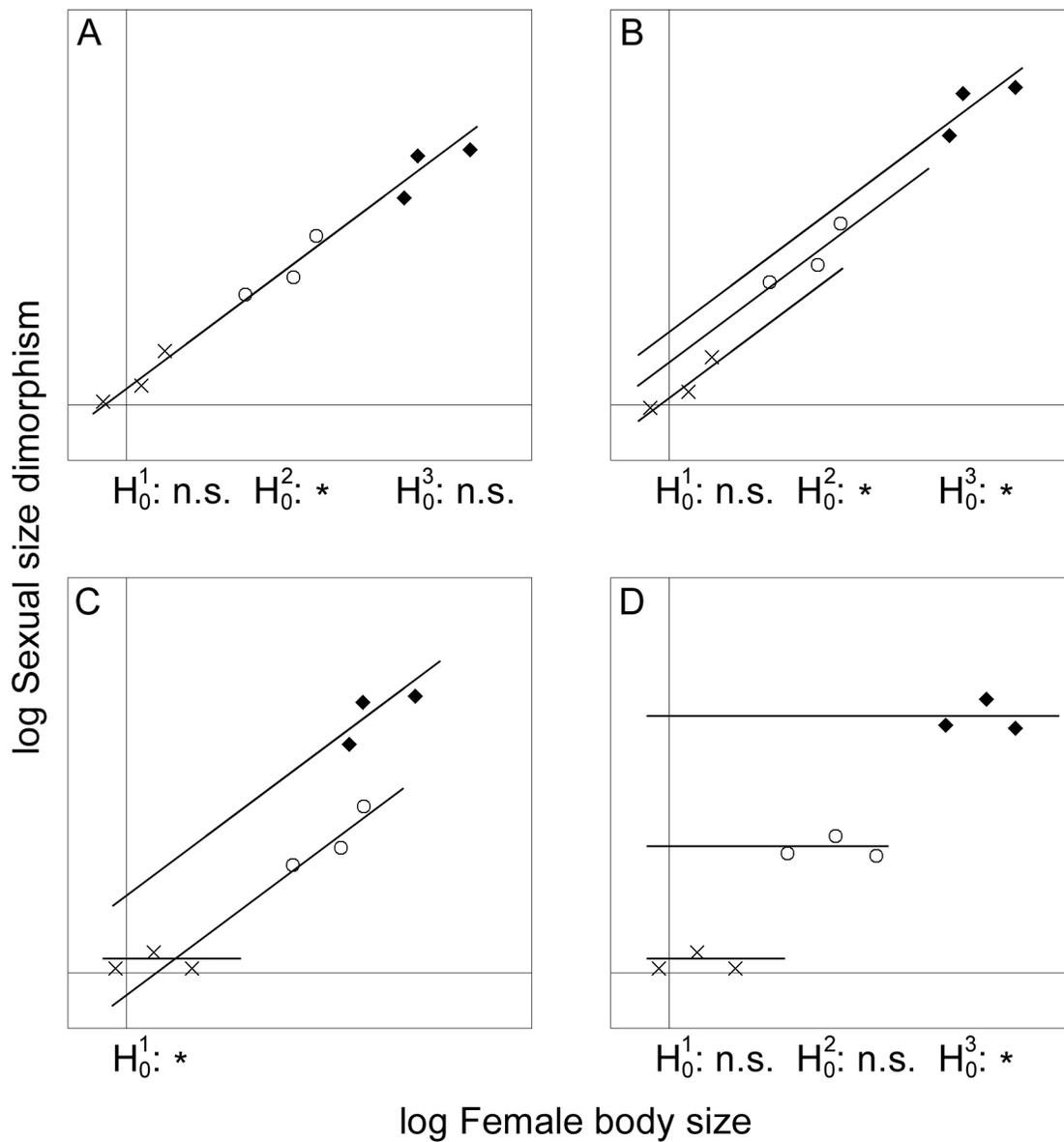


Figure 4.1. Hypothetical relationships between body size, sexual size dimorphism, and sexual selection.

Symbols are as follows: ×, low sexual selection; ○, intermediate sexual selection; ◆, high sexual selection. The three null hypotheses are as follows: H₀¹: no difference in slopes between mating systems; H₀²: common slope among mating systems is not different from zero; H₀³: no difference in intercepts between mating systems; “n.s.” indicates that no significant difference is found for that null hypothesis; an asterisk indicates a significant difference. In each of the four diagrams SSD scales positively with size when sexual selection is not taken into account. See text for discussion.

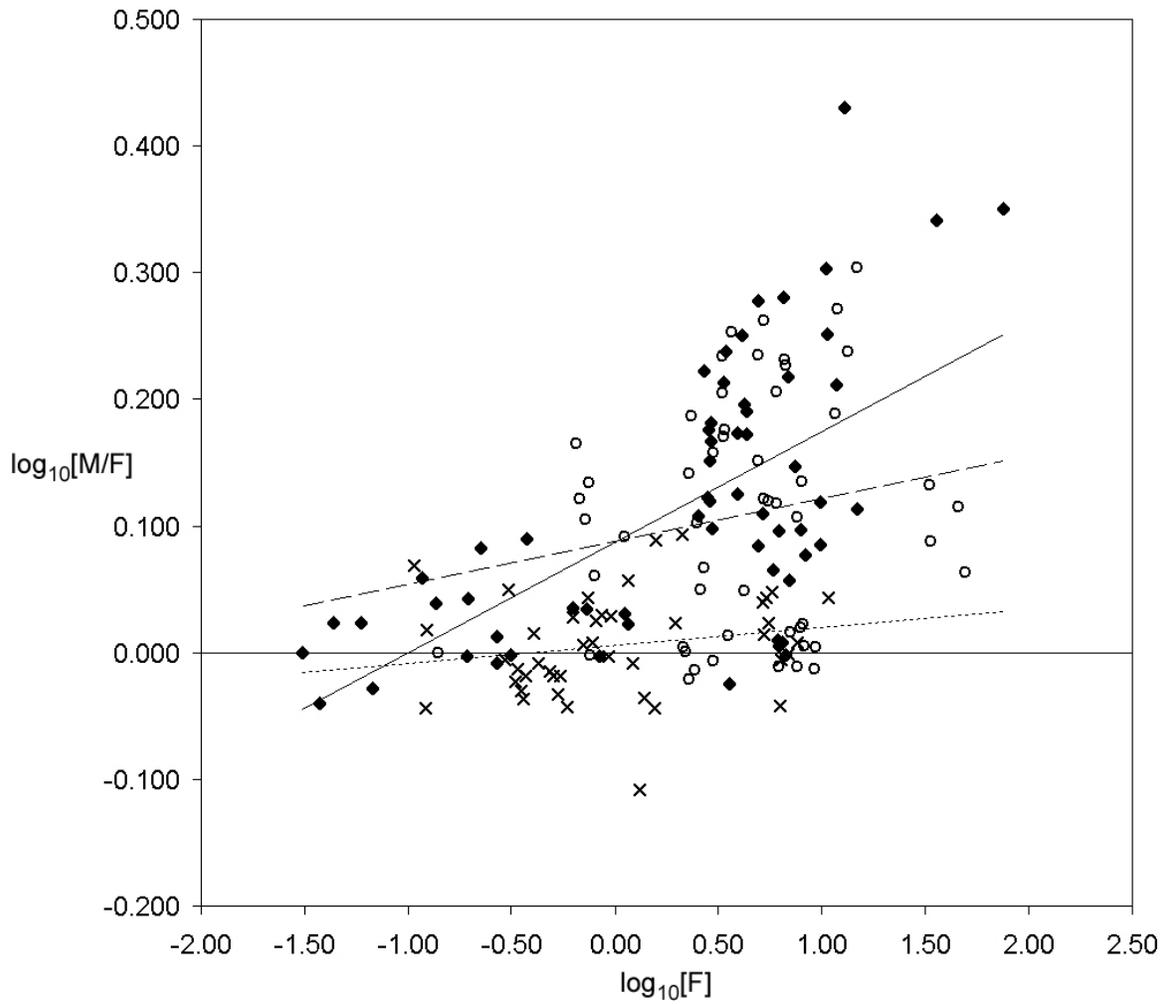


Figure 4.2. Separate OLS regressions of $\log_{10}[M/F]$ against $\log_{10}[F]$ for each mating system in Primates (reduced data set).

Symbols are as follows: \times , monogamous (*Mon*); \circ , multi-male (*MM*); \blacklozenge , uni-male (*UM*). Regression lines: dotted, *Mon*; dashed, *MM*; solid, *UM*. Uni-male regression line is significantly positive at $\alpha = 0.05$.

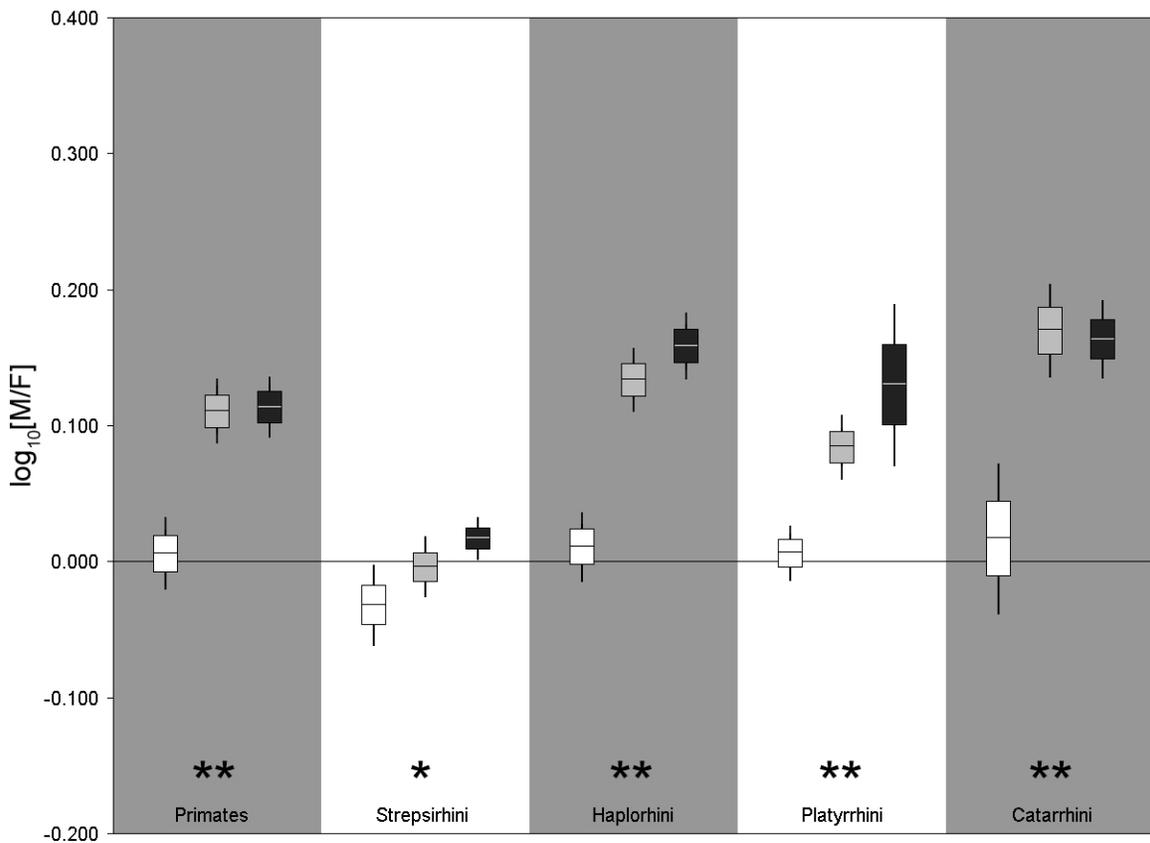


Figure 4.3a. Means of $\log_{10}[M/F]$ by mating system (reduced data set): traditional ANOVA.

Box colors are as follows: white, *Mon*; light gray, *MM*; dark gray, *UM*. Horizontal lines are means, boxes are one standard error above and below the mean, and bars are 95% confidence intervals for the mean. The zero line corresponds to monomorphism (males and females equal size). * indicates significant difference between means at alpha = 0.05; ** indicates significant difference at alpha = 0.01. Means do not significantly differ in Strepsirhini for the full data set (not shown here). Note that *UM* species have a lower mean than *MM* species in Catarrhini.

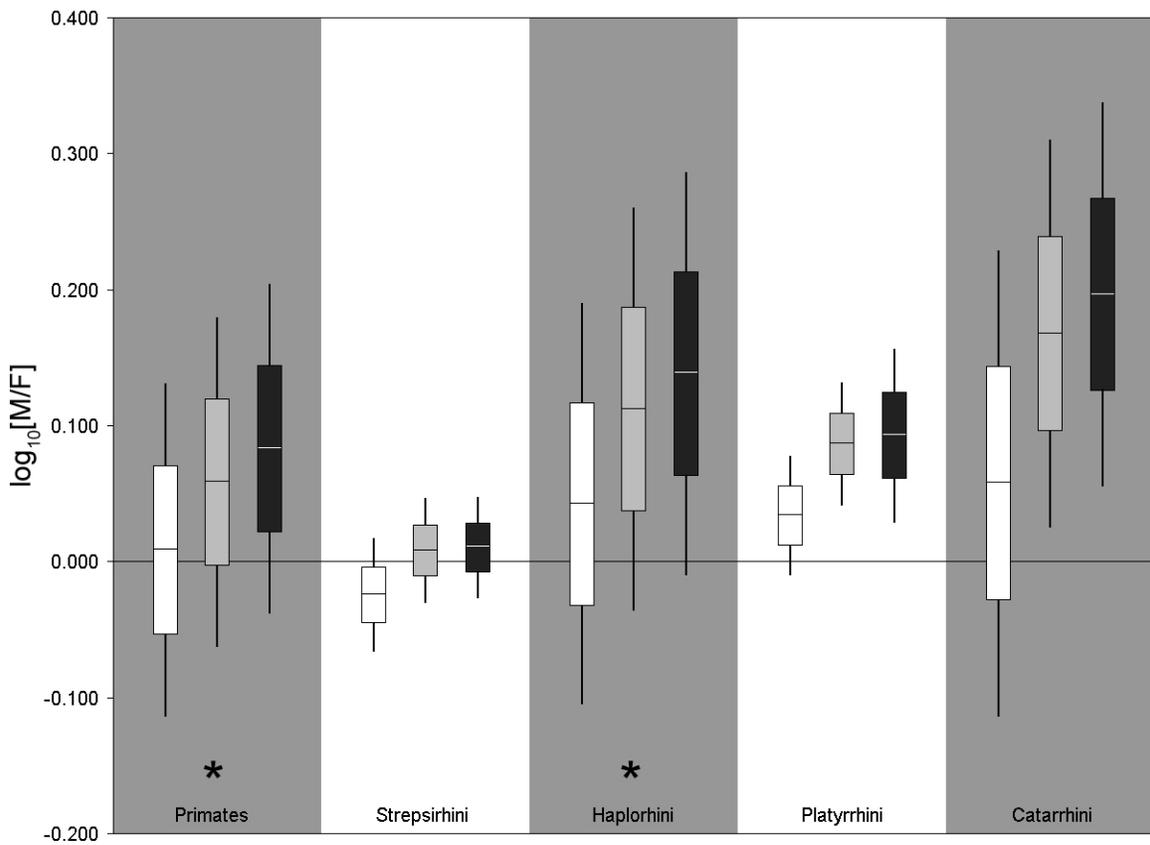


Figure 4.3b. Means of $\log_{10}[M/F]$ by mating system (reduced data set): PGLM ANOVA.

Boxes, bars, lines, and asterisks are as in Figure 4.3a. Note that *UM* species have a higher mean than *MM* species in Catarrhini, unlike in the traditional ANOVA results. Differences between means in Catarrhini approach significance ($p = 0.068$). Means differ significantly in Catarrhini and Platyrrhini for the full data set (not shown here).

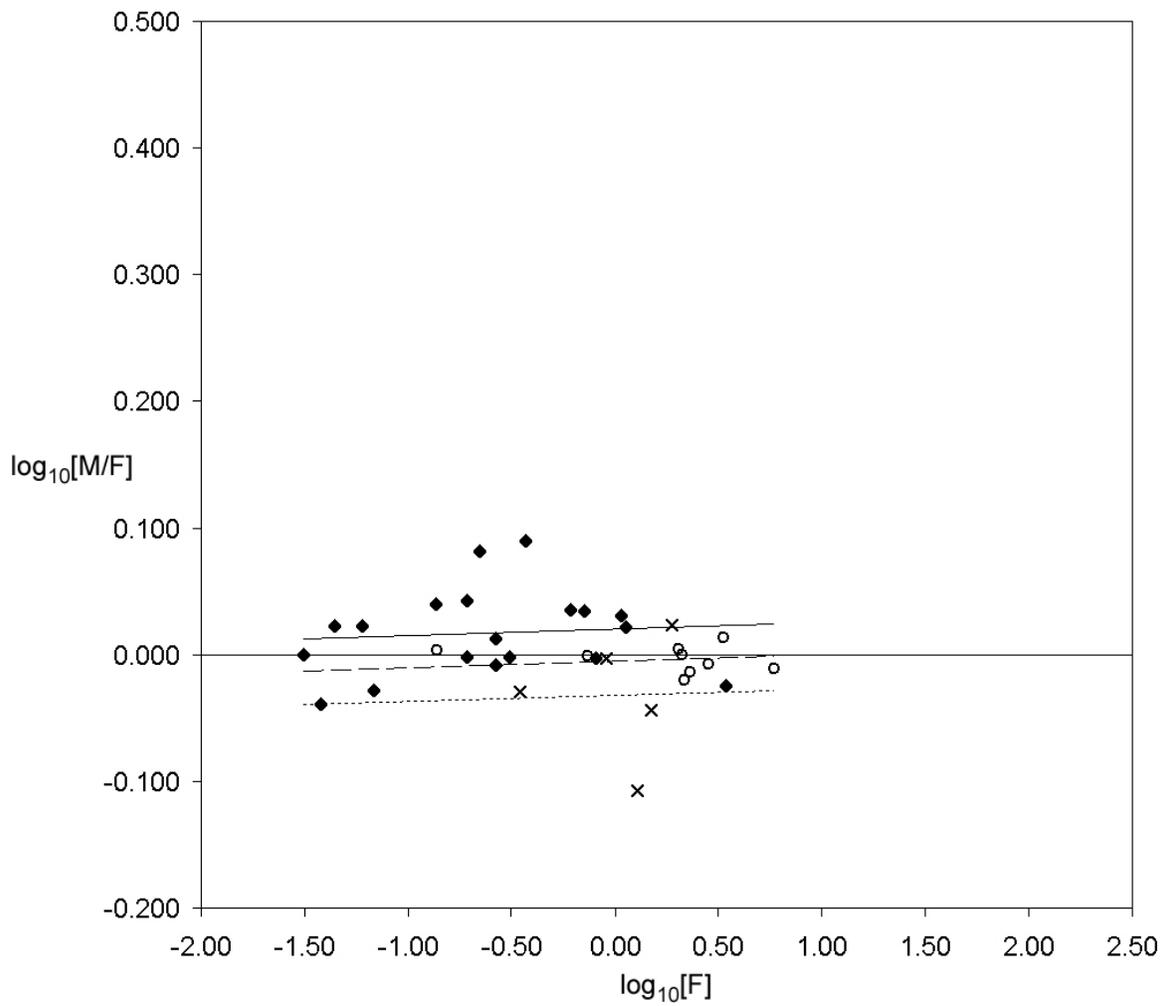


Figure 4.4. ANCOVA of $\log_{10}[M/F]$ dependent on $\log_{10}[F]$ and mating system in Strepsirhini (reduced data set).

Symbols and lines are as in Figure 4.2. Common slope is not significantly different from zero.

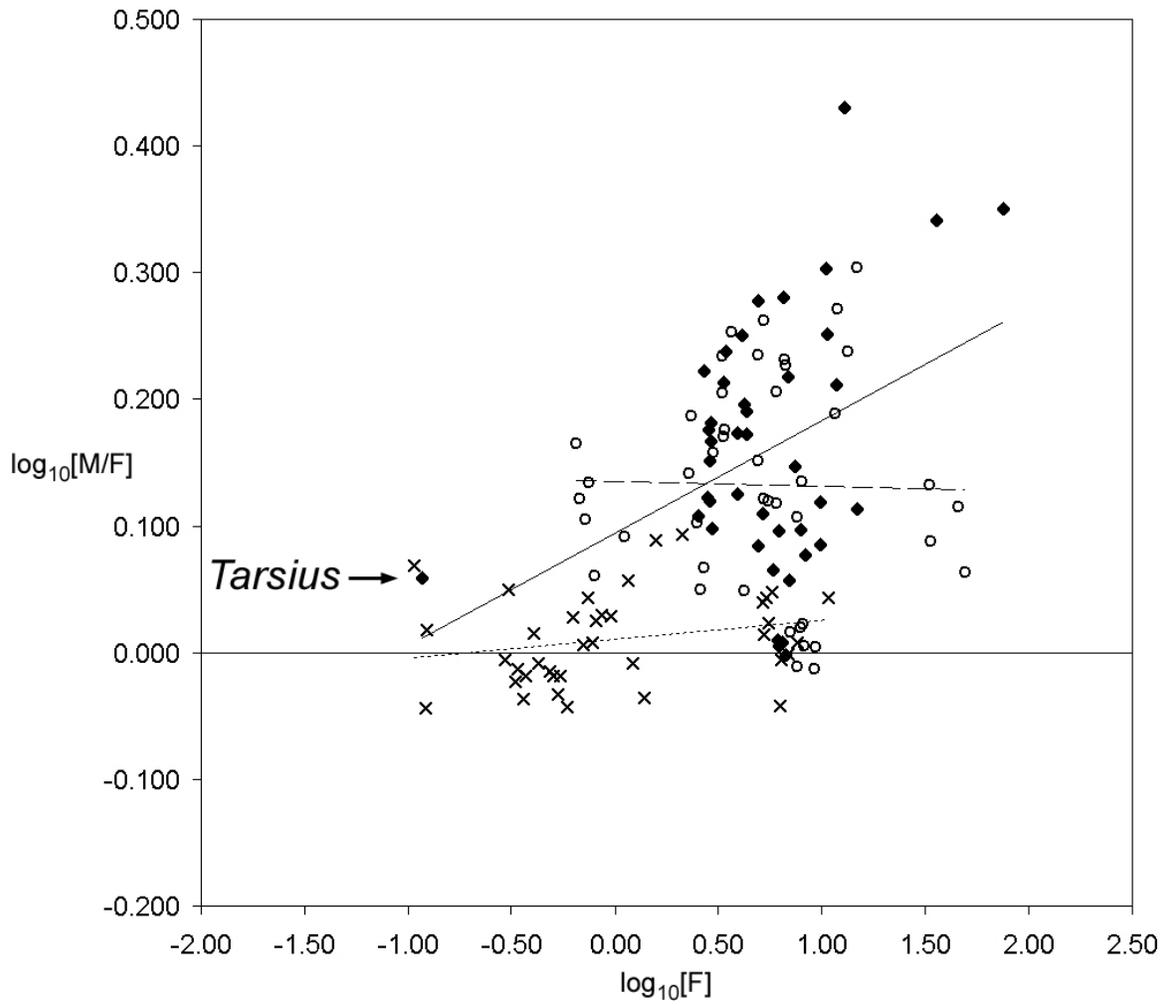


Figure 4.5. Separate OLS regressions of $\log_{10}[M/F]$ against $\log_{10}[F]$ for each mating system in Haplorthini (reduced data set).

Symbols and lines are as in Figure 4.2. Uni-male haplorthines have a significantly positive slope, although note that it is leveraged by *Tarsius syrichta*.

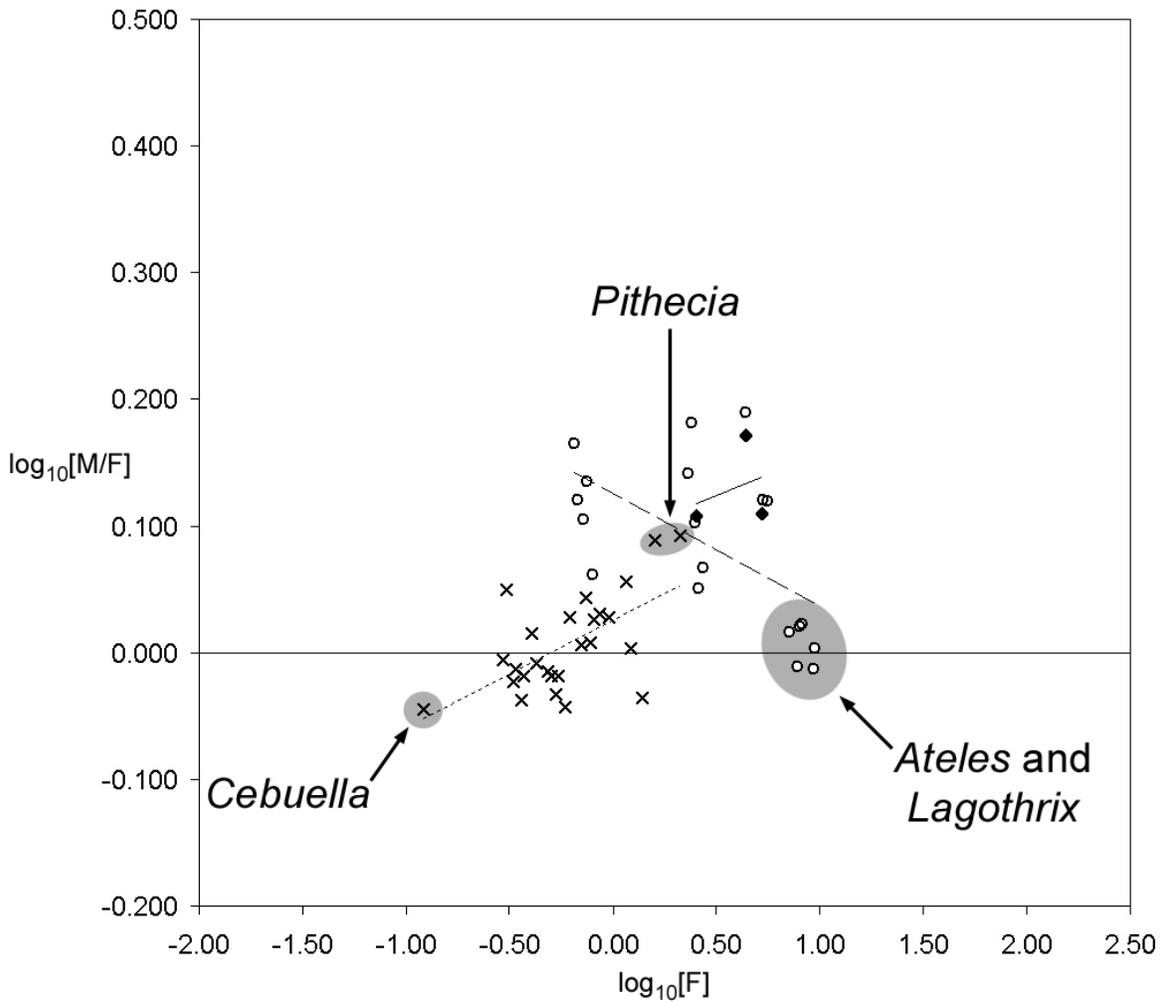


Figure 4.6. Separate OLS regressions of $\log_{10}[M/F]$ against $\log_{10}[F]$ for each mating system in Platyrrhini (reduced data set).

Symbols and lines are as in Figure 4.2. Monogamous platyrrhines have a significantly positive slope; multi-male slope is significantly negative. These slopes are driven by relatively few species: *Cebuella pygmaea*, *Pithecia monachus*, and *P. pithecia* for the *Mon* slope and a cluster of the *Ateles* species and *Lagothrix lagothricha* for the *MM* slope.

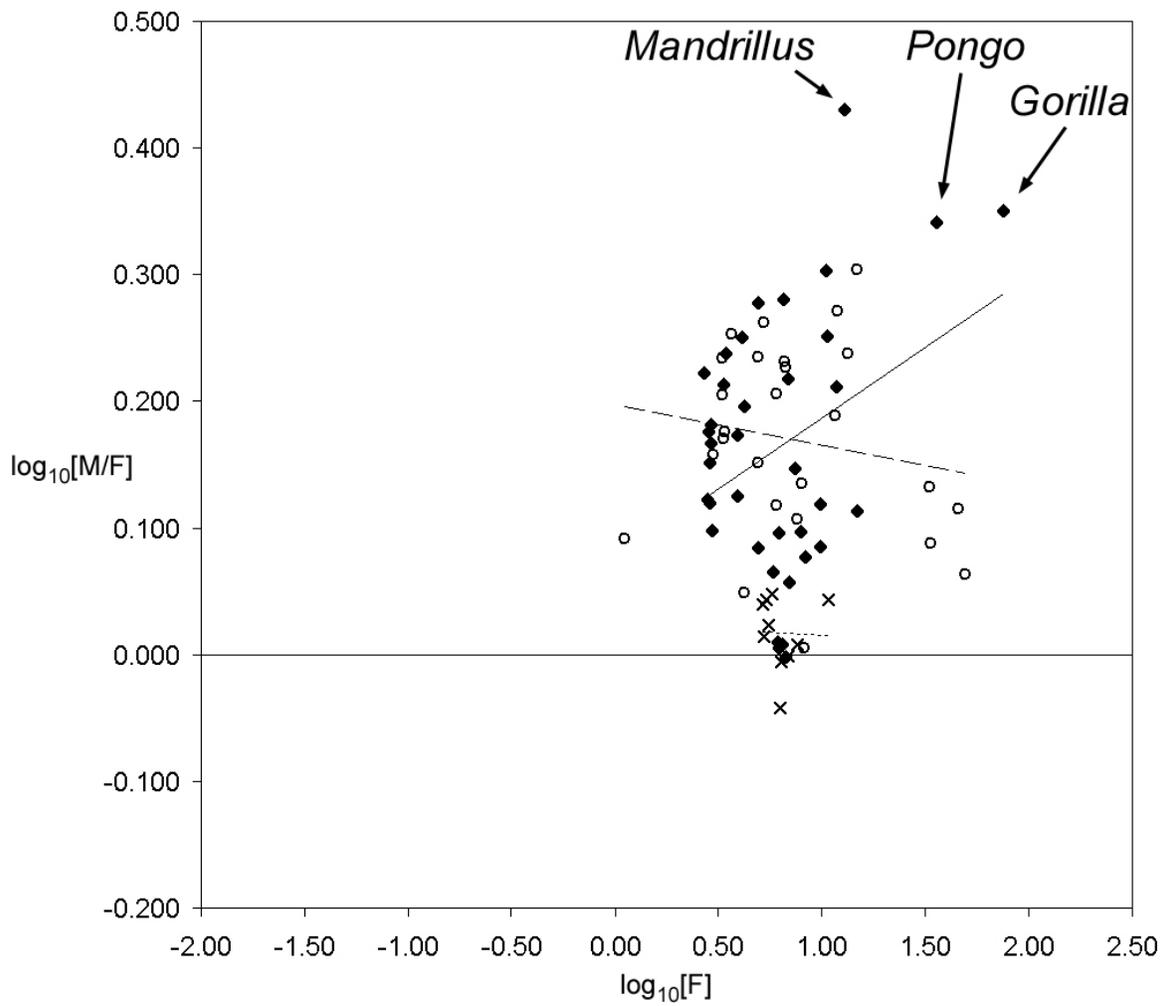


Figure 4.7. Separate OLS regressions of $\log_{10}[M/F]$ against $\log_{10}[F]$ for each mating system in Catarrhini (reduced data set).

Symbols and lines are as in Figure 4.2. Uni-male catarrhines have a significantly positive slope. This slope is highly leveraged by three species: *Mandrillus sphinx*, *Pongo pygmaeus*, and *Gorilla gorilla*.

| Taxon | Sample | Male N | Female N | Male mean (kg) | Female mean (kg) | Mating System | Substrate | Body Mass Source | Mating System Source |
|------------------------------------|--------|--------|----------|----------------|------------------|---------------|-----------|--------------------------------------|--------------------------------------|
| Cheirogaleidae | | | | | | | | | |
| <i>Allocebus trichotis</i> | F | 2 | 2 | 0.092 | 0.084 | Mon | A | Meier & Albignac (1991) | Nowak (1999) |
| <i>Cheirogaleus major</i> | F | 3 | 6 | 0.438 | 0.362 | UM or MM | A | Stephan & Bauchot (1965) | Lindenfors & Tullberg (1998) |
| <i>Cheirogaleus medius</i> | F, R | W | W | 0.140 | 0.139 | MM | A | Hladik <i>et al.</i> (1980) | Fietz <i>et al.</i> (2000) |
| | | 7 | 6 | 0.188 | 0.172 | | | Kathrin Dausmann, pc | |
| | | 36 | 43 | 0.128 | 0.134 | | | Alexandra Mueller, pc | |
| | | 4 | 3 | 0.159 | 0.150 | | | | |
| <i>Microcebus berthae</i> | F, R | 10 | 10 | 0.0341 | 0.0373 | UM or MM | A | Manfred Eberle, pc | Lindenfors & Tullberg (1998) |
| <i>Microcebus murinus</i> | F, R | 127 | 120 | 0.0630 | 0.0672 | UM or MM | A | Manfred Eberle, pc | Lindenfors & Tullberg (1998) |
| <i>Microcebus myoxinus</i> | F, R | 81 | 48 | 0.0307 | 0.0307 | UM or MM | A | Schwab (2000) | Lindenfors & Tullberg (1998) |
| <i>Microcebus rufus</i> | F, R | 17 | 15 | 0.0458 | 0.0435 | UM or MM | A | Atsalis (1999) | Lindenfors & Tullberg (1998) |
| <i>Mirza coquereli</i> | F, R | P | P | 0.311 | 0.312 | UM or MM | A | | Lindenfors & Tullberg (1998) |
| | | 68 | 77 | 0.309 | 0.299 | | | Peter Kappeler, pc | |
| <i>Phaner furcifer</i> | F, R | 8 | 6 | 0.328 | 0.351 | Mon | A | Oliver Schuelke, pc | Schulke & Kappeler (2003) |
| Megaladapidae | | | | | | | | | |
| <i>Lepilemur edwardsi</i> | F, R | 10 | 10 | 0.928 | 0.934 | Mon | A | Rasoloharijaona <i>et al.</i> (2003) | Rasoloharijaona <i>et al.</i> (2003) |
| <i>Lepilemur leucopus</i> | F | 2 | 5 | 0.617 | 0.594 | MM | A | Smith & Jungers (1997) | Zinner <i>et al.</i> (2003) |
| <i>Lepilemur ruficaudatus</i> | F, R | P | P | 0.753 | 0.755 | MM | A | | Ganzhorn & Kappeler (1996) |
| | | 28 | 19 | 0.800 | 0.827 | | | R. Hilgartner & D. Zinner, pc | |
| | | 8 | 8 | 0.705 | 0.682 | | | Schmid & Ganzhorn (1996) | |
| Lemuridae | | | | | | | | | |
| <i>Eulemur coronatus</i> | F | 2 | 2 | 1.28 | 1.08 | MM | A | Terranova & Coffman (1997) | Kappeler (2000) |
| <i>Eulemur fulvus albocollaris</i> | F, R | P | P | 2.15 | 2.13 | MM | A | | Kappeler (2000) |
| | | 15 | 9 | 2.20 | 2.16 | | | Johnson <i>et al.</i> , in review | |
| | | 7 | 5 | 2.10 | 2.10 | | | Bradley <i>et al.</i> (1997) | |
| <i>Eulemur fulvus rufus</i> | F, R | P | P | 2.17 | 2.27 | MM | A | | Kappeler (2000) |
| | | 20 | 13 | 2.18 | 2.25 | | | Glander <i>et al.</i> (1992) | |
| | | 23 | 15 | 2.15 | 2.29 | | | Johnson <i>et al.</i> , in review | |
| <i>Eulemur fulvus sanfordi</i> | F | 2 | 2 | 1.87 | 1.83 | MM | A | Terranova & Coffman (1997) | Kappeler (2000) |

| Taxon | Sample | Male | | Mating System | Substrate | Body Mass Source | Mating System Source |
|-------------------------------------|--------|------|-----------|---------------|-----------|------------------|------------------------------|
| | | N | mean (kg) | | | | |
| <i>Eulemur macaco</i> | F, R | W | 2.35 | 2.43 | MM | A | Kappeler (2000) |
| | | 46 | 2.37 | 2.51 | | | |
| | | 2 | 1.88 | 1.76 | | | |
| <i>Eulemur mongoz</i> | F, R | 4 | 1.41 | 1.56 | Mon | A | Terranova & Coffman (1997) |
| <i>Eulemur rubriventer</i> | F, R | 9 | 2.07 | 1.96 | Mon | A | Terranova & Coffman (1997) |
| <i>Hapalemur aureus</i> | F | 2 | 1.60 | 1.50 | Mon | A | Glander <i>et al.</i> (1992) |
| <i>Hapalemur griseus</i> | F | 2 | 0.748 | 0.670 | Mon | A | Glander <i>et al.</i> (1992) |
| <i>Hapalemur simus</i> | F | 2 | 2.15 | 1.3 | Mon | A | Smith & Jungers (1997) |
| <i>Lemur catta</i> | F, R | 41 | 2.21 | 2.21 | MM | A | Kappeler (1991) |
| <i>Varecia variegata</i> | F, R | 13 | 3.63 | 3.52 | MM | A | Sussman (1991) |
| | | 5 | 3.63 | 3.52 | MM | A | Terranova & Coffman (1997) |
| Indriidae | | | | | | | |
| <i>Avahi lamiger</i> | F, R | 4 | 1.03 | 1.32 | Mon | A | Glander <i>et al.</i> (1992) |
| <i>Avahi occidentalis</i> | F | 6 | 0.814 | 0.777 | Mon | A | Lindenfors & Tullberg (1998) |
| <i>Indri indri</i> | F | 2 | 5.83 | 7.14 | Mon | A | Bauchot & Stephan (1966) |
| <i>Propithecus diadema</i> | F, R | P | 6.05 | 6.21 | MM | A | Powzyk (1996) |
| | | 8 | 5.59 | 5.90 | | | Glander <i>et al.</i> (1992) |
| | | 5 | 6.50 | 6.51 | | | Powzyk (1996) |
| <i>Propithecus tattersalli</i> | F, R | 10 | 3.39 | 3.59 | UM and MM | A | Ravosa <i>et al.</i> (1993) |
| <i>Propithecus verreauxi</i> | F, R | P | 2.93 | 2.98 | MM | A | Kappeler (2000) |
| | | 46 | 3.02 | 3.20 | | | Kappeler (2000) |
| | | 119 | 2.84 | 2.76 | | | Lewis & Kappeler, in review |
| | | | | | | | Richard <i>et al.</i> (2000) |
| Daubentoniidae | | | | | | | |
| <i>Daubentonia madagascariensis</i> | F | 3 | 2.63 | 2.30 | UM or MM | A | Glander (1994) |
| | | 4 | 2.63 | 2.30 | | | Lindenfors & Tullberg (1998) |
| Lorisidae | | | | | | | |
| <i>Arctocebus calabarensis</i> | F | 2 | 0.324 | 0.301 | UM or MM | A | Jewell & Oates (1969) |
| <i>Eooticus elegantulus</i> | F | 5 | 0.287 | 0.261 | UM or MM | A | Dixson (1998) |
| <i>Eooticus matschiei</i> | F | 2 | 0.207 | 0.212 | UM or MM | A | Dixson (1998) |
| <i>Galago moholi</i> | F, R | P | 0.214 | 0.194 | UM or MM | A | Dixson (1998) |
| | | 13 | 0.217 | 0.200 | | | Dixson (1998) |
| | | 53 | 0.211 | 0.188 | | | Dixson (1998) |
| | | | | | | | Bearder & Martin (1980) |
| | | | | | | | Harcourt & Bearder (1989) |

| Taxon | Sample | Male N | Female N | Male mean (kg) | Female mean (kg) | Mating System | Substrate | Body Mass Source | Mating System Source |
|--|--------|--------|----------|----------------|------------------|---------------|-----------|------------------------------|------------------------------|
| <i>Galago senegalensis</i> | F, R | P | P | 0.271 | 0.225 | UM or MM | A | | Lindenfors & Tullberg (1998) |
| | | 80 | 67 | 0.227 | 0.199 | | | Smith & Jungers (1997) | |
| | | 8 | 9 | 0.315 | 0.250 | | | Smith & Jungers (1997) | |
| <i>Galagoides alleni</i> | F, R | 9 | 30 | 0.277 | 0.269 | UM or MM | A | Charles-Dominique (1977a) | Dixson (1998) |
| <i>Galagoides demidoff</i> | F, R | 19 | 9 | 0.0628 | 0.0596 | UM or MM | A | Charles-Dominique (1972) | Dixson (1998) |
| <i>Galagoides thomasi</i> | F | 2 | 1 | 0.103 | 0.130 | UM or MM | A | Smith & Jungers (1997) | Lindenfors & Tullberg (1998) |
| <i>Galagoides zanzibaricus</i> | F, R | 35 | 38 | 0.150 | 0.137 | UM or MM | A | Harcourt & Nash (1989) | extrapolation |
| <i>Loris tardigradus hydekkerianus</i> | F, R | 7 | 4 | 0.264 | 0.269 | UM or MM | A | Smith & Jungers (1997) | Dixson (1998) |
| <i>Loris tardigradus malabaricus</i> | F, R | 10 | 8 | 0.192 | 0.193 | UM or MM | A | Kappeler (1991) | Dixson (1998) |
| <i>Nycticebus coucang bengalensis</i> | F | W | W | 1.10 | 1.02 | UM or MM | A | | Dixson (1998) |
| | | 2 | 1 | 0.890 | 0.900 | | | Fooden (1971) | |
| | | 2 | 1 | 1.31 | 1.14 | | | Smith & Jungers (1997) | |
| <i>Nycticebus coucang coucang</i> | F, R | 56 | 44 | 0.679 | 0.626 | UM or MM | A | Smith & Jungers (1997) | Dixson (1998) |
| <i>Nycticebus pygmaeus</i> | F, R | 7 | 5 | 0.462 | 0.376 | UM or MM | A | Kappeler (1991) | Lindenfors & Tullberg (1998) |
| <i>Otolemur crassicaudatus</i> | F, R | 66 | 35 | 1.19 | 1.11 | UM or MM | A | Skinner & Smithers (1990) | Dixson (1998) |
| <i>Otolemur garnettii</i> | F, R | 120 | 134 | 0.794 | 0.734 | UM or MM | A | Smith & Jungers (1997) | Dixson (1998) |
| <i>Perodicticus potto potto</i> | F, R | 17 | 15 | 0.830 | 0.836 | UM or MM | A | Smith & Jungers (1997) | Dixson (1998) |
| <i>Perodicticus potto edwardsi</i> | F, R | 4 | 4 | 1.22 | 1.16 | UM or MM | A | Malbrant & Maclatchy (1949) | Dixson (1998) |
| Tarsiidae | | | | | | | | | |
| <i>Tarsius bancanus</i> | F, R | P | P | 0.128 | 0.123 | Mon | A | | Wright <i>et al.</i> (2003) |
| | | 21 | 16 | 0.128 | 0.117 | | | Niemitz (1984) | |
| | | 6 | 6 | 0.128 | 0.128 | | | Wright <i>et al.</i> (2003) | |
| <i>Tarsius diana</i> | F | 1 | 2 | 0.104 | 0.107 | Mon | A | Niemitz <i>et al.</i> (1991) | Gursky (2003) |

| Taxon | Sample | Male | | Female | | Mating System | Substrate | Body Mass Source | Mating System Source |
|---|--------|------|----|-----------|-----------|---------------|-----------|------------------------------------|------------------------------|
| | | N | N | mean (kg) | mean (kg) | | | | |
| <i>Tarsius spectrum</i> | F, R | 5 | 8 | 0.125 | 0.107 | Mon | A | Gursky (1998) | Gursky (2003) |
| <i>Tarsius syrichta</i> | F, R | 10 | 17 | 0.134 | 0.117 | UM and MM | | Kappeler (1991) | Lindenfors & Tullberg (1998) |
| Callitrichidae | | | | | | | | | |
| <i>Callithrix argentata</i> | F, R | 8 | 10 | 0.330 | 0.360 | Mon (PA) | A | Smith & Jungers (1997) | Dixson (1998) |
| <i>Callithrix emiliae</i> | F, R | 12 | 5 | 0.313 | 0.330 | Mon (PA) | A | Ford & Davis (1992) | Dixson (1998) |
| <i>Callithrix humeralifer</i> | F, R | P | P | 0.418 | 0.426 | Mon (PA) | A | | Dixson (1998) |
| <i>Callithrix jacchus</i> | F | 3 | 2 | 0.362 | 0.381 | Mon (PA) | A | Epple (1970) | Dixson (1998) |
| <i>Callithrix mauesi</i> | F | 2 | 2 | 0.345 | 0.398 | Mon (PA) | A | Mittermeier <i>et al.</i> (1992) | Dixson (1998) |
| <i>Callithrix nigriceps</i> | F | 3 | 1 | 0.370 | 0.390 | Mon (PA) | A | Ferrari <i>et al.</i> (1993) | Dixson (1998) |
| <i>Callithrix penicillata</i> | F, R | 8 | 8 | 0.344 | 0.307 | Mon (PA) | A | Smith & Jungers (1997) | Dixson (1998) |
| <i>Cebuella pygmaea</i> | F, R | 36 | 27 | 0.110 | 0.122 | Mon (PA) | A | Soini (1988) | Heymann (2000) |
| <i>Leontopithecus chrysomelas</i> | F | 2 | 6 | 0.620 | 0.535 | Mon (PA) | A | Rosenberger & Coimbra-Filho (1984) | Heymann (2000) |
| <i>Leontopithecus rosalia</i> | F, R | 9 | 9 | 0.663 | 0.622 | Mon (PA) | A | Dietz <i>et al.</i> (1994) | Heymann (2000) |
| <i>Saguinus bicolor</i> | F | 3 | 4 | 0.431 | 0.430 | Mon (PA) | A | Smith & Jungers (1997) | Dixson (1998) |
| <i>Saguinus fuscicollis fuscicollis</i> | F, R | 9 | 10 | 0.328 | 0.338 | Mon (PA) | A | Soini (1990) | Dunbar (2000) |
| <i>Saguinus fuscicollis illigeri</i> | F, R | 9 | 4 | 0.292 | 0.296 | Mon (PA) | A | Soini (1990) | Dunbar (2000) |
| <i>Saguinus fuscicollis nigrifons</i> | F, R | P | P | 0.354 | 0.369 | Mon (PA) | A | | Dunbar (2000) |
| | | 9 | 7 | 0.350 | 0.376 | | | Soini (1990) | |
| | | 17 | 19 | 0.352 | 0.366 | | | Soini (1990) | |
| | | 25 | 15 | 0.359 | 0.366 | | | Soini (1990) | |

| Taxon | Sample | Male N | Female N | Male mean (kg) | Female mean (kg) | Mating System | Substrate | Body Mass Source | Mating System Source |
|-----------------------------|--------|--------|----------|----------------|------------------|---------------|-----------|-----------------------------------|------------------------------|
| <i>Saguinus Geoffroyi</i> | F, R | 55 | 40 | 0.482 | 0.503 | Mon (PA) | A | Dawson & Dukelow (1976) | Heymann (2000) |
| <i>Saguinus labiatus</i> | F, R | 136 | 77 | 0.490 | 0.529 | Mon (PA) | A | Puertas <i>et al.</i> (1995) | Heymann (2000) |
| <i>Saguinus leucopus</i> | F | 2 | 2 | 0.494 | 0.490 | Mon (PA) | A | Hernandez-Camacho & Defler (1985) | Dixon (1998) |
| <i>Saguinus midas</i> | F, R | P | P | 0.535 | 0.591 | Mon (PA) | A | | Lindenfors & Tullberg (1998) |
| <i>Saguinus mystax</i> | F, R | P | P | 0.522 | 0.545 | Mon (PA) | A | | Dunbar (2000) |
| | | 18 | 10 | 0.568 | 0.585 | | | Garber <i>et al.</i> , 1993 | |
| | | 95 | 80 | 0.491 | 0.511 | | | Moya, <i>et al.</i> (1990) | |
| | | 79 | 48 | 0.525 | 0.561 | | | Soini & Soini (1990) | |
| | | 48 | 30 | 0.472 | 0.490 | | | Soini & Soini (1990) | |
| | | 34 | 26 | 0.505 | 0.540 | | | Soini & Soini (1990) | |
| | | 6 | 13 | 0.550 | 0.561 | | | Garber <i>et al.</i> (1993) | |
| | | 6 | 6 | 0.545 | 0.564 | | | Garber <i>et al.</i> (1993) | |
| <i>Saguinus nigricollis</i> | F, R | 8 | 6 | 0.468 | 0.484 | Mon (PA) | A | Hershkovitz (1977) | Heymann (2000) |
| <i>Saguinus oedipus</i> | F, R | 37 | 29 | 0.418 | 0.404 | Mon (PA) | A | Savage <i>et al.</i> (1993) | Dunbar (2000) |
| Cebidae | | | | | | | | | |
| <i>Alouatta belzebul</i> | F, R | 27 | 26 | 7.27 | 5.52 | MM | A | Peres (1994) | Plavcan (1999) |
| <i>Alouatta caraya</i> | F, R | 58 | 117 | 6.42 | 4.33 | UM and MM | A | Rumiz (1990) | Lindenfors & Tullberg (1998) |
| <i>Alouatta fusca</i> | F, R | 4 | 5 | 6.73 | 4.35 | MM | A | Smith & Jungers (1997) | Lindenfors & Tullberg (1998) |
| <i>Alouatta palliata</i> | F, R | P | P | 6.96 | 5.28 | MM | A | | Dunbar (2000) |
| | | 14 | 18 | 6.53 | 4.02 | | | Glander <i>et al.</i> (1991) | |
| | | 15 | 15 | 7.80 | 6.60 | | | Thorington <i>et al.</i> , 1979 | |
| | | 8 | 10 | 8.35 | 6.17 | | | Scott <i>et al.</i> (1976) | |
| | | 4 | 17 | 4.95 | 4.25 | | | Scott <i>et al.</i> (1976) | |
| | | 110+ | 177+ | 7.17 | 5.35 | | | Peres (1994) | |
| <i>Alouatta pigra</i> | F | 2 | 4 | 11.4 | 6.43 | UM and MM | A | Peres (1994) | Lindenfors & Tullberg (1998) |

| Taxon | Sample | Male N | Female N | Male mean (kg) | Female mean (kg) | Mating System | Substrate | Body Mass Source | Mating System Source |
|--------------------------------|--------|--------|----------|----------------|------------------|---------------|-----------|-----------------------------------|------------------------------|
| <i>Alouatta seniculus</i> | F, R | P | P | 6.66 | 5.18 | UM and MM | A | | Strier (2000) |
| | | 28 | 34 | 7.62 | 6.02 | | | Smith & Jungers (1997) | |
| | | 31 | 29 | 5.62 | 4.03 | | | Braza <i>et al.</i> (1983) | |
| | | 8 | 9 | 7.54 | 6.30 | | | Hernandez-Camacho & Defler (1985) | |
| | | 14 | 4 | 6.70 | 4.50 | | | Rudran (1979) | |
| | | 10 | 4 | 6.50 | 4.50 | | | Thorington <i>et al.</i> (1979) | |
| | | 7 | 4 | 6.00 | 5.70 | | | Rodriguez & Boher (1988) | |
| | F, R | 5 | 5 | 1.23 | 1.22 | Mon | A | AMNH (this study) | Lindenfors & Tullberg (1998) |
| | F | 1 | 1 | 1.19 | 1.24 | Mon | A | Fernandes (1993) | Lindenfors & Tullberg (1998) |
| | | 7 | 6 | 0.921 | 0.859 | Mon | A | Hernandez-Camacho & Defler (1985) | Lindenfors & Tullberg (1998) |
| <i>Aotus lemurinus</i> | F, R | 32 | 24 | 0.795 | 0.78 | Mon | A | Aquino & Encarnacion (1986) | Lindenfors & Tullberg (1998) |
| | F, R | 20 | 17 | 0.813 | 0.736 | Mon | A | Smith & Jungers (1997) | Lindenfors & Tullberg (1998) |
| | F, R | 20 | 20 | 0.708 | 0.698 | Mon | A | Montoya <i>et al.</i> (1990) | Lindenfors & Tullberg (1998) |
| | F, R | 10 | 16 | 8.26 | 7.88 | MM | A | Smith & Jungers (1997) | Dunbar (2000) |
| | F, R | 4 | 8 | 9.41 | 9.33 | MM | A | Smith & Jungers (1997) | Dunbar (2000) |
| | F, R | 6 | 11 | 8.89 | 9.16 | MM | A | Crile & Quiring (1940) | Lindenfors & Tullberg (1998) |
| | F, R | 20 | 32 | 7.45 | 7.64 | MM | A | Schultz (1941) | Lindenfors & Tullberg (1998) |
| | F, R | P | P | 8.49 | 8.07 | MM | A | | Dunbar (2000) |
| | | 20 | 42 | 9.11 | 8.44 | | | Smith (1996) | |
| | | 5 | 7 | 7.86 | 7.69 | | | Fleagle & Mittermeier (1980) | |
| <i>Brachyteles arachnoides</i> | F | 3 | 3 | 9.42 | 8.33 | MM | A | Lemos de Sa & Glander (1993) | Dixon (1998) |
| | F | 1 | 2 | 3.45 | 2.88 | MM | A | Smith & Jungers (1997) | Lindenfors & Tullberg (1998) |
| | F, R | 5 | 6 | 3.16 | 2.71 | MM | A | Smith & Jungers (1997) | extrapolation |
| | F, R | 6 | 4 | 0.854 | 0.805 | Mon | A | Ford & Davis (1992) | Lindenfors & Tullberg (1998) |
| | F | 10 | 2 | 1.02 | 1.12 | Mon | A | Hershkovitz (1990) | Lindenfors & Tullberg (1998) |
| | F | 5 | 2 | 0.991 | 0.909 | Mon | A | Smith & Jungers (1997) | Lindenfors & Tullberg (1998) |
| | F | 1 | 3 | 1.09 | 1.07 | Mon | A | Smith & Jungers (1997) | Lindenfors & Tullberg (1998) |
| | F, R | 10 | 19 | 1.02 | 0.956 | Mon | A | Smith & Jungers (1997) | Lindenfors & Tullberg (1998) |
| | F, R | 5 | 7 | 1.27 | 1.38 | Mon | A | Hershkovitz (1990) | Lindenfors & Tullberg (1998) |

| Taxon | Sample | | Male Female | | Male Female | | Mating System | Substrate | Body Mass Source | Mating System Source |
|--------------------------------------|--------|----|-------------|---|-------------|-----------|---------------|-----------|-----------------------------------|------------------------------|
| | N | P | N | P | mean (kg) | mean (kg) | | | | |
| <i>Callicebus torquatus</i> | F, R | | | | 1.32 | 1.16 | Mon | A | Hernandez-Camacho & Defler (1985) | Lindenfors & Tullberg (1998) |
| | | 5 | 9 | | 1.49 | 1.27 | | | Smith & Jungers (1997) | |
| <i>Cebus albifrons</i> | F, R | W | W | | 3.18 | 2.29 | MM | A | Hernandez-Camacho & Defler (1985) | Lindenfors & Tullberg (1998) |
| | | 8 | 6 | | 1.15 | 1.05 | | | Smith & Jungers (1997) | |
| <i>Cebus apella</i> | F, R | P | P | | 3.64 | 2.39 | MM | A | Hernandez-Camacho & Defler (1985) | Dunbar (2000) |
| | | 18 | 15 | | 3.07 | 2.18 | | | Smith & Jungers (1997) | |
| | | 9 | 5 | | 3.74 | 2.33 | | | Hernandez-Camacho & Defler (1985) | |
| <i>Cebus capucinus</i> | F | 3 | 2 | | 3.66 | 2.50 | MM | A | AMNH (this study) | Dunbar (2000) |
| <i>Cebus olivaceus</i> | F, R | W | W | | 3.24 | 2.52 | UM and MM | A | Smith & Jungers (1997) | Dixson (1998) |
| | | 15 | 3 | | 3.10 | 1.90 | | | Rodriguez & Boher (1988) | |
| <i>Chiropotes albinasus</i> | F, R | 7 | 7 | | 3.15 | 2.49 | MM | A | Smith & Jungers (1997) | Lindenfors & Tullberg (1998) |
| <i>Chiropotes satamus satanus</i> | F | 4 | 3 | | 3.25 | 3.11 | MM | A | Hershkovitz (1985) | Lindenfors & Tullberg (1998) |
| <i>Chiropotes satamus chiropotes</i> | F, R | 20 | 19 | | 2.90 | 2.58 | MM | A | Smith & Jungers (1997) | Lindenfors & Tullberg (1998) |
| <i>Lagothrix lagothricha</i> | F, R | 16 | 9 | | 7.28 | 7.02 | MM | A (T) | Hershkovitz (1985) | Lindenfors & Tullberg (1998) |
| <i>Pithecia irrorata</i> | F | 2 | 2 | | 2.25 | 2.07 | Mon | A | Smith & Jungers (1997) | Lindenfors & Tullberg (1998) |
| <i>Pithecia monachus</i> | F, R | 16 | 10 | | 2.61 | 2.11 | Mon | A | Hershkovitz (1987) | Lindenfors & Tullberg (1998) |
| <i>Pithecia pithecia</i> | F, R | 10 | 4 | | 1.94 | 1.58 | Mon | A | Smith & Jungers (1997) | Lindenfors & Tullberg (1998) |
| <i>Saimiri boliviensis</i> | F, R | 14 | 13 | | 1.02 | 0.75 | MM | A | Fooden (1976b) | Lindenfors & Tullberg (1998) |
| <i>Saimiri oerstedii</i> | F, R | W | W | | 0.897 | 0.680 | MM | A | AMNH (this study) | Lindenfors & Tullberg (1998) |
| | | 3 | 3 | | 0.907 | 0.603 | | | Crile & Quiring (1940) | Dunbar (2000) |
| <i>Saimiri sciureus</i> | F, R | 8 | 4 | | 0.893 | 0.737 | MM | A | Schultz (1941) | Dunbar (2000) |
| | | 8 | 5 | | 0.740 | 0.635 | | | Fleagle & Mittermeier (1980) | |
| | | 17 | 58 | | 1.02 | 0.699 | | | Scollay (1980) | |
| | | 9 | 5 | | 1.08 | 0.859 | | | Hernandez-Camacho & Defler (1985) | |
| | | 29 | 34 | | 0.840 | 0.698 | | | Ique (1990) | |

| Taxon | Sample | Male | | Female | | Mating System | Substrate | Body Mass Source | Mating System Source |
|---|--------|-----------|-----|-----------|-----------|---------------|-----------|-------------------------------|------------------------------|
| | | N | N | mean (kg) | mean (kg) | | | | |
| <i>Saimiri ustus</i> | F, R | 11 | 6 | 0.921 | 0.799 | MM | A | Ford & Davis (1992) | Dunbar (2000) |
| <i>Saimiri vanzolinii</i> | F, R | 9 | 4 | 0.950 | 0.650 | MM | A | Smith & Jungers (1997) | Dunbar (2000) |
| Cercopithecinae | | | | | | | | | |
| <i>Allenopithecus nigroviridis</i> | F | 5 | 1 | 6.13 | 3.18 | MM | T | Smith & Jungers (1997) | Lindenfors & Tullberg (1998) |
| <i>Cercocebus agilis</i> | F | 2 | 2 | 9.50 | 5.66 | MM | A | Colyn (1994) | Plavcan (1999) |
| <i>Cercocebus atys</i> | F | 3 | 4 | 11.0 | 6.20 | MM | A (T) | Oates <i>et al.</i> (1990) | Lindenfors & Tullberg (1998) |
| <i>Cercocebus galeritus</i> | F, R | W | W | 9.61 | 5.26 | MM | A (T) | | Lindenfors & Tullberg (1998) |
| | | 3 | 3 | 10.19 | 5.47 | | | Gautier-Hion & Gautier (1976) | |
| | | 3 | 4 | 9.03 | 5.10 | | | Smith & Jungers (1997) | |
| <i>Cercocebus torquatus</i> | F | 3 | 1 | 8.01 | 5.50 | MM | A (T) | Sanders & Bodenbender (1994) | Lindenfors & Tullberg (1998) |
| <i>Cercopithecus ascanius schmidti</i> | F, R | 37 | 55 | 3.69 | 2.79 | UM | A | Colyn (1994) | Cords (2000) |
| <i>Cercopithecus ascanius katangae</i> | F, R | 32 | 187 | 3.71 | 2.97 | UM | A | Colyn (1994) | Cords (2000) |
| <i>Cercopithecus campbelli</i> | F, R | 10 | 9 | 4.50 | 2.70 | UM | A (T) | Oates <i>et al.</i> (1990) | Cords (2000) |
| <i>Cercopithecus cephus</i> | F, R | 8 | 10 | 4.09 | 2.88 | UM | A | Gautier-Hion & Gautier (1976) | Cords (2000) |
| <i>Cercopithecus denti</i> | F, R | 4 | 36 | 4.25 | 2.83 | UM | A | Colyn (1994) | Lindenfors & Tullberg (1998) |
| <i>Cercopithecus diana</i> | F, R | 4 | 11 | 5.20 | 3.90 | UM | A | Oates <i>et al.</i> (1990) | Cords (2000) |
| <i>Cercopithecus hamlyni</i> | F, R | 11 | 9 | 5.49 | 3.36 | UM | A | Colyn (1994) | Lindenfors & Tullberg (1998) |
| <i>Cercopithecus lhoesti</i> | F, R | 19 | 50 | 5.97 | 3.45 | UM | A (T) | Colyn (1994) | Lindenfors & Tullberg (1998) |
| <i>Cercopithecus mitis stuhlmanni</i> | F, R | 41 | 94 | 5.85 | 3.93 | UM | A | Colyn (1994) | Cords (2000) |
| <i>Cercopithecus mitis erythrarchus</i> | F, R | 6 | 6 | 9.31 | 4.91 | UM | A | Skinner & Smithers (1990) | Cords (2000) |
| <i>Cercopithecus neglectus</i> | F, R | W | W | 7.35 | 4.13 | UM | A (T) | | Cords (2000) |
| | | 4 | 4 | 7.00 | 3.96 | | | Gautier-Hion & Gautier (1976) | |
| | | 2 | 2 | 8.05 | 4.46 | | | Napier (1981) | |
| <i>Cercopithecus nictitans</i> | F, R | P | P | 6.67 | 4.25 | UM | A | | Cords (2000) |
| | | 16 | 9 | 6.61 | 4.22 | | | Gautier-Hion & Gautier (1976) | |
| | | 17 | 21 | 6.73 | 4.28 | | | Colyn (1994) | |
| <i>Cercopithecus petaurista</i> | F, R | 13 | 7 | 4.40 | 2.90 | UM | A | Oates <i>et al.</i> (1990) | Cords (2000) |
| <i>Cercopithecus pogonias</i> | F, R | W | W | 4.26 | 2.90 | UM | A | | Cords (2000) |
| | | 4 | 6 | 4.50 | 3.03 | | | Gautier-Hion & Gautier (1976) | |
| | | 1 | 4 | 3.30 | 2.70 | | | Colyn (1994) | |
| <i>Cercopithecus wolffi</i> | F, R | 13 | 84 | 3.80 | 2.88 | UM | A | Colyn (1994) | Lindenfors & Tullberg (1998) |
| <i>Chlorocebus aethiops</i> | F, R | P | P | 4.94 | 3.34 | MM | A (T) | | Cords (2000) |
| | | 109 total | | 4.21 | 2.74 | | | Anapol <i>et al.</i> (1995) | |
| | | 21 | 15 | 5.77 | 3.53 | | | Bolter & Zihlman (2003) | |
| | | 29 | 30 | 5.51 | 4.09 | | | Skinner & Smithers (1990) | |
| | | 60 | 90 | 4.26 | 2.98 | | | Turner <i>et al.</i> (1994) | |

| Taxon | Sample | Male N | Female N | Male mean (kg) | Female mean (kg) | Mating System | Substrate | Body Mass Source | Mating System Source |
|-------------------------------------|--------|--------|----------|----------------|------------------|---------------|-----------|----------------------------------|------------------------------|
| <i>Chlorocebus pygerythrus</i> | F, R | P | P | 4.28 | 2.98 | MM | A (T) | Turner <i>et al.</i> (1997) | Cords (2000) |
| | | 26 | 36 | 4.13 | 2.57 | | | Turner <i>et al.</i> (1997) | |
| | | 12 | 31 | 4.43 | 3.44 | | | Turner <i>et al.</i> (1997) | |
| | | 18 | 15 | 4.33 | 3.15 | | | Turner <i>et al.</i> (1997) | |
| | | 4 | 10 | 4.24 | 2.75 | | | Turner <i>et al.</i> (1997) | |
| <i>Chlorocebus sabaeus</i> | F, R | 61 | 71 | 5.30 | 3.30 | MM | A (T) | Horrocks (1986) | Cords (2000) |
| <i>Erythrocebus patas</i> | F, R | 9 | 14 | 12.40 | 6.50 | UM | T | Galat-Luong <i>et al.</i> (1996) | Cords (2000) |
| <i>Lophocebus albigena</i> | F, R | W | W | 7.89 | 6.01 | MM | A | | Dunbar (2000) |
| | | 5 | 6 | 8.98 | 6.40 | | | Gautier-Hion & Gautier (1976) | |
| | | 4 | 6 | 7.65 | 6.50 | | | Colyn (1994) | |
| | | 4 | 4 | 7.34 | 4.93 | | | Colyn (1994) | |
| | | 4 | 3 | 7.31 | 5.67 | | | Napier (1981) | |
| <i>Lophocebus aterrimus</i> | F | 1 | 4 | 7.90 | 5.64 | MM | A | Colyn (1994) | Lindenfors & Tullberg (1998) |
| <i>Macaca arctoides</i> | F | 7 | 3 | 12.20 | 8.40 | MM | T | Fooden (1990) | Lindenfors & Tullberg (1998) |
| <i>Macaca assamensis assamensis</i> | F, R | 16 | 12 | 11.30 | 6.70 | MM | A | Fooden (1988) | Lindenfors & Tullberg (1998) |
| <i>Macaca assamensis pelops</i> | F | 5 | 3 | 11.50 | 7.80 | MM | A | Fooden (1988) | Lindenfors & Tullberg (1998) |
| <i>Macaca cyclops</i> | F, R | 7 | 4 | 6.00 | 4.94 | UM and MM | A (T) | Rothenfluh (1976) | Lindenfors & Tullberg (1998) |
| <i>Macaca fascicularis</i> | F, R | P | P | 5.11 | 3.41 | MM | A | | Dunbar (2000) |
| | | 69 | 46 | 5.36 | 3.59 | | | Fooden (1995) | |
| | | 13 | 14 | 4.85 | 3.22 | | | MCZ (this study) | |
| <i>Macaca fuscata</i> | F, R | 10 | 23 | 10.97 | 8.03 | MM | A (T) | Kimura & Hanada (1995) | Dixson (1998) |
| <i>Macaca maura</i> | F, R | 17 | 4 | 9.72 | 6.05 | MM | A | Smith & Jungers (1997) | extrapolation |
| <i>Macaca mulatta</i> | F, R | 5 | 6 | 6.99 | 4.94 | MM | A (T) | Napier (1981) | Dunbar (2000) |
| <i>Macaca nemestrina nemestrina</i> | F, R | W | W | 11.2 | 6.59 | MM | A (T) | | Dixson (1998) |
| | | 3 | 5 | 10.6 | 6.14 | | | Fooden (1975) | |
| | | 5 | 4 | 11.6 | 7.15 | | | Fooden (1975) | |
| <i>Macaca nemestrina leonina</i> | F, R | 4 | 7 | 8.48 | 4.93 | MM | A (T) | Fooden (1975) | Dixson (1998) |
| <i>Macaca nigra</i> | F | 11 | 3 | 9.89 | 5.47 | MM | A (T) | Smith & Jungers (1997) | Lindenfors & Tullberg (1998) |
| <i>Macaca radiata</i> | F, R | 8 | 8 | 6.6 | 3.69 | MM | A (T) | Hartman (1938) | Dunbar (2000) |
| <i>Macaca sinica</i> | F, R | 14 | 26 | 5.66 | 3.3 | MM | A | Cheverud <i>et al.</i> (1992) | Dunbar (2000) |
| <i>Macaca tonkeana</i> | F | 6 | 3 | 14.9 | 9 | MM | A (T) | Smith & Jungers (1997) | Plavean (1999) |
| <i>Mandrillus sphinx</i> | F, R | 5 | 7 | 34.4 | 12.8 | UM | T | Setchell <i>et al.</i> (2001) | Lindenfors & Tullberg (1998) |
| <i>Miopithecus talapoin</i> | F, R | 7 | 9 | 1.38 | 1.12 | MM | A | Gautier-Hion & Gautier (1976) | Lindenfors & Tullberg (1998) |

| Taxon | Sample | Male N | Female N | Male mean (kg) | Female mean (kg) | Mating System | Substrate | Body Mass Source | Mating System Source |
|----------------------------------|--------|--------|----------|----------------|------------------|---------------|-----------|--------------------------------|------------------------------|
| <i>Papio anubis</i> | F, R | P | P | 23.0 | 13.3 | MM | T | | Dunbar (2000) |
| | | 177 | 237 | 21.1 | 12.2 | | | Berger (1972) | |
| | | 10 | 39 | 22.79 | 12.26 | | | Popp (1983) | |
| | | 39 | 35 | 21.2 | 11.7 | | | Phillips-Conroy & Jolly (1981) | |
| | | 43 | 26 | 21.46 | 12.54 | | | Popp (1983) | |
| | | 54 | 23 | 27.1 | 14.0 | | | Popp (1983) | |
| | | 18 | 18 | 21.9 | 12.7 | | | Gest & Siegel (1983) | |
| | | 5 | 10 | 22.72 | 15.16 | | | Eley <i>et al.</i> (1989) | |
| | | 9 | 17 | 23.88 | 13.01 | | | Eley <i>et al.</i> (1989) | |
| | | 4 | 9 | 24.80 | 16.07 | | | Eley <i>et al.</i> (1989) | |
| <i>Papio cynocephalus</i> | F, R | P | P | 22.3 | 12.0 | MM | T | | Dunbar (2000) |
| | | 37 | 21 | 21.8 | 12.3 | | | Smith & Jungers (1997) | |
| | | 12 | 11 | 22.32 | 11.65 | | | UTA (this study) | |
| | | 5 | 5 | 22.8 | 11.9 | | | Popp (1983) | |
| <i>Papio hamadryas</i> | F, R | P | P | 18.0 | 10.3 | UM | T | | Dunbar (2000) |
| | | 41 | 39 | 16.9 | 9.9 | | | Phillips-Conroy & Jolly (1981) | |
| | | 15 | 24 | 16.18 | 9.73 | | | Popp (1983) | |
| | | 7 | 13 | 21.0 | 11.4 | | | Popp (1983) | |
| <i>Papio ursinus</i> | F, R | 28 | 22 | 29.8 | 14.8 | MM | T | Bulger & Hamilton (1987) | Dunbar (2000) |
| <i>Theropithecus gelada</i> | F, R | 5 | 8 | 19.0 | 11.7 | UM and MM | T | Dechow (1983) | Dunbar (2000) |
| Colobinae | | | | | | | | | |
| <i>Colobus angolensis</i> | F, R | P | P | 9.71 | 7.59 | MM | A | | Lindenfors & Tullberg (1998) |
| | | 4 | 6 | 9.8 | 7.4 | | | Oates <i>et al.</i> (1994) | |
| | | 8 | 5 | 9.62 | 7.77 | | | Colyn (1994) | |
| <i>Colobus guereza guereza</i> | F | 3 | 4 | 13.5 | 9.2 | UM and MM | A | Oates <i>et al.</i> (1994) | Lindenfors & Tullberg (1998) |
| <i>Colobus guereza matschiei</i> | F, R | 13 | 14 | 9.89 | 7.9 | UM and MM | A | Smith & Jungers (1997) | Lindenfors & Tullberg (1998) |
| <i>Colobus polykomos</i> | F, R | 5 | 10 | 9.9 | 8.3 | UM and MM | A | Oates <i>et al.</i> (1994) | Lindenfors & Tullberg (1998) |
| <i>Colobus satanas</i> | F, R | 5 | 5 | 10.4 | 7.42 | UM and MM | A | Malbrant & Maclatchy (1949) | Lindenfors & Tullberg (1998) |
| <i>Colobus vellerosus</i> | F | 3 | 5 | 8.5 | 6.9 | UM and MM | A | Oates <i>et al.</i> (1990) | Lindenfors & Tullberg (1998) |
| <i>Nasalis larvatus</i> | F, R | 6 | 10 | 21.02 | 10.48 | UM and MM | A | MCZ (this study) | Lindenfors & Tullberg (1998) |

| Taxon | Sample | Male | | Female | | Mating System | Substrate | Body Mass Source | Mating System Source |
|---|--------|------|----|-----------|-----------|---------------|-----------|--------------------------------|------------------------------|
| | | N | N | mean (kg) | mean (kg) | | | | |
| <i>Ptilocolobus badius badius</i> | F, R | 9 | 14 | 8.3 | 8.2 | MM | A | Oates <i>et al.</i> (1990) | Struhsaker (2000) |
| <i>Ptilocolobus badius rufomitratatus</i> | F | 3 | 7 | 9.67 | 7.21 | UM and MM | A | Smith & Jungers (1997) | Struhsaker (2000) |
| <i>Presbytis comata</i> | F, R | 4 | 6 | 6.68 | 6.71 | UM | A | Rothenthal (1976) | Lindenfors & Tullberg (1998) |
| <i>Presbytis femoralis</i> | F, R | 23 | 18 | 6.26 | 6.19 | UM | A | Willis (1995) | Lindenfors & Tullberg (1998) |
| <i>Presbytis hosei</i> | F | 7 | 3 | 6.18 | 5.63 | UM | A | Willis (1995) | Lindenfors & Tullberg (1998) |
| <i>Presbytis melalophos</i> | F, R | 11 | 12 | 6.59 | 6.47 | UM | A | Willis (1995) | Plavcan (1999) |
| <i>Presbytis potenziani</i> | F, R | W | W | 6.31 | 6.40 | Mon | A | | Dixson (1998) |
| | | 7 | 2 | 6.14 | 6.41 | | | Brandon-Jones (1993) | |
| | | 6 | 4 | 6.5 | 6.4 | | | Tilson & Tenaza (1976) | |
| <i>Presbytis rubicunda</i> | F, R | P | P | 6.26 | 6.11 | UM | A | | Plavcan (1999) |
| | | 16 | 14 | 6.22 | 6.04 | | | MCZ (this study) | |
| | | 35 | 38 | 6.29 | 6.17 | | | Willis (1995) | |
| <i>Presbytis thomasi</i> | F | 3 | 5 | 6.77 | 6.69 | UM | A | Willis (1995) | Lindenfors & Tullberg (1998) |
| <i>Procolobus verus</i> | F, R | 20 | 14 | 4.7 | 4.2 | MM | A | Oates <i>et al.</i> (1990) | Lindenfors & Tullberg (1998) |
| <i>Pygathrix nemaeus</i> | F | 2 | 1 | 11.0 | 8.18 | UM and MM | A | Smith & Jungers (1997) | Lindenfors & Tullberg (1998) |
| <i>Rhinopithecus roxellana</i> | F, R | 7 | 4 | 17.9 | 11.6 | MM | A (T) | Jablonski & Pan Ruliang (1995) | Lindenfors & Tullberg (1998) |
| <i>Sennopithecus entellus entellus</i> | F, R | 9 | 11 | 13.0 | 9.89 | UM and MM | A (T) | Willis (1995) | Dixson (1998) |
| | | 5 | 9 | 19.2 | 14.8 | UM and MM | A (T) | Willis (1995) | Dixson (1998) |
| <i>Sennopithecus entellus schistacea</i> | F, R | 14 | 11 | 11.4 | 6.91 | UM and MM | A (T) | Willis (1995) | Dixson (1998) |
| <i>Sennopithecus entellus thersites</i> | F | 3 | 3 | 9.15 | 6.80 | UM | A | Napier (1985) | Plavcan (1999) |
| <i>Simias concolor</i> | F, R | 11 | 19 | 6.72 | 5.78 | UM | A | MCZ (this study) | Dixson (1998) |
| <i>Trachypithecus cristatus</i> | F | 3 | 2 | 7.70 | 7.35 | UM | A | Willis (1995) | extrapolation |
| <i>Trachypithecus francoisi</i> | F | 4 | 1 | 10.8 | 9.5 | UM | A | Oates <i>et al.</i> (1994) | extrapolation |
| <i>Trachypithecus geei</i> | F | 7 | 3 | 12.0 | 11.2 | UM | A | Willis (1995) | Dixson (1998) |
| <i>Trachypithecus johnii</i> | F, R | 7 | 8 | 7.77 | 6.22 | UM and MM | A | Fooden (1971) | Lindenfors & Tullberg (1998) |
| <i>Trachypithecus obscurus</i> | F, R | 8 | 5 | 7.93 | 6.95 | UM | A | Napier (1985) | Dixson (1998) |
| <i>Trachypithecus phayrei</i> | F, R | 7 | 5 | 12.0 | 9.86 | UM | A | Willis (1995) | Lindenfors & Tullberg (1998) |
| <i>Trachypithecus pileatus</i> | F | 3 | 3 | 8.17 | 5.90 | UM | A | Napier (1985) | Dixson (1998) |

| Taxon | Sample | Male N | Female N | Male mean (kg) | Female mean (kg) | Mating System | Substrate | Body Mass Source | Mating System Source |
|------------------------------------|--------|--------|----------|----------------|------------------|---------------|-----------|---------------------------|------------------------------|
| Hylobatidae | | | | | | | | | |
| <i>Hylobates agilis albibarbis</i> | F, R | 5 | 5 | 5.71 | 6.30 | Mon | A | Geissmann (1993) | Lindenfors & Tullberg (1998) |
| <i>Hylobates agilis unko</i> | F, R | 12 | 4 | 5.85 | 5.55 | Mon | A | Geissmann (1993) | Lindenfors & Tullberg (1998) |
| <i>Hylobates concolor</i> | F, R | 7 | 13 | 7.77 | 7.62 | Mon | A | Geissmann (1993) | Lindenfors & Tullberg (1998) |
| <i>Hylobates hooLOCK</i> | F, R | 13 | 5 | 6.87 | 6.88 | Mon | A | Geissmann (1993) | Lindenfors & Tullberg (1998) |
| <i>Hylobates klossii</i> | F | 2 | 4 | 5.67 | 5.89 | Mon | A | Geissmann (1993) | Lindenfors & Tullberg (1998) |
| <i>Hylobates lar lar</i> | F | 2 | 2 | 5.56 | 4.65 | Mon | A | Geissmann (1993) | Lindenfors & Tullberg (1998) |
| <i>Hylobates lar carpenteri</i> | F, R | 33 | 24 | 5.92 | 5.36 | Mon | A | MCZ (this study) | Lindenfors & Tullberg (1998) |
| <i>Hylobates lar entelloides</i> | F, R | P | P | 6.44 | 5.77 | Mon | A | | Lindenfors & Tullberg (1998) |
| | | 8 | 6 | 5.65 | 4.89 | | | Geissmann (1993) | |
| | | 11 | 3 | 7.23 | 6.65 | | | Geissmann (1993) | |
| <i>Hylobates lar vestitus</i> | F | 5 | 3 | 5.01 | 5.25 | Mon | A | Geissmann (1993) | Lindenfors & Tullberg (1998) |
| <i>Hylobates leucogenys</i> | F | 6 | 2 | 7.27 | 7.65 | Mon | A | Geissmann (1993) | Lindenfors & Tullberg (1998) |
| <i>Hylobates moloch</i> | F | 1 | 1 | 6.58 | 6.25 | Mon | A | Geissmann (1993) | Lindenfors & Tullberg (1998) |
| <i>Hylobates muelleri muelleri</i> | F, R | 5 | 7 | 5.44 | 5.27 | Mon | A | Geissmann (1993) | Lindenfors & Tullberg (1998) |
| <i>Hylobates muelleri abbotti</i> | F | 5 | 3 | 6.28 | 5.82 | Mon | A | Geissmann (1993) | Lindenfors & Tullberg (1998) |
| <i>Hylobates muelleri funereus</i> | F, R | W | W | 5.66 | 5.16 | Mon | A | | Lindenfors & Tullberg (1998) |
| | | 6 | 3 | 5.63 | 5.37 | | | Geissmann (1993) | |
| | | 2 | 4 | 5.75 | 5.01 | | | Geissmann (1993) | |
| <i>Hylobates pileatus</i> | F | 1 | 1 | 5.50 | 5.44 | Mon | A | Geissmann (1993) | Lindenfors & Tullberg (1998) |
| <i>Hylobates syndactylus</i> | F, R | P | P | 11.79 | 10.70 | Mon | A | | Lindenfors & Tullberg (1998) |
| | | 7 | 10 | 11.88 | 10.71 | | | Orgeldinger (1994) | |
| | | 5 | 7 | 11.70 | 10.68 | | | Geissmann (1993) | |
| Hominidae | | | | | | | | | |
| <i>Gorilla gorilla</i> | R | W | W | 169.3 | 75.7 | UM | T | | Lindenfors & Tullberg (1998) |
| <i>Gorilla gorilla gorilla</i> | F | 10 | 3 | 170.4 | 71.5 | UM | T | Smith & Jungers (1997) | Lindenfors & Tullberg (1998) |
| <i>Gorilla gorilla graueri</i> | F | 4 | 2 | 175.2 | 71.0 | UM | T | Smith & Jungers (1997) | Lindenfors & Tullberg (1998) |
| <i>Gorilla gorilla beringei</i> | F | 5 | 1 | 162.5 | 97.5 | UM | T | Smith & Jungers (1997) | Dixson (1998) |
| <i>Homo sapiens</i> | F, R | P | P | 57.4 | 49.7 | MM | T | | see below |
| | | 49 | 49 | 53.9 | 45.8 | | | Diaz <i>et al.</i> (1991) | |
| | | 121 | 162 | 60.2 | 53.6 | | | Jones & White (1994) | |
| | | 194 | 193 | 58.1 | 49.7 | | | Friedlaender (1987) | |
| <i>Pan paniscus</i> | F, R | 7 | 6 | 45.0 | 33.2 | MM | A (T) | Jungers & Susman (1984) | Dixson (1998) |

| Taxon | Sample | Male | | Female | | Mating System | Substrate | Body Mass Source | Mating System Source |
|--------------------------------------|--------|------|----|-----------|-----------|---------------|-----------|-------------------------|----------------------|
| | | N | N | mean (kg) | mean (kg) | | | | |
| <i>Pan troglodytes schweinfurthi</i> | F, R | W | W | 41.4 | 33.1 | MM | A (T) | | Dixson (1998) |
| | | 9 | 6 | 39.5 | 29.8 | | | Wrangham & Smuts (1980) | |
| | | 6 | 8 | 42.0 | 35.2 | | | Uehara & Nishida (1987) | |
| <i>Pan troglodytes troglodytes</i> | F, R | W | W | 59.7 | 45.8 | MM | A (T) | | Dixson (1998) |
| | | 3 | 3 | 60.0 | 47.4 | | | Jungers & Susman (1984) | |
| | | 2 | 1 | 59.3 | 41.0 | | | Smith & Jungers (1997) | |
| <i>Pan troglodytes verus</i> | F | 1 | 3 | 46.3 | 41.6 | MM | A (T) | Smith & Jungers (1997) | Dixson (1998) |
| <i>Pongo pygmaeus abelli</i> | F | 3 | 4 | 77.9 | 35.6 | UM and MM | A | Jungers (1988) | Dixson (1998) |
| <i>Pongo pygmaeus pygmaeus</i> | F, R | 7 | 13 | 78.5 | 35.8 | UM and MM | A | Jungers (1988) | Dixson (1998) |

Table 4.1. Sex-specific mean body mass, mating system, and substrate use for taxa included in this study.

Abbreviations: F, full sample; R, reduced sample; W, weighted mean of sex-specific population values; P, unweighted mean of sex-specific population values; Mon, monogamous; MM, multi-male, multi-female; UM, uni-male, multi-female; A, arboreal; T, terrestrial. *Homo sapiens* is designated here as MM rather than Mon to reflect the fact that many pair-bond relationships in humans occur serially and/or in parallel. *Most of these references are cited in Smith & Jungers (1997). I used their compilation as a starting point, then searched for later references. In some cases I went back to references cited in Smith & Jungers (1997) to look for standard deviation data to use in the quantitative genetics portion of this study. In other cases I simply used the mass data in their compilation, in which case I cite the original article but designate it with an asterisk. In some cases, groups designated here as distinct species are sometimes grouped with another species and no separate mating system data is available; in that case I assign the same mating system category to both taxa. Substrate information taken from Nowak (1999) and Nunn & van Schaik (2002).

| Full Sample | Traditional ANCOVA | | | | | | PGLS Best Branches | | | | | | PGLS Divergence Dates | | | | | | PGLS Equal Branch Lengths | | | | | |
|--------------|--------------------|-----|---------|--------|----------------|----------------|--------------------|---------|--------|----------------|----------------|----------------|-----------------------|--------|----------------|----------------|----------------|---------|---------------------------|----------------|----------------|----------------|--|--|
| | Group | N | Slope | SE | p ¹ | p ² | r ² | Slope | SE | p ¹ | p ² | r ² | Slope | SE | p ¹ | p ² | r ² | Slope | SE | p ¹ | p ² | r ² | | |
| Primates | Mon | 221 | 0.061* | 0.0087 | <0.001 | <0.001 | 0.378 | -0.007 | 0.0240 | 0.763 | 0.275 | 0.062 | -0.050 | 0.0291 | 0.088 | 0.522 | 0.089 | 0.015* | 0.0193 | 0.425 | 0.030 | 0.110 | | |
| | MM | 49 | 0.001 | 0.0154 | 0.940 | 0.254 | 0.011 | -0.006 | 0.0225 | 0.791 | 0.255 | 0.026 | -0.020 | 0.0261 | 0.440 | 0.153 | 0.065 | -0.022 | 0.0258 | 0.408 | 0.372 | 0.075 | | |
| | UM | 172 | 0.031* | 0.0128 | 0.016 | 0.003 | 0.429 | -0.009 | 0.0352 | 0.800 | 0.604 | 0.069 | -0.069 | 0.0405 | 0.090 | 0.808 | 0.097 | 0.039* | 0.0269 | 0.144 | 0.008 | 0.141 | | |
| Strepsirhini | Mon | 64 | -0.018* | 0.0203 | 0.388 | <0.001 | 0.498 | -0.030* | 0.0347 | 0.392 | 0.034 | 0.130 | -0.104 [†] | 0.0401 | 0.012 | 0.069 | 0.154 | -0.010* | 0.0401 | 0.812 | 0.005 | 0.088 | | |
| | MM | 104 | 0.047* | 0.0259 | 0.072 | 0.002 | 0.318 | 0.006 | 0.0505 | 0.898 | 0.605 | 0.070 | -0.070 | 0.0550 | 0.204 | 0.639 | 0.098 | 0.046 | 0.0459 | 0.315 | 0.086 | 0.154 | | |
| | UM | | | | | | | | | | | | | | | | | | | | | | | |
| Haplorhini | Mon | | | | | | | | | | | | | | | | | | | | | | | |
| | MM | | | | | | | | | | | | | | | | | | | | | | | |
| | UM | | | | | | | | | | | | | | | | | | | | | | | |
| Platyrrhini | Mon | | | | | | | | | | | | | | | | | | | | | | | |
| | MM | | | | | | | | | | | | | | | | | | | | | | | |
| | UM | | | | | | | | | | | | | | | | | | | | | | | |
| Catarrhini | Mon | | | | | | | | | | | | | | | | | | | | | | | |
| | MM | | | | | | | | | | | | | | | | | | | | | | | |
| | UM | | | | | | | | | | | | | | | | | | | | | | | |

Table 4.2a. Analysis of covariance (ANCOVA) and phylogenetic generalized linear model (PGLM) parameters and standard errors for models of $\log_{10}[M/F]$ dependent on $\log_{10}[F]$ and mating system: Full sample.

Probability 1 for slopes corresponds to Ho: difference between mating system slopes = 0; probability 2 for slopes corresponds to Ho: common slope for all mating systems = 0; probability for intercepts corresponds to Ho: difference of mating system intercepts = 0. * indicates significant difference between slopes or intercepts at $\alpha = 0.05$. † indicates significant difference of common slope from zero at $\alpha = 0.05$.

| Reduced Sample | Traditional ANCOVA | | | | | PGLS Best Branches | | | | | PGLS Divergence Dates | | | | | PGLS Equal Branch Lengths | | | | | | | |
|----------------|--------------------|---------------------|--------|---------|----------------|--------------------|----------------|--------|--------|----------------|-----------------------|----------------|---------|---------------------|----------------|---------------------------|--------------------|--------|-------|----------------|----------------|----------------|--|
| | Group | N | Slope | SE | p ¹ | p ² | r ² | Slope | SE | p ¹ | p ² | r ² | Slope | SE | p ¹ | p ² | r ² | Slope | SE | p ¹ | p ² | r ² | |
| Primates | 157 | 0.062 ^{2*} | 0.0103 | < 0.001 | 0.009 | 0.376 | 0.021 | 0.0231 | 0.373 | 0.429 | 0.053 | -0.024 | 0.0278 | 0.397 | 0.540 | 0.025 | 0.046 [†] | 0.0188 | 0.016 | 0.020 | 0.156 | | |
| Strepsirhini | 33 | 0.005 | 0.0116 | 0.669 | 0.882 | 0.250 | 0.003 | 0.0149 | 0.863 | 0.890 | 0.128 | 0.005 | 0.0178 | 0.773 | 0.794 | 0.066 | -0.003 | 0.0176 | 0.886 | 0.786 | 0.123 | | |
| Haplorhini | 124 | 0.027 | 0.0150 | 0.078 | 0.056 | 0.412 | 0.027 | 0.0342 | 0.430 | 0.416 | 0.059 | -0.044 | 0.0392 | 0.265 | 0.642 | 0.033 | 0.066 [†] | 0.0255 | 0.010 | 0.003 | 0.191 | | |
| Platyrrhini | 48 | -0.025 [*] | 0.0223 | 0.261 | < 0.001 | 0.452 | -0.016 | 0.0335 | 0.641 | 0.130 | 0.097 | -0.053 | 0.0360 | 0.146 | 0.480 | 0.063 | 0.006 | 0.0382 | 0.880 | 0.114 | 0.073 | | |
| Catarrhini | 73 | 0.035 | 0.0317 | 0.270 | 0.086 | 0.279 | 0.056 | 0.0519 | 0.281 | 0.503 | 0.090 | -0.048 | 0.0551 | 0.390 | 0.496 | 0.037 | 0.110 [†] | 0.0454 | 0.018 | 0.026 | 0.260 | | |
| Group | | Int. | SE | p | Int. | SE | p | Int. | SE | p | Int. | SE | p | Int. | SE | p | Int. | SE | p | | | | |
| Primates: | Mon | 0.006 [*] | 0.0121 | < 0.001 | 0.013 | 0.0621 | 0.086 | 0.009 | 0.140 | 0.310 | 0.014 [*] | 0.0371 | < 0.001 | 0.014 [*] | 0.0371 | < 0.001 | | | | | | | |
| | MM | 0.072 [*] | 0.0125 | | 0.059 | 0.0612 | | 0.057 | 0.139 | | 0.052 [*] | 0.0369 | | 0.052 [*] | 0.0369 | | | | | | | | |
| | UM | 0.095 [*] | 0.0107 | | 0.082 | 0.0612 | | 0.078 | 0.139 | | 0.088 [*] | 0.0360 | | 0.088 [*] | 0.0360 | | | | | | | | |
| Strepsirhini | | | | | | | | | | | | | | | | | | | | | | | |
| | Mon | -0.032 | 0.0147 | 0.057 | -0.024 | 0.0211 | 0.268 | -0.016 | 0.0535 | 0.602 | -0.018 | 0.0253 | 0.276 | -0.018 | 0.0253 | 0.276 | | | | | | | |
| | MM | -0.005 | 0.0113 | | 0.009 | 0.0192 | | 0.012 | 0.0522 | | 0.014 | 0.0236 | | 0.014 | 0.0236 | | | | | | | | |
| | UM | 0.020 | 0.0103 | | 0.011 | 0.0193 | | 0.008 | 0.0524 | | 0.014 | 0.0214 | | 0.014 | 0.0214 | | | | | | | | |
| Haplorhini: | Mon | 0.011 [*] | 0.0126 | < 0.001 | 0.043 | 0.0744 | 0.144 | 0.046 | 0.164 | 0.340 | 0.061 [*] | 0.0393 | 0.004 | 0.061 [*] | 0.0393 | 0.004 | | | | | | | |
| | MM | 0.115 [*] | 0.0156 | | 0.106 | 0.0752 | | 0.119 | 0.165 | | 0.105 [*] | 0.0414 | | 0.105 [*] | 0.0414 | | | | | | | | |
| | UM | 0.1390 [*] | 0.0164 | | 0.131 | 0.0753 | | 0.143 | 0.165 | | 0.145 [*] | 0.0402 | | 0.145 [*] | 0.0402 | | | | | | | | |
| Platyrrhini: | Mon | 0.0001 [*] | 0.0112 | < 0.001 | 0.033 | 0.0219 | 0.243 | 0.043 | 0.0368 | 0.646 | 0.043 | 0.0259 | 0.451 | 0.043 | 0.0259 | 0.451 | | | | | | | |
| | MM | 0.096 [*] | 0.0156 | | 0.092 | 0.0253 | | 0.093 | 0.0403 | | 0.091 | 0.0364 | | 0.091 | 0.0364 | | | | | | | | |
| | UM | 0.145 [*] | 0.0321 | | 0.099 | 0.0343 | | 0.091 | 0.0470 | | 0.075 | 0.0417 | | 0.075 | 0.0417 | | | | | | | | |
| Catarrhini: | Mon | -0.011 [*] | 0.0374 | < 0.001 | 0.005 | 0.0981 | 0.242 | 0.119 | 0.194 | 0.535 | -0.026 [*] | 0.0670 | 0.016 | -0.026 [*] | 0.0670 | 0.016 | | | | | | | |
| | MM | 0.139 [*] | 0.0324 | | 0.107 | 0.0907 | | 0.223 | 0.180 | | 0.049 [*] | 0.0644 | | 0.049 [*] | 0.0644 | | | | | | | | |
| | UM | 0.136 [*] | 0.0288 | | 0.132 | 0.0925 | | 0.249 | 0.181 | | 0.092 [*] | 0.0679 | | 0.092 [*] | 0.0679 | | | | | | | | |

Table 4.2b. Analysis of covariance (ANCOVA) and phylogenetic generalized linear model (PGLM) parameters and standard errors for models of $\log_{10}[M/F]$ dependent on $\log_{10}[F]$ and mating system: Reduced sample.

Probability 1 for slopes corresponds to Ho: difference between mating system slopes = 0; probability 2 for slopes corresponds to Ho: common slope for all mating systems = 0; probability for intercepts corresponds to Ho: difference of mating system intercepts = 0. * indicates significant difference between slopes or intercepts at alpha = 0.05. † indicates significant difference of common slope from zero at alpha = 0.05.

| Group | MS | Full Sample OLS Regression | | | | | Reduced Sample OLS Regression | | | | |
|-------------|-----|----------------------------|---------|--------|---------|----------------|-------------------------------|---------|--------|---------|----------------|
| | | N | Slope | SE | p | r ² | N | Slope | SE | p | r ² |
| Primates | Mon | 68 | 0.007 | 0.0106 | 0.498 | 0.007 | 43 | 0.014 | 0.0114 | 0.223 | 0.036 |
| | MM | 71 | 0.039 | 0.0233 | 0.095 | 0.040 | 54 | 0.034 | 0.0259 | 0.189 | 0.033 |
| | UM | 82 | 0.089* | 0.0120 | < 0.001 | 0.410 | 60 | 0.087* | 0.0141 | < 0.001 | 0.396 |
| Haplorhini | Mon | 57 | 0.014 | 0.0084 | 0.104 | 0.047 | 38 | 0.015 | 0.0105 | 0.170 | 0.052 |
| | MM | 59 | -0.008 | 0.0261 | 0.772 | 0.001 | 45 | -0.003 | 0.0279 | 0.915 | 0.000 |
| | UM | 56 | 0.102* | 0.0305 | 0.002 | 0.170 | 41 | 0.089* | 0.0368 | 0.021 | 0.130 |
| Platyrrhini | Mon | 37 | 0.072* | 0.0205 | 0.001 | 0.258 | 26 | 0.085* | 0.0227 | 0.001 | 0.370 |
| | MM | 23 | -0.090* | 0.0290 | 0.005 | 0.315 | 19 | -0.089* | 0.0304 | 0.009 | 0.337 |
| | UM | 4 | 0.261 | 0.1981 | 0.318 | 0.465 | 3 | 0.067 | 0.2101 | 0.803 | 0.092 |
| Catarrhini | Mon | 17 | -0.074 | 0.0916 | 0.430 | 0.042 | 10 | -0.011 | 0.1050 | 0.918 | 0.001 |
| | MM | 36 | -0.057 | 0.0330 | 0.092 | 0.081 | 26 | -0.030 | 0.0384 | 0.440 | 0.025 |
| | UM | 51 | 0.126* | 0.0387 | 0.002 | 0.177 | 37 | 0.110* | 0.0524 | 0.043 | 0.112 |

| Group | MS | N | Int. | SE | p | N | Int. | SE | p |
|-------------|-----|----|--------|--------|---------|----|--------|--------|---------|
| | | | | | | | | | |
| | MM | 71 | 0.092* | 0.0182 | < 0.001 | 54 | 0.089* | 0.0204 | < 0.001 |
| | UM | 82 | 0.077* | 0.0104 | < 0.001 | 60 | 0.087* | 0.0117 | < 0.001 |
| Haplorhini | Mon | 57 | 0.007 | 0.0047 | 0.118 | 38 | 0.011 | 0.0058 | 0.071 |
| | MM | 59 | 0.145* | 0.0217 | < 0.001 | 45 | 0.136* | 0.0232 | < 0.001 |
| | UM | 56 | 0.071* | 0.0281 | 0.014 | 41 | 0.093* | 0.0307 | 0.004 |
| Platyrrhini | Mon | 37 | 0.019* | 0.0068 | 0.010 | 26 | 0.025* | 0.0079 | 0.004 |
| | MM | 23 | 0.127* | 0.0179 | < 0.001 | 19 | 0.126* | 0.0189 | < 0.001 |
| | UM | 4 | -0.008 | 0.1302 | 0.959 | 3 | 0.091 | 0.1258 | 0.603 |
| Catarrhini | Mon | 17 | 0.073 | 0.0724 | 0.330 | 10 | 0.026 | 0.0848 | 0.770 |
| | MM | 36 | 0.226* | 0.0311 | < 0.001 | 26 | 0.196* | 0.0367 | < 0.001 |
| | UM | 51 | 0.047 | 0.0363 | 0.200 | 37 | 0.076 | 0.0445 | 0.095 |

Table 4.3. OLS regressions of $\log_{10}[M/F]$ against $\log_{10}[F]$ by mating system (MS).

Probabilities correspond to $H_0 = 0$. * indicates significant difference from H_0 at $\alpha = 0.05$.

| Full Sample | Traditional ANOVA | | | | PGLS Best Branches | | | | PGLS Divergence Dates | | | | PGLS Equal Branch Lengths | | | | | |
|---------------|-------------------|---|--------|--------|--------------------|----------------|--------|--------|-----------------------|----------------|--------|--------|---------------------------|----------------|--------|--------|--------|----------------|
| | Group | N | Mean | SE | p | r ² | Mean | SE | p | r ² | Mean | SE | p | r ² | Mean | SE | p | r ² |
| Primates: | Mon 68 | | 0.009* | 0.0107 | <0.001 | 0.235 | 0.016* | 0.0721 | <0.001 | 0.062 | 0.014* | 0.1721 | <0.001 | 0.077 | 0.001* | 0.0421 | <0.001 | 0.107 |
| | MM 71 | | 0.117* | 0.0105 | | | 0.051* | 0.0717 | | | 0.043* | 0.1717 | | | 0.038* | 0.0424 | | |
| | UM 82 | | 0.111* | 0.0098 | | | 0.097* | 0.0717 | | | 0.104* | 0.1717 | | | 0.089* | 0.0417 | | |
| Strepsirhini: | Mon 11 | | 0.010 | 0.0156 | 0.776 | 0.011 | 0.001 | 0.0309 | 0.566 | 0.024 | -0.006 | 0.0863 | 0.292 | 0.052 | -0.012 | 0.0407 | 0.239 | 0.060 |
| | MM 12 | | 0.005 | 0.0149 | | | 0.020 | 0.0314 | | | 0.030 | 0.0863 | | | 0.017 | 0.0405 | | |
| | UM 26 | | 0.018 | 0.0101 | | | 0.030 | 0.0294 | | | 0.034 | 0.0856 | | | 0.036 | 0.0362 | | |
| Haplorhini: | Mon 57 | | 0.008* | 0.0105 | <0.001 | 0.409 | 0.040* | 0.0860 | 0.002 | 0.069 | 0.048* | 0.2023 | <0.001 | 0.082 | 0.034* | 0.0432 | <0.001 | 0.130 |
| | MM 59 | | 0.140* | 0.0104 | | | 0.094* | 0.0863 | | | 0.078* | 0.2029 | | | 0.089* | 0.0461 | | |
| | UM 56 | | 0.155* | 0.0106 | | | 0.143* | 0.0863 | | | 0.143* | 0.2028 | | | 0.144* | 0.0451 | | |
| Platyrrhini: | Mon 37 | | 0.004* | 0.0082 | <0.001 | 0.492 | 0.030* | 0.0232 | 0.021 | 0.119 | 0.038 | 0.0471 | 0.153 | 0.060 | 0.035 | 0.0275 | 0.061 | 0.088 |
| | MM 23 | | 0.083* | 0.0104 | | | 0.085* | 0.0241 | | | 0.076 | 0.0493 | | | 0.089 | 0.0355 | | |
| | UM 4 | | 0.160* | 0.0250 | | | 0.128* | 0.0319 | | | 0.124 | 0.0551 | | | 0.125 | 0.0412 | | |
| Catarrhini: | Mon 17 | | 0.015* | 0.0213 | <0.001 | 0.295 | 0.066* | 0.0958 | 0.026 | 0.070 | 0.092* | 0.2247 | 0.012 | 0.083 | 0.087* | 0.0572 | <0.001 | 0.146 |
| | MM 36 | | 0.176* | 0.0147 | | | 0.150* | 0.0795 | | | 0.136* | 0.2049 | | | 0.160* | 0.0512 | | |
| | UM 51 | | 0.156* | 0.0123 | | | 0.196* | 0.0789 | | | 0.202* | 0.2046 | | | 0.222* | 0.0493 | | |

| Reduced Sample | Traditional ANOVA | | | | PGLS Best Branches | | | | PGLS Divergence Dates | | | | PGLS Equal Branch Lengths | | | | | |
|----------------|-------------------|---|---------|--------|--------------------|----------------|--------|--------|-----------------------|----------------|--------|--------|---------------------------|----------------|---------|--------|--------|----------------|
| | Group | N | Mean | SE | p | r ² | Mean | SE | p | r ² | Mean | SE | p | r ² | Mean | SE | p | r ² |
| Primates: | Mon 43 | | 0.006* | 0.0134 | <0.001 | 0.229 | 0.009* | 0.0619 | 0.022 | 0.048 | 0.013 | 0.1396 | 0.197 | 0.021 | -0.002* | 0.0373 | <0.001 | 0.123 |
| | MM 54 | | 0.111* | 0.0120 | | | 0.059* | 0.0611 | | | 0.058 | 0.1389 | | | 0.043* | 0.0376 | | |
| | UM 60 | | 0.114* | 0.0113 | | | 0.083* | 0.0612 | | | 0.079 | 0.1390 | | | 0.082* | 0.0367 | | |
| Strepsirhini: | Mon 5 | | -0.032* | 0.0145 | 0.015 | 0.245 | -0.024 | 0.0204 | 0.131 | 0.127 | -0.018 | 0.0523 | 0.373 | 0.064 | -0.018 | 0.0244 | 0.141 | 0.122 |
| | MM 9 | | -0.004* | 0.0108 | | | 0.008 | 0.0188 | | | 0.011 | 0.0512 | | | 0.014 | 0.0230 | | |
| | UM 19 | | 0.017* | 0.0074 | | | 0.010 | 0.0181 | | | 0.006 | 0.0513 | | | 0.015 | 0.0203 | | |
| Haplorhini: | Mon 38 | | 0.011* | 0.0127 | <0.001 | 0.396 | 0.043* | 0.0743 | 0.034 | 0.054 | 0.046 | 0.1645 | 0.246 | 0.023 | 0.042* | 0.0398 | <0.001 | 0.146 |
| | MM 45 | | 0.134* | 0.0117 | | | 0.112* | 0.0747 | | | 0.112 | 0.1652 | | | 0.100* | 0.0427 | | |
| | UM 41 | | 0.158* | 0.0123 | | | 0.138* | 0.0746 | | | 0.134 | 0.1650 | | | 0.145* | 0.0415 | | |
| Platyrrhini: | Mon 26 | | 0.006* | 0.0100 | <0.001 | 0.435 | 0.034 | 0.0216 | 0.114 | 0.092 | 0.045 | 0.0373 | 0.692 | 0.016 | 0.043 | 0.0255 | 0.184 | 0.072 |
| | MM 19 | | 0.084* | 0.0117 | | | 0.087 | 0.0224 | | | 0.077 | 0.0391 | | | 0.094 | 0.0325 | | |
| | UM 3 | | 0.130* | 0.0294 | | | 0.093 | 0.0315 | | | 0.073 | 0.0461 | | | 0.077 | 0.0404 | | |
| Catarrhini: | Mon 10 | | 0.017* | 0.0276 | <0.001 | 0.266 | 0.058 | 0.0857 | 0.068 | 0.074 | 0.072 | 0.1860 | 0.388 | 0.027 | 0.079* | 0.0529 | <0.001 | 0.198 |
| | MM 26 | | 0.170* | 0.0171 | | | 0.168 | 0.0713 | | | 0.172 | 0.1697 | | | 0.156* | 0.0479 | | |
| | UM 37 | | 0.163* | 0.0143 | | | 0.197 | 0.0706 | | | 0.194 | 0.1691 | | | 0.216* | 0.0459 | | |

Table 4.4. Analysis of variance (ANOVA) parameters and confidence intervals (CI) for means of $\log_{10}[M/F]$ by mating system.

Probabilities are for F-tests for significant differences of means. * indicates significant difference at $\alpha = 0.05$.

| Group | Variables | N | df | Traditional | | Best Branches | | Divergence Dates | | Equal Branch Lengths | | | | | |
|----------------|----------------------|-----|--------|----------------|-------|---------------|----------------|------------------|--------|----------------------|-------|--------|-------|-------|--------|
| | | | | r ² | F | p | r ² | F | p | r ² | F | p | | | |
| All Primates F | size, MS, Arb, Ter | 221 | 5, 215 | 0.491 | 41.4 | <0.001 | 0.098 | 4.66 | <0.001 | 0.117 | 5.68 | <0.001 | 0.131 | 6.50 | <0.001 |
| All Primates R | size, MS, Arb, Ter | 157 | 5, 151 | 0.485 | 28.4 | <0.001 | 0.110 | 3.74 | 0.003 | 0.075 | 2.45 | 0.036 | 0.176 | 6.44 | <0.001 |
| Strepsirhini F | size, MS, Arb or Ter | 49 | 4, 44 | 0.011 | 0.126 | 0.972 | 0.030 | 0.345 | 0.846 | 0.066 | 0.783 | 0.543 | 0.081 | 0.966 | 0.436 |
| Strepsirhini R | size, MS, Arb or Ter | 33 | 4, 28 | 0.251 | 2.34 | 0.079 | 0.128 | 1.03 | 0.408 | 0.067 | 0.501 | 0.735 | 0.129 | 1.04 | 0.406 |
| Haplorhini F | size, MS, Arb, Ter | 172 | 5, 166 | 0.566 | 43.2 | <0.001 | 0.114 | 4.26 | 0.001 | 0.131 | 5.02 | <0.001 | 0.168 | 6.69 | <0.001 |
| Haplorhini R | size, MS, Arb, Ter | 124 | 5, 118 | 0.553 | 29.1 | <0.001 | 0.126 | 3.40 | 0.007 | 0.096 | 2.52 | 0.033 | 0.213 | 6.40 | <0.001 |
| Platyrrhini F | size, MS, Ter | 64 | 4, 59 | 0.511 | 15.4 | <0.001 | 0.138 | 2.35 | 0.064 | 0.156 | 2.72 | 0.038 | 0.097 | 1.58 | 0.191 |
| Platyrrhini R | size, MS, Ter | 48 | 4, 43 | 0.470 | 9.52 | <0.001 | 0.113 | 1.36 | 0.262 | 0.068 | 0.786 | 0.541 | 0.093 | 1.10 | 0.369 |
| Catarrhini F | size, MS, Arb, Ter | 104 | 5, 98 | 0.476 | 17.8 | <0.001 | 0.122 | 2.73 | 0.024 | 0.134 | 3.03 | 0.014 | 0.189 | 4.57 | 0.001 |
| Catarrhini R | size, MS, Arb, Ter | 73 | 5, 67 | 0.459 | 11.3 | <0.001 | 0.154 | 2.44 | 0.043 | 0.103 | 1.54 | 0.188 | 0.273 | 5.03 | 0.001 |

Table 4.5. Coefficients of determination and F-tests for complete linear models.

Complete models are presented for each clade. Abbreviations: F, full data set; R, reduced data set; MS, mating system; Arb, arboreality; Ter, terrestriality; df, degrees of freedom. Arboreality and terrestriality are the same variable for Strepsirhini, so the complete model only contains one substrate variable. All Platyrrhini in this study are primarily arboreal, thus the arboreality variable carries no information for platyrrhines and is not included in the complete model.

Chapter 5: Global Skeletal Size Variables and Comparative Primatology

INTRODUCTION

Many primatological comparative studies take into consideration the effects of size. Such studies include investigations of morphological, ecological, behavioral, and/or physiological traits in one or more species, and may be concerned with establishing the relationship between size and other factors or demonstrating that size has no effect whatsoever on particular factors. The importance of incorporating size into comparative studies makes the selection of an appropriate size variable for a given research question critical.

When a measure of overall body size is appropriate, body mass is often considered to be the best choice: since the density of all animals is roughly the same, body mass is a directly comparable measure of size (as a proxy for volume) between organisms of different shape (Jungers, 1985). However, body mass is highly variable over time in response to many factors (*e.g.*, environmental, physiological, reproductive, *etc.*). Longitudinal studies in non-pregnant adult primates show that body mass measurements can change by more than 20% over relatively short periods of time (weeks or months), even in primates that do not enter a torpor state (*e.g.*, Du Mond & Hutchison, 1967; Goldizen *et al.*, 1988; Bernstein *et al.*, 1989; Glander *et al.*, 1992; Dietz *et al.*, 1994; Richard *et al.*, 2000; Perret & Aujard, 2001). For longitudinal studies of living primates, temporal variation in body size may be the variable of interest. However, what is usually appropriate for comparative studies of skeletal specimens is not the variability in mass over time for a single individual, but a measure of central tendency of body size for each individual included in a particular analysis.

In addition, although body mass is measurable for any animal given an appropriate measuring tool, many existing museum specimens often were not weighed prior to being skeletonized. One technique for dealing with the missing data problem is to predict body mass from postcranial measurements. Several studies have generated such prediction equations (*e.g.*, Aiello, 1981; Jungers, 1987; Ruff, 1987; 1988; Ruff *et al.*, 1989; 1990a; 1990; Dagosto & Terranova, 1992; Rafferty *et al.*, 1995; Delson *et al.*, 2000; 2002). However, comparisons between two or more predictions are often shown to be meaningless once prediction intervals are taken into account (Jungers reply to Smith, 1996).

This paper addresses the needs of those researchers who would like to have a stable measure of overall adult size that is available for every individual in a skeletal collection. I rely on the demonstration by Mosimann (1970) that geometric means of variables measured in the same units (*e.g.*, all linear measures in millimeters or all area measures in mm²) are robust size variables that can be used to demonstrate equivalence with, or deviation from, geometric similarity (*i.e.*, isometry and allometry, respectively), and the observation of Jungers *et al.* (1995) that variables which scale isometrically are directly proportional to each other (*i.e.*, raw variables X and Y can be expressed as $Y=cX$, where c is a constant).

Here I distinguish between two types of adult body mass variables: **point body mass (PBM)** and **central tendency mass (CTM)**. Point body mass refers to a single measurement of mass taken at a particular point in time for an individual adult specimen. For example, if a wild-caught museum specimen is weighed once in the field prior to the removal of the soft tissue, that weight is a measure of PBM¹. Central tendency mass is an idealized central tendency of adult body mass about which PBM varies for a particular

¹ Although weight is technically a force, weight and mass are used interchangeably throughout the text.

individual. CTM can be approximated by an arithmetic mean of several PBM measurements from a single individual (*e.g.*, Leigh, 1992). The PBM measurements used in the mean should include only those measurements taken during adulthood.

The mathematical relationship between PBM and CTM can be stated explicitly ([Appendix H](#)). Of primary importance here is that the mean of PBM and CTM for a large number of individuals will converge on the same value. Therefore, analyses of sex-specific means of PBM measurements will not differ significantly from the same analyses performed using sex-specific means of CTM, provided the sample of each sex-specific group is large enough. Thus inter-specific relationships that have been demonstrated to exist between sex-specific PBM and other variables can also be said to apply to sex-specific CTM. Consideration of the variability of individual PBM measurements about CTM ([Appendix H](#)) indicates that the same cannot be said for analyses that treat individuals (rather than groups) as data.

Size measured directly from the postcranial skeleton may provide a better approximation of CTM than does PBM since postcranial skeletal size is expected to vary less over time than body mass for a given individual (Hartwig-Scherer & Martin, 1992). In addition, a skeletal measure of size enjoys the advantage of potentially being measurable for every specimen in analysis, even those that were not weighed at the time of collection. One way that skeletal size can be measured is through the use of a geometric mean of multiple measurements. This approach has been successfully used in developing regional size variables for primate morphometrics (*i.e.*, variables that measure the size of a particular skeletal element such as the femur or the cranium, *e.g.*, Falsetti *et al.*, 1993; Jungers *et al.*, 1995; Richmond & Jungers, 1995; Lague & Jungers, 1996; Ravosa, 1998) as well as an overall size variable (*e.g.*, Jantz & Jantz, 1999). Geometric means that scale isometrically with CTM are particularly useful because many ratios,

distribution parameters, and regression parameters will be identical regardless of whether CTM or an isometric variable is used for a set of analyses ([Appendix I](#)). Also, because skeletal size measures should vary less than PBM over time, measure of relative variability (such as coefficients of variation) of skeletal size should provide better approximations for variability of CTM.

If the goal is to represent overall body size, a geometric mean should incorporate measurements from multiple elements of the postcranium (*e.g.*, femur, tibia, humerus, radius). Although it is possible to find single variables that scale isometrically with CTM (*e.g.*, acetabulum height in hominoids, Jungers, 1990b), measurements of a particular anatomical region may underestimate or overestimate body size in a given individual due to pathology, measurement error, atypical loading regime, or some other cause. By sampling across multiple elements, not only is a variable more representative of overall size than regional size, it is also less likely to be significantly affected by one unusually high or low measurement. Geometric means that sample across multiple postcranial elements are referred to here as **skeletal size variables (SSV)**. Skeletal size variables that are shown to scale isometrically with CTM are defined as **global skeletal size variables (GSV)**.

Why Use Global Skeletal Size Variables?

At this point the reader may question why one should use a GSV if CTM must be known to verify the utility of the GSV, particularly since CTM data are rarely available. However, because sample means of PBM and CTM converge on the same value, PBM data may be used to determine whether a SSV qualifies as a GSV. If a stable measure of body size is desired, a GSV is preferable over PBM, even when both variables are available. More importantly, a GSV can be verified using published sex-specific PBM data. Then the GSV can be used in intra-specific analyses that were previously

unfeasible due to the small number of specimens with recorded PBM (as will be shown below). The ability to conduct morphological research at low taxonomic levels represents a significant advance for studies of evolution, a process that occurs at the level of populations rather than species or genera.

SAMPLE AND METHODS

Sample

Empirical comparisons of PBM and CTM in a primate population are performed using longitudinal body mass data drawn from records at the Duke University Primate Center for free-ranging *Lemur catta* (32 males, 31 females). Each individual is represented by a minimum of 5 adult PBM measurements.

Two examples are presented in this paper that test whether an SSV can be found that is a GSV for the skeletal samples under consideration. The first example uses a sample of wild adult *Saimiri boliviensis boliviensis* postcranial skeletons (11 males, 12 females); all specimens have an associated PBM measured at the time of capture. The second example considers 760 wild adult skeletons from 20 primate species in addition to the first sample; most specimens do not have associated body mass data ([Table 5.1](#)). The 21 species represent several major primate radiations and most of the size range of extant primates. Specimens are identified as adult if epiphyseal fusion is complete in the measured postcranial elements.

Methods

Measurements include maximum breadths along anatomical planes as well as anatomical major and minor axes at midshaft and articular surfaces for the femur, tibia, humerus, and radius ([Table 5.2](#)). The major axis is the largest diameter of a shape. The minor axis is a shorter diameter that is perpendicular to the major axis at the widest point

in the shape. These axes sometimes coincide with anatomical planes, but not always (Fig. 5.1).

A skeletal size variable (SSV1) is constructed from the 16 measurements in Table 5.2. Each bone is represented by four measurements. SSV1 is the geometric mean of the 16 measurements, raised to the third power. Cubing the geometric mean renders it volumetric, rendering direct comparisons to body mass in raw data space meaningful². SSV1 is calculated for each individual in the sample.

Comparison of PBM and CTM

Comparison of body mass variables are made for *Lemur catta* to illustrate the variability of PBM about CTM. CTM is approximated in ring-tailed lemurs by calculation of an arithmetic mean of all adult PBM measurements available for each individual. PBM is highly variable about CTM, and individual measures of PBM can be up to 33% larger or smaller than CTM for a given individual (Fig. 5.2a, Table 5.3). Regression of a random sample of PBM measurements against corresponding CTM yields an isometric scaling slope, but over 40% of the variation in PBM is unaccounted for by CTM (Fig. 5.2b).

Identifying Global Skeletal Size Variables

Since a GSV is only needed in those situations where CTM is unavailable, demonstrating that a SSV is directly proportional to CTM is, strictly speaking, impossible. However, it can be shown that a SSV behaves as if it were directly proportional to CTM at the scale and resolution used for a particular study. A two-step strategy is set forth here: 1) demonstrate that a SSV is possibly directly proportional to

² It has been argued that the cube root of body mass should be the preferred size variable for many comparisons Vogel, S. (1988). *Life's Devices: The Physical World of Animals and Plants*: Princeton University Press.. A geometric mean of linear dimensions can be compared directly (without first being cubed) to the cube root of body mass.

CTM by regressing PBM against SSV, and 2) demonstrate that results of analyses based on SSV and PBM (*e.g.*, comparison of dimorphism ratios or allometric relationships) are statistically indistinguishable at a given alpha level of interest (typically 0.05) for those taxa where PBM is known for the sample specimens or from published sources. Step one excludes those SSV that are unlikely to be GSV, and step two determines whether or not a SSV that has passed step one behaves as a GSV.

The first step requires further consideration of the relationship between CTM and PBM. As shown in [Figure 5.2a](#), PBM can vary considerably about the value of CTM. Any particular sample of PBM measurements will not be directly proportional to CTM, as the data points will not all fall on a line passing through the origin of a bivariate plot in raw data space (*i.e.*, not logarithmically transformed) ([Fig. 5.2b](#)). However, because the means of PBM and CTM converge on the same value, a regression line passing through the data in raw data space should have an intercept that does not significantly differ from zero. If a variable (such as a GSV) is directly proportional to CTM, a bivariate plot of the two would show data points falling directly on a line passing through the origin. A plot of PBM against GSV will be similar to a plot of PBM against CTM. It will resemble [Figure 5.2b](#) in that data points will vary about the regression line and the intercept will not significantly differ from zero; it will differ in that the slope of a regression line passing through the origin will be the value of the proportionality constant (c in equation [I.1](#) from [Appendix I](#)) rather than the identity value of one.

When performing these regressions, Model I regression is preferred to Model II because of the large component of additional error in the PBM term (that is, the component that accounts for the difference between PBM and CTM). Two ordinary least squares (OLS) regressions are performed: 1) an unconstrained regression to test for a slope different from zero and an intercept not different from zero, and 2) a regression

constrained to intercept the Y-axis at zero to test for a slope not different from the slope of the first regression.

Accepting the null hypotheses that the intercept of the first regression is equal to zero and that the two slopes are equal to each other is subject to Type II error, which is more likely to occur than Type I error. Accordingly, a SSV for which these null hypotheses are not rejected cannot be said to be directly proportional to CTM; rather, the possibility that the SSV is directly proportional is not rejected. This possibility is further tested in the second step.

Step two involves generating parameters and confidence intervals using a SSV and PBM for all groups for which mass data is available. Since the means of PBM and CTM are expected to be equal, while variances (and thus coefficients of variation) of PBM are not expected to be equal to those of CTM, expectations of equality only apply to means ratios and slopes from regressions that use log-transformed means as data points. Most often this will require comparing parameters calculated from the SSV as measured in the study sample to parameters reported in published sources. Examples are provided in the results. If parameters are not significantly different at the desired alpha level, then the SSV behaves as if it is directly proportional to CTM, regardless of whether or not it is exactly directly proportional. Thus the SSV qualifies as a GSV.

RESULTS

Example 1: Individuals with Known PBM

GSV Verification – Step 1

The value of SSV1 was calculated for each individual specimen of *Saimiri boliviensis boliviensis* (Table 5.4). Two OLS regressions of PBM against SSV1 in raw data space were performed (Fig. 5.3). One regression constrains the intercept to the origin, the other does not. Visual comparison of the two regression lines shows very little

difference between them, as do statistical comparisons (regressions 1 and 2 in [Table 5.5](#)). The intercept of the unconstrained regression is not significantly different from zero. Slopes of both regressions are significantly different from zero ($P < 0.05$), even when using Smith's (1994) adjustment to degrees of freedom to account for clumping of the data points. Slopes of the two regressions do not differ significantly from each other at $P < 0.05$.

GSV Verification – Step 2

Size dimorphism ratios (mean male size divided by mean female size) were calculated for PBM and SSV1. Ninety-five percent confidence limits were generated for these ratios using the percentile bootstrap method (Chernick, 1999). Size dimorphism ratio using PBM is 1.39 (95% confidence interval = 1.25 - 1.56); ratio using SSV1 is 1.37 (95% confidence interval = 1.29 - 1.45). There is no significant difference in the size dimorphism ratios based on PBM and SSV1.

Example 2: Individuals with Unknown PBM

GSV Verification – Step 1

The value of SSV1 was calculated for each individual summarized in [Table 5.1](#) and used to determine sex-specific means for those 21 taxa ([Table 5.6](#)). Sex-specific body mass values were taken from Smith and Jungers' (1997) compilation of primate body mass. A plot of constrained and unconstrained OLS regressions of mean PBM against mean SSV1 shows 1) tight agreement between the lines and 2) an unconstrained regression that does not significantly differ from zero in the value of its intercept ([Fig. 5.4a](#), regressions 3 and 4 in [Table 5.5](#)). However, a bivariate plot of these same data in logarithmic data space shows the regressions to be dominated by the largest primates; *i.e.*, the hominoids ([Fig. 5.4b](#)).

Restricting the analysis to the hominoids in the sample (*Hylobates*, *Pan*, *Pongo*, and *Gorilla*) reduces the size range considerably and limits the analysis to those taxa that acted as leverage points when considering the full sample. A plot of constrained and unconstrained OLS regressions of mean PBM against mean SSV1 shows 1) highly similar lines and 2) an unconstrained regression that does not significantly differ from zero in the value of its intercept (Fig. 5.5, regressions 5 and 6 in Table 5.5). Reanalysis of the hominoids with the largest and smallest taxa removed (*Gorilla* and *Hylobates*) yields regression lines that do not differ significantly from those generated for the full hominoid sample (regressions 7 and 8 in Table 5.5).

GSV Verification – Step 2

Slopes of regressions of logarithmically-transformed linear dimensions against log-transformed SSV1 were compared to published slopes calculated for PBM using a similar data set. Jungers' (1990b) non-human hominoid data set is composed of the same taxa in the present sample plus *Hylobates syndactylus* (an intermediate-sized hominoid that falls in the mid-range of all regressions). Jungers analyzes the allometric relationship between sex-specific mean PBM and sixteen linear dimensions of postcranial joints; the same analyses were performed on the sample in this study for the five linear dimensions in common between these two studies (dimensions 2, 5, 9, 13, and 14 in Jungers' study) (Table 5.7). In all cases there are no significant differences between the slopes found by Jungers and the slopes in this study ($\alpha = 0.05$). Additionally, in the one case for these five variables that Jungers finds significant negative allometry (TPLAP), the slope is also negatively allometric in this study. A slope that approaches significance in Jungers' study is found to be negatively allometric here (RHMaj).

Intra-specific Scaling Relationships

Regressions of log-transformed linear dimensions against log-transformed SSV1 were also performed separately for each taxon in the hominoid sample using individuals as data points. Several intra-specific regressions were found to differ significantly from the inter-specific regressions, well more than the 1.25 differences expected by chance in a collection of 25 regressions (Table 5.8). For example, Figure 5.6 shows a bivariate plot of log-transformed RHMaj against log-transformed SSV1; the significantly positively allometric intra-specific regressions for *Hylobates lar* and *Gorilla gorilla* are superimposed on the significantly negative allometric inter-specific regression for the full hominoid sample.

DISCUSSION

Example 1: Individuals with Known PBM

As noted in the methods, if a SSV is directly proportional to CTM (*i.e.*, scales isometrically with CTM and thus is a GSV) then plots of CTM against SSV should place all data points on a line passing through the origin. Plots of PBM against SSV should resemble Figure 5.2b. Therefore the variance about the regression line of PBM against a GSV is due to the variability of PBM about CTM. In the case of squirrel monkeys (the taxon under consideration in this example), particularly high values of PBM compared to CTM should be expected occasionally for males since they have been observed to increase their body mass by over 10% on average just prior to breeding seasons (Du Mond & Hutchison, 1967; Coe & Rosenblum, 1978). Visual comparison of Figures 5.2b and 5.3 shows them to be quite similar, differing only in the slope as expected.

If SSV1 is directly proportional to CTM then SSV1 is a GSV, and thus an ideal size variable. Application of the two-step method demonstrates clear support for the hypothesis that SSV1 behaves as a GSV for *Saimiri boliviensis*. The regression analysis

of SSV1 and PBM (step 1) does not falsify this hypothesis: the intercept of the unconstrained regression is not significantly different from zero, and the slopes of the two regressions do not differ significantly. The comparison of ratios of size dimorphism for SSV1 and PBM (step 2) shows that the two ratios are statistically indistinguishable at $\alpha = 0.05$. Thus SSV1 behaves as if it is directly proportional to CTM at that alpha level, regardless of whether the relationship is exactly directly proportional or not. It can be concluded that SSV1 acts as a GSV, and thus an ISV, for use with this taxon.

Example 2: Individuals with Unknown PBM

The second example differs from the first in that the second example uses mean PBM data, while the first uses individual PBM data. Individual PBM data points are expected to vary about CTM (*e.g.*, [Figure 5.2b](#)). However, because the population means of PBM and CTM are equal ([Appendix H](#)), a plot of PBM against CTM using taxon- or sex-specific means as data points would place all points directly on a line passing through the origin with a slope of one, given infinitely large sample sizes. Since sample sizes are not infinite, PBM means are expected to converge on CTM means but will rarely equal them. Means based on small samples of PBM can be quite different from population means due to random sampling error. Therefore plots of mean PBM against mean CTM will have some scatter, but in general will not have as much scatter as plots of individual measurements. Similarly, a plot of PBM against a GSV using means as data points is expected to have some scatter, but much less than that observed when using individual data points. Scatter is also expected to increase when mean PBM and mean GSV are calculated for different samples (*e.g.*, published mean body mass data calculated based on one sample, and mean GSV calculated from skeletons of different animals belonging to the same taxon). Reference samples should be selected with care, as means can vary greatly within the same species; *e.g.*, Smith and Jungers (1997) report mean male body

mass as 7.93 kg for *Cercopithecus mitis* (Anapol *et al.*, 1995), 5.85 kg for *C. m. stuhlmanni* (Colyn, 1994), and 9.31 kg for *C. m. erythrarchus* (Skinner & Smithers, 1990).

The plot of sex-specific mean PBM against sex-specific mean SSV1 for the hominoid sample (Fig. 5.5) has a coefficient of determination (r^2) of 98.7%, quite high for a sample of ten data points and indicative of a tight fit of the data to the regression lines (lines which are virtually indistinguishable from each other). The data points that differ most from the regression lines have mean PBM based on extremely small samples. For example, the most divergent point, female gorillas, is based on a sample of three individuals (Table 5.1, Smith & Jungers, 1997).

The two-step method supports the hypothesis that SSV1 behaves as a GSV for these taxa. The regression analysis of SSV1 and PBM (step 1) does not falsify the hypothesis that SSV1 is directly proportional to CTM: the intercept of the unconstrained regression is not significantly different from zero, and the slopes of the two regressions do not differ significantly, even when possible leverage points are removed (regressions 5 through 8 in Table 5.5). The comparison of slopes for regressions of log-transformed linear dimensions against log-transformed SSV1 and log-transformed PBM (step 2) demonstrates that the two ratios are statistically indistinguishable at $\alpha = 0.05$, and therefore SSV1 behaves as if it is directly proportional to CTM at that alpha level. Thus SSV1 acts as a GSV for use within comparisons of *Hylobates lar*, *Pan paniscus*, *Pan troglodytes*, *Pongo pygmaeus*, and *Gorilla gorilla*.

Analysis of the full sample of 21 primate species produces a valuable insight into the utility of skeletal size variables when attempting to make comparisons across large size ranges. Although the hominoid data points generally fall quite close to a regression line passing directly through the origin, all other data points in the sample plot above that

line (*i.e.*, they have positive residuals) (Figure 5.4b). In general, significant and/or systematic deviations from regression lines are likely to be the product of one or more of three types of causes.

First, the deviations may result from systematic error in the measurement of skeletal dimensions. For example, a systematic increase in skeletal measurements for a taxon will produce a larger SSV, which will right-shift data points to fall below regression lines. Second, deviations may be a product of body mass measurement error. For example, a set of male squirrel monkey weights might be measured while they were “fatted” for the breeding season, resulting in overly high mean male mass; another error can result from the use of an inappropriate or small reference sample. Third, deviations may be due to differences in the scaling relationship between CTM and a SSV. Systematic deviations for several taxa can result from size-dependency in the scaling relationship, whereas isolated deviations for single taxa or non-systematic deviations for multiple taxa can result from differences in overall robusticity of the postcranium.

In this case, the scaling relationship between CTM and SSV1 appears to change with size, with lower regression slopes for larger taxa (Table 5.5). This observation is consistent with empirical evidence that cross-sectional properties of long bones scale with positive allometry with respect to body mass across primates (*e.g.*, Ruff, 1987; Demes & Jungers, 1993; Jungers & Burr, 1994). If linear dimensions increase faster than predicted by geometric similarity with body mass, then larger animals will have disproportionately larger linear dimensions, disproportionately larger geometric means of linear dimensions, and thus lower CTM:SSV ratios (*i.e.*, the proportionality constant c in equation I.1 in Appendix I and the slope of regressions of CTM against SSV; this is also the constant in a regression of \log [CTM] against \log [SSV]).

That does not preclude SSV1 from acting as a GSV for the smaller, non-hominoid taxa. As demonstrated earlier, SSV1 acts as a GSV for *S. boliviensis*. What these two examples show is that because the proportionality constant differs between the *Saimiri* regression and the hominoid regression, direct comparisons of GSV between these groups are not meaningful in terms of body mass. For example, although mean male squirrel monkey size is 10.9% that of mean male gibbon size as measured in SSV1, that does not correspond to the same percentage in body mass (which is 15.4%). In contrast, direct comparisons within a regression sample are valid; mean male gibbon size is 9.6% of mean male chimpanzee size as measured in SSV1 and 9.9% as measured in PBM. Although direct comparisons of SSV1 values between regression samples are not appropriate, comparisons of values in which the proportionality constant c has cancelled are appropriate; *e.g.*, comparisons of means ratios, coefficients of variation, and slopes for regressions of log-transformed data ([Appendix I](#)). Size correction using a GSV (*e.g.*, dividing a linear measurement by the cube root of GSV) does not cause the proportionality constant to cancel, and thus should only be used when comparing measurements within a regression sample.

GSV and Sample Size

One of the primary advantages to using a skeletal size variable is the ability to generate size measurements for large samples of primate postcranial material, which in turn allows for fine-grained analyses at low taxonomic levels (populations, sub-species, species) for taxa where previously only analyses at higher taxonomic levels were possible. For example, Jungers' (1990b) study of postcranial dimensions in hominoids (which is referred to earlier in this study for assessing the relationship between SSV1 and CTM) is limited to between-species comparisons due to small within-species sample sizes. The present study is different in that it is also able to analyze within-species

relationships due to the relatively large sample of individuals of known size (as measured by SSV1).

The ability to conduct analyses at lower taxonomic levels is particularly important in light of the results found in this study – that within-species and between-species scaling patterns are not always the same. The scaling of RHMaj with body size is a good example: although the between-species relationship is significantly negatively allometric, within-species relationships are significantly positively allometric for gorillas, bonobos, and gibbons (Tables 5.5 and 5.6, Fig. 5.6). Similarly, within-species scaling patterns of both tibial plateau dimensions (TPMAP and TPLAP) do not differ significantly from isometry in orangutans, bonobos, or chimpanzees, while they are significantly positively allometric in gorillas and significantly negatively allometric in gibbons.

Positive allometry in gorillas is observed in four of the five variables analyzed here, occurring in both forelimb and hindlimb, and may reflect an overall pattern of response to larger size in a predominantly quadrupedal animal. In contrast, gibbons exhibit positive allometry in the forelimb and negative allometry in the hindlimb, consistent with a suspensory animal that transmits most of its weight through its forelimbs. Clearly the higher resolution gained by performing within-species analyses can be quite informative. In general, it may be the case that inter-specific scaling patterns reflect the interaction of functional differences and size differences (*i.e.*, change in shape and size between species) while intra-specific patterns reflect the response of a particular body plan to differences in size (*i.e.*, change in size alone within a species); it is certainly the case that one cannot assume that inter-specific scaling patterns are duplicated at the species level. Using a GSV allows researchers to investigate these relationships further and expand our knowledge of evolutionary relationships.

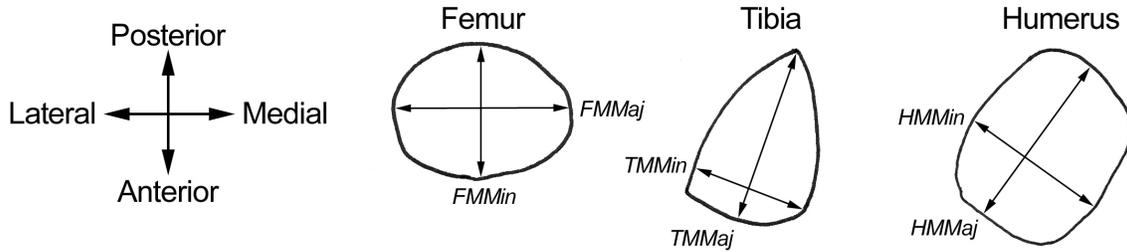
SUMMARY

Postcranial variables that scale isometrically with body mass can be used for direct measurement of size of skeletal specimens and direct comparison with analyses based on body mass. Geometric means of multiple skeletal elements from different regions of the postcranial skeleton (skeletal size variables, or SSV) are preferred over single variables because geometric means are more representative of overall size and are less susceptible to error. Any SSV that scales isometrically with body mass is defined as a global skeletal size variable (GSV). A GSV is unnecessary if CTM data are available for all specimens in a sample; as a result, when a GSV is useful, CTM data are not available to definitively prove direct proportionality between GSV and CTM. However, a two-step process of regression and parameter comparison using PBM and SSV can demonstrate whether or not a SSV behaves as if it is a GSV for a particular study. Two examples have been provided in this paper.

Use of a global skeletal size variable in comparative studies enjoys two considerable advantages over the use of PBM. First, a GSV is more stable over time than PBM, a property that is often desirable for comparative studies. Assessments of variability will be limited to variation in a relatively stable size variable, which avoids compounding that variation with an additional component resulting from causes such as seasonality, reproductive status, *etc.* Second, study samples are not limited to those skeletons that have recorded body mass – all specimens with relatively complete postcrania can have a known body size, allowing for larger samples at lower taxonomic levels than are available using PBM. In addition to these advantages, parameters such as means ratios, coefficients of variation, and slopes for regressions of log-transformed data are directly comparable between studies based on GSV and CTM (and PBM in the case of means ratios and regression slopes). The combination of these factors suggests that

global skeletal size variables can be powerful new tools in the study of primate evolutionary relationships.

Midshaft Cross-sections



Articular Surfaces

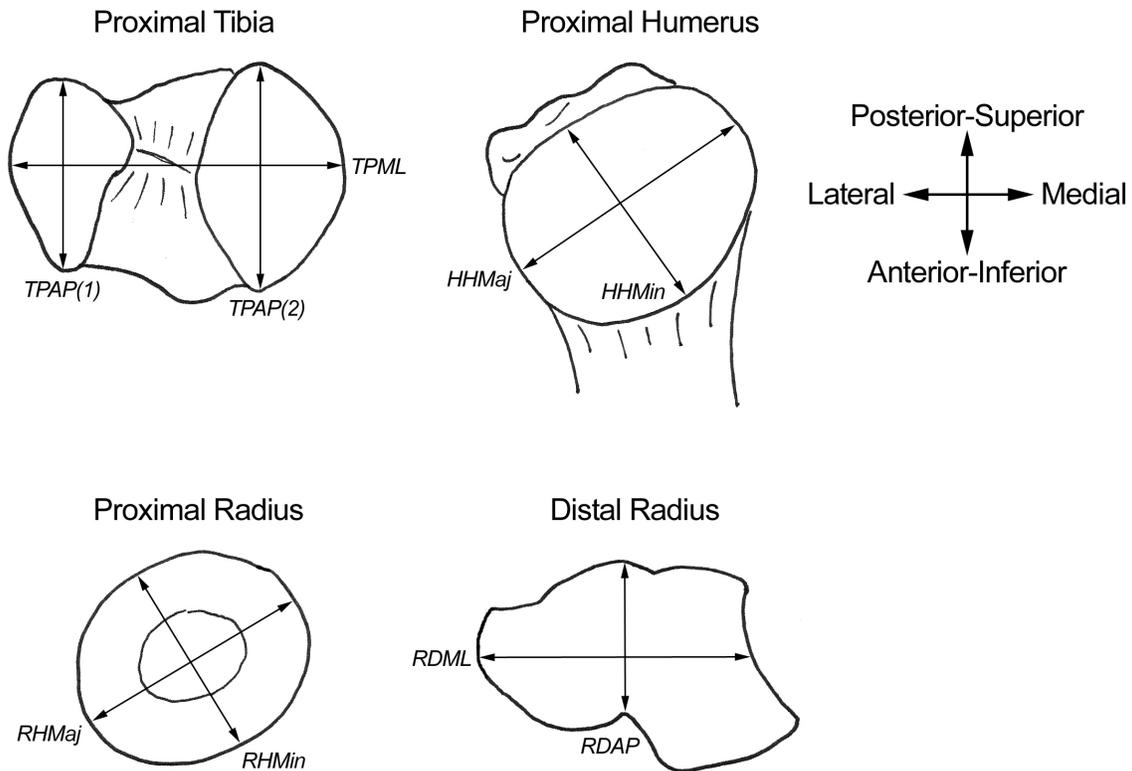


Figure 5.1. Linear dimensions used in this study (shown here for a male gorilla).

Anatomical directions are as indicated in upper left-hand corner except for proximal humerus. Proximal humerus shown in oblique view; anatomical directions are located at right center. TPAP is the mean of TPAP(1) and TPAP(2). Femoral head measurements (FHSI and FHAP) are standard measurements and are not shown here.

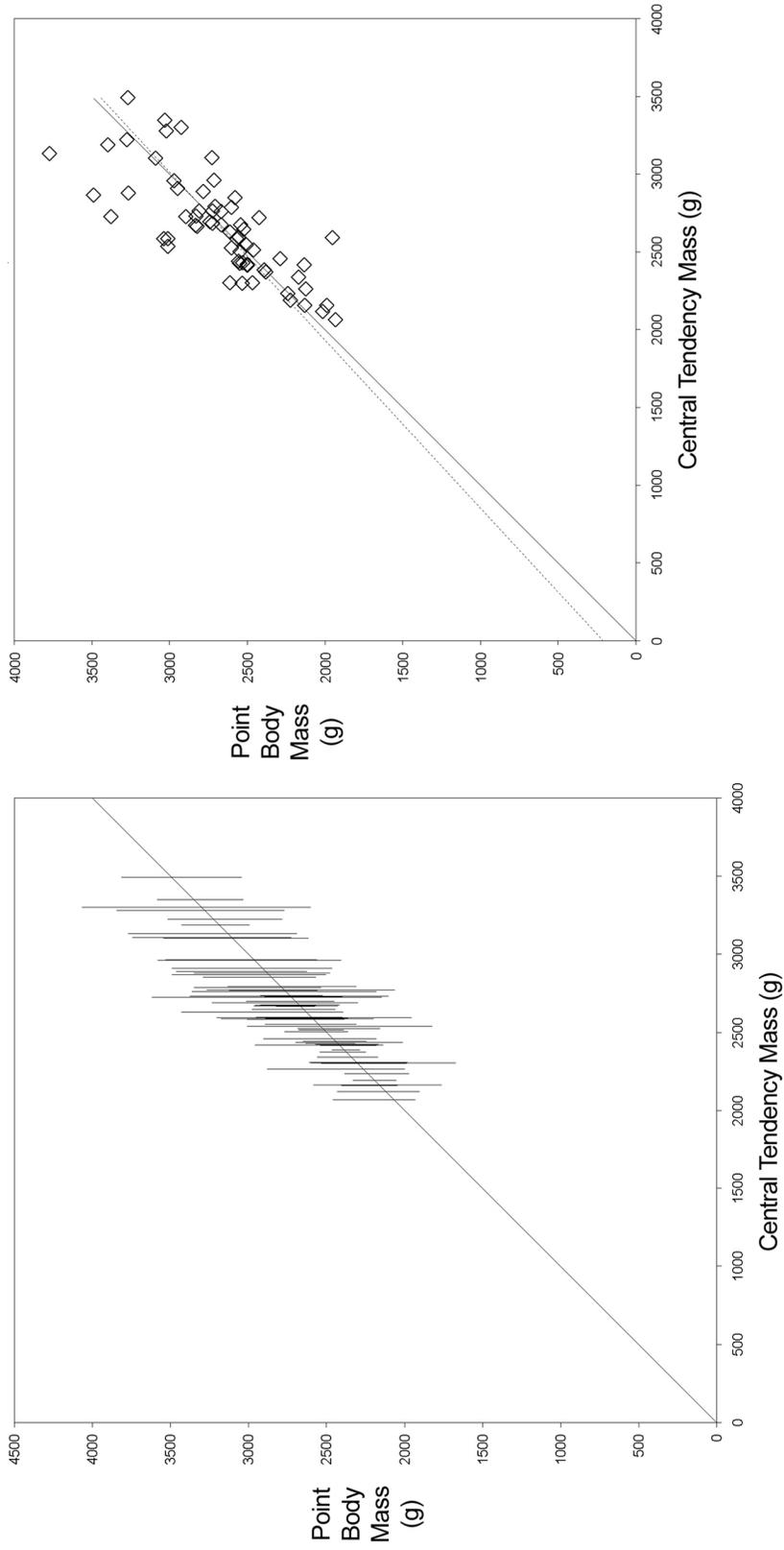


Figure 5.2. PBM and CTM for 63 free-ranging *Lemur catta*.

(a) left, (b) right. (a) Observed range of PBM (vertical bars) plotted against CTM (as approximated by arithmetic mean of PBM measurements) for 63 free-ranging *Lemur catta* from the Duke University Primate Center. Only adult measurements of PBM are included. The line of identity is shown, *i.e.*, the expected value of PBM for a given CTM (slope = 1). (b) Randomly selected sample of single PBM measurements plotted against CTM for 63 free-ranging *Lemur catta*. The solid line is the line of identity; the dotted line is the OLS regression line. Note the high variability of individual point body mass measurements about the mean values. The coefficient of determination (r^2) for these data is 0.599; the slope is significantly different from zero ($P < 0.0001$) while the intercept is not ($P = 0.421$).

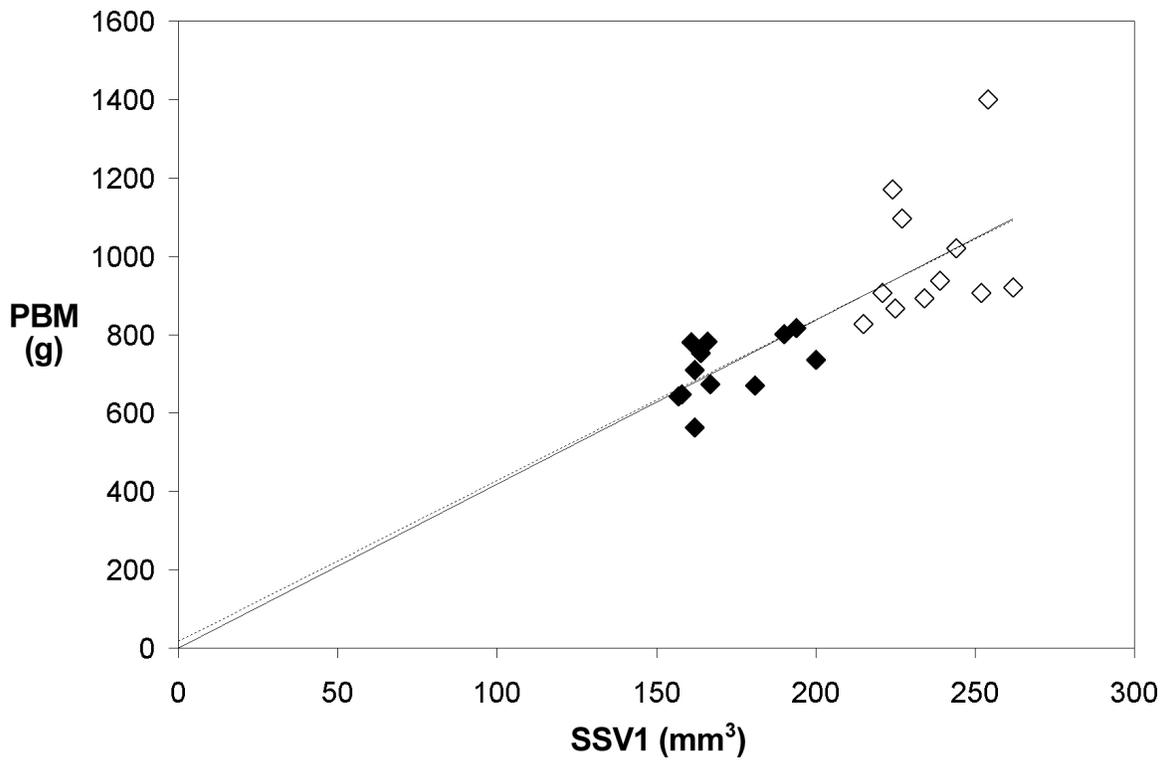


Figure 5.3. Bivariate plot of PBM against SSV1 for *Saimiri boliviensis*.

Closed symbols are females, open symbols are males. Solid line represents the OLS regression of mass against SSV that has been constrained to intercept the origin; dotted line represents the OLS regression of mass against SSV in which the intercept is unconstrained.

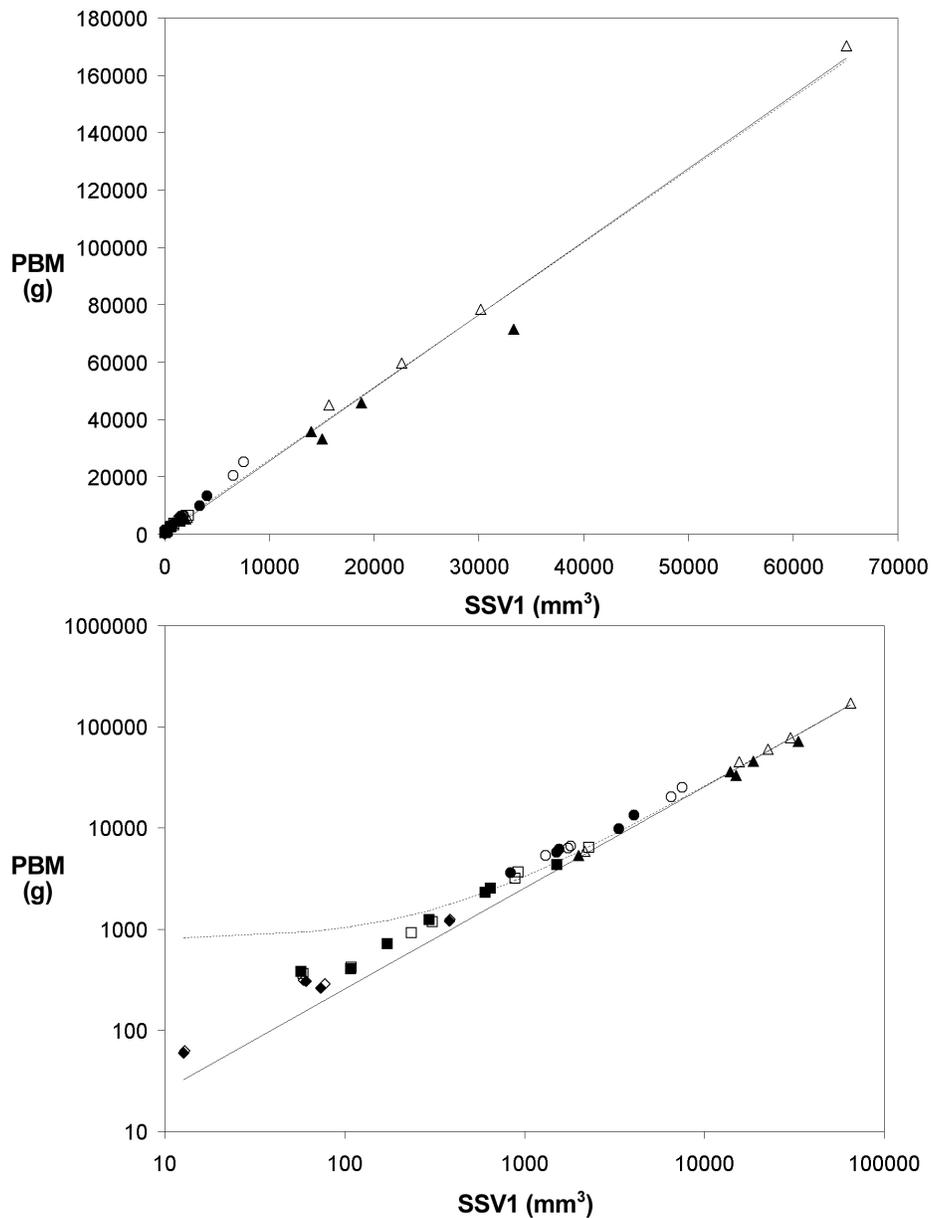


Figure 5.4. Bivariate plots of PBM against SSV1 using sex-specific means for 21 primate species.

(a) top, (b) bottom. Symbols are as follows: prosimians, \diamond ; platyrrhines, \square ; cercopithecoids, \circ ; hominoids, \triangle . Closed symbols are females, open symbols are males. (a) Data plotted in raw data space. (b) Data plotted in log-log space for better visibility. In both plots, the dotted line is an unconstrained OLS regression in raw data space; the solid line is an OLS regression constrained to pass through the origin in raw data space. Note that all non-hominoid points plot above the constrained regression line.

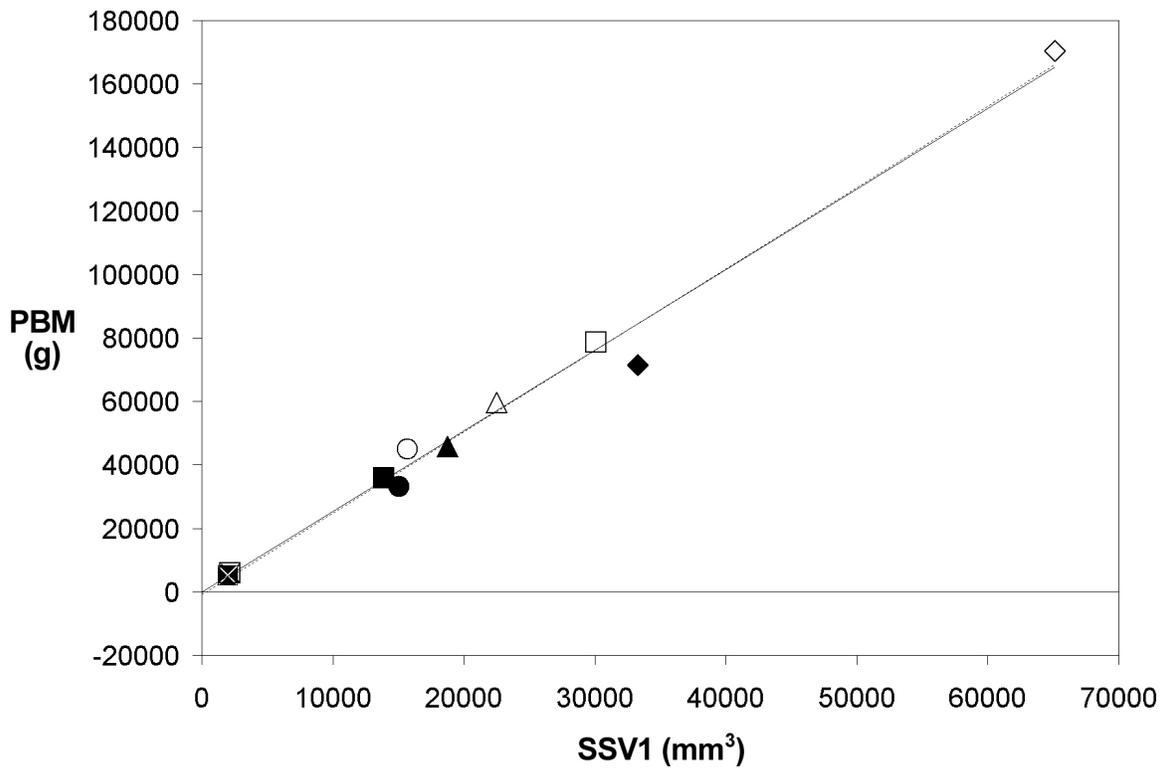


Figure 5.5. Bivariate plot of PBM against SSV1 using sex-specific means for five hominoid species.

Hylobates lar, \boxtimes ; *Pongo pygmaeus*, \square ; *Pan paniscus*, \circ ; *Pan troglodytes*, \triangle ; *Gorilla gorilla*, \diamond . Closed symbols are females, open symbols are males. Lines are as explained in Fig. 5.3.

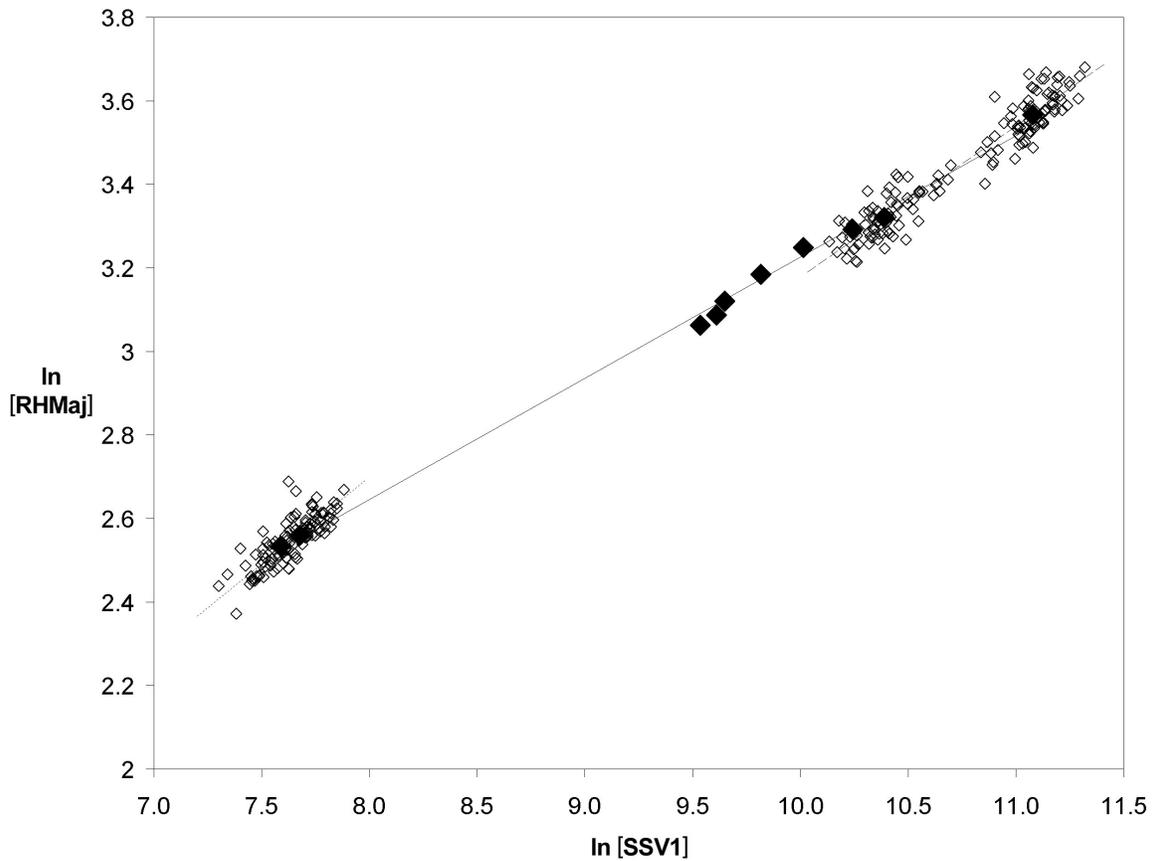


Figure 5.6. Bivariate plot of the natural logarithm of RHMaj against the natural logarithm of SSV1 for five hominoid species.

Closed diamonds represent sex-specific means; open diamonds represent individuals (gibbons on the left side of the plot, gorillas on the right). All lines are major axis regression lines, as follows: solid, sex-specific means; dotted, individual *Hylobates lar*; dashed, individual *Gorilla gorilla*. The inter-specific (solid) regression line is significantly negatively allometric; the two intra-specific regression lines are significantly positively allometric.

| Taxon | N males | N females | Collection | Superfamily | Family/ Subfamily |
|---|-------------|-------------|------------|-----------------|----------------------|
| <i>Arctocebus calabarensis</i> | 7 (3) | 5 (9) | AIMZ | Lorisoidea | Lorisidae |
| <i>Perodicticus potto</i> | 15 (5) | 11 (5) | AIMZ | Lorisoidea | Lorisidae |
| <i>Euoticus elegantulus</i> | 18 (5) | 14 (3) | PCM | Lorisoidea | Galagidae |
| <i>Galagoides demidoff</i> | 11 (54) | 11 (19) | PCM | Lorisoidea | Galagidae |
| <i>Callithrix jacchus jacchus</i> | 10 (3) | 9 (2) | AIMZ | Ceboidea | Callitrichidae |
| <i>Saguinus oedipus</i> | 18 (37) | 8 (29) | NMNH | Ceboidea | Callitrichidae |
| <i>Saimiri boliviensis boliviensis</i> | 11 (17) | 12 (19) | AMNH | Ceboidea | Cebidae |
| <i>Cebus albifrons</i> | 13 (26) | 12 (15) | AMNH | Ceboidea | Cebidae |
| <i>Cebus apella paraguayanus</i> | 8 (51) | 11 (38) | AMNH | Ceboidea | Cebidae |
| <i>Alouatta caraya</i> | 10 (58) | 12 (117) | AMNH | Ceboidea | Atelidae |
| <i>Aotus azarae boliviensis</i> | 15 (4) | 13 (8) | AMNH | Ceboidea | Aotinae |
| <i>Nasalis larvatus</i> | 6 (46) | 10 (48) | MCZ | Cercopthicoidea | Colobinae |
| <i>Presbytis rubicunda</i> | 17 (35) | 15 (38) | MCZ | Cercopthicoidea | Colobinae |
| <i>Trachypithecus cristata ultima</i> | 13 (26) | 26 (49) | MCZ | Cercopthicoidea | Colobinae |
| <i>Macaca fascicularis fascicularis</i> | 14 (60) | 16 (46) | MCZ | Cercopthicoidea | Cercopithecinae |
| <i>Papio cynocephalus anubis</i> | 16 (100) | 17 (116) | UTA | Cercopthicoidea | Cercopithecinae |
| <i>Hylobates lar</i> | 17, 43 (84) | 16, 36 (66) | AIMZ, MCZ | Hominoidea | Hylobatidae |
| <i>Pongo pygmaeus</i> | 7 (7) | 14 (13) | NMNH | Hominoidea | Pongidae |
| <i>Pan paniscus</i> | 6 (7) | 9 (6) | MRAC | Hominoidea | Hominidae |
| <i>Pan troglodytes troglodytes</i> | 16, 18 (5) | 27, 48 (4) | CMNH, PCM | Hominoidea | Hominidae |
| <i>Gorilla gorilla gorilla</i> | 36, 25 (10) | 25, 36 (3) | CMNH, PCM | Hominoidea | Hominidae |

Table 5.1. Skeletal sample for evaluation of SSV.

Values in parentheses are sample sizes used to generate sex-specific means for these taxa in Smith and Jungers (1997). Values separated by commas indicate sample size from each collection when two collections were sampled. Abbreviations: AIMZ, Anthropologisches Institut und Museum (Zürich, Switzerland); AMNH, American Museum of Natural History; CMNH, Cleveland Museum of Natural History; MCZ, Museum of Comparative Zoology (Cambridge, MA); MRAC, Musée Royal de l'Afrique Centrale (Tervuren, Belgium); NMNH, National Museum of Natural History; PCM, Powell-Cotton Museum (Kent, England); UTA, University of Texas at Austin.

| | | | |
|--------------|---|--------------|--------------------------------------|
| <i>FHAP</i> | Femoral head anteroposterior diameter | <i>HHMaj</i> | Humeral head major axis diameter |
| <i>FHSI</i> | Femoral head superoinferior diameter | <i>HHMin</i> | Humeral head minor axis diameter |
| <i>FMMaj</i> | Femoral midshaft major axis diameter | <i>HMMaj</i> | Humeral midshaft major axis diameter |
| <i>FMMin</i> | Femoral midshaft minor axis diameter | <i>HMMin</i> | Humeral midshaft minor axis diameter |
| <i>TPAP</i> | Tibial plateau anteroposterior width (mean of medial and lateral surfaces) | <i>RHMaj</i> | Radial head major axis diameter |
| <i>TPML</i> | Tibial plateau mediolateral width | <i>RHMin</i> | Radial head minor axis diameter |
| <i>TMMaj</i> | Tibial midshaft major axis diameter | <i>RDAP</i> | Distal radius anteroposterior width |
| <i>TMMin</i> | Tibial midshaft minor axis diameter | <i>RDML</i> | Distal radius mediolateral width |

Table 5.2. Postcranial measurements diagrammed in Figure 5.1.

| Name | ID | Sex | Mean | | | | Max | | | | Name | ID | Sex | Mean | | | | Max | | | |
|-----------|------|-----|------|------|--------|--------|-------|--------|--------------|------|------|----|------|--------|--------|-------|--------|-----|-----|-----|-----|
| | | | N | PBM | Min | Max | SD | Error | N | PBM | | | | Min | Max | SD | Error | N | PBM | Min | Max |
| Agatha | 942 | F | 6 | 2439 | 2243 | 2653 | 160.9 | 8.79% | Agnostes | 903 | M | 8 | 2673 | 2566 | 2960 | 124.5 | 10.73% | | | | |
| Alice | 1034 | F | 6 | 2232 | 1970 | 2384 | 148.3 | 11.74% | Ajax | 992 | M | 11 | 2765 | 2060 | 3270 | 325.9 | 25.49% | | | | |
| Anemone | 501 | F | 13 | 2878 | 2477 | 3350 | 263.1 | 16.40% | Alcibiades | 51 | M | 17 | 2263 | 1998 | 2880 | 191.1 | 27.29% | | | | |
| Aspasia | 290 | F | 5 | 2157 | 2043 | 2406 | 143.2 | 11.54% | Brennus | 972 | M | 14 | 2300 | 1670 | 2600 | 256.3 | 27.40% | | | | |
| Atossa | 683 | F | 10 | 3222 | 2783 | 3519 | 236.1 | 13.63% | Cato | 126 | M | 11 | 3189 | 2991 | 3430 | 151.2 | 7.54% | | | | |
| Baucis | 627 | F | 9 | 2593 | 1952 | 3205 | 452.3 | 24.73% | Cercolas | 665 | M | 7 | 2731 | 2523 | 2924 | 151.2 | 7.61% | | | | |
| Bias | 1088 | F | 12 | 2063 | 1930 | 2460 | 144.5 | 19.25% | Cleomedon | 1161 | M | 12 | 2189 | 2050 | 2330 | 96.7 | 6.46% | | | | |
| Calpurnia | 137 | F | 17 | 2761 | 2179 | 3363 | 318.1 | 21.82% | Croesus | 846 | M | 5 | 2584 | 2383.5 | 3009.5 | 248.6 | 16.46% | | | | |
| Chloris | 949 | F | 12 | 2299 | 1988 | 2532 | 171.7 | 13.53% | Dion | 741 | M | 19 | 2728 | 2100 | 3378 | 266.3 | 23.81% | | | | |
| Cleis | 803 | F | 12 | 2889 | 2624 | 3463.5 | 265.5 | 19.90% | Ephialtes | 840 | M | 5 | 2646 | 2442 | 2978 | 212.3 | 12.56% | | | | |
| Cleomenis | 889 | F | 12 | 2431 | 2010 | 2697 | 158.8 | 17.31% | Erato | 266 | M | 8 | 2426 | 2315 | 2633 | 114.4 | 8.52% | | | | |
| Clytie | 482 | F | 12 | 2370 | 2248 | 2542 | 97.9 | 7.26% | Glaucon | 911 | M | 18 | 2537 | 1820 | 3009.5 | 317.1 | 28.28% | | | | |
| Corinna | 694 | F | 12 | 2586 | 2197 | 3178 | 325.6 | 22.88% | Hesper | 929 | M | 8 | 2685 | 2297 | 3236.5 | 276.0 | 20.54% | | | | |
| Dory | 1020 | F | 6 | 2385 | 2284 | 2466 | 63.1 | 4.22% | Hieron | 762 | M | 10 | 2787 | 2533 | 3350 | 235.9 | 20.22% | | | | |
| Eranthe | 937 | F | 5 | 2303 | 1979 | 2610.5 | 228.9 | 14.05% | Ion | 442 | M | 20 | 2675 | 2415 | 2925 | 165.0 | 9.72% | | | | |
| Galatea | 543 | F | 5 | 2665 | 2574 | 2823 | 94.2 | 5.92% | Juba | 882 | M | 6 | 2595 | 2397 | 2951 | 189.2 | 13.74% | | | | |
| Kamala | 173 | F | 23 | 2958 | 2406 | 3583.5 | 276.7 | 21.13% | Lent | 217 | M | 11 | 2587 | 2360 | 2890 | 175.3 | 11.73% | | | | |
| Katrina | 851 | F | 9 | 2763 | 2555.5 | 3123 | 158.3 | 13.04% | Leonidas | 709 | M | 26 | 2629 | 2393 | 3432 | 230.8 | 30.54% | | | | |
| Lysis | 307 | F | 26 | 2722 | 2147 | 3620 | 345.2 | 33.00% | Lycus | 791 | M | 9 | 2867 | 2503 | 3490.5 | 297.2 | 21.75% | | | | |
| Melinna | 861 | F | 5 | 2727 | 2397 | 2896 | 195.4 | 12.11% | Nemo | 866 | M | 8 | 2850 | 2566 | 3291.5 | 258.5 | 15.49% | | | | |
| Nicias | 250 | F | 6 | 2415 | 2179 | 2540 | 135.4 | 9.77% | Omar | 196 | M | 8 | 2419 | 2164 | 2569 | 131.0 | 10.54% | | | | |
| Ninna | 1046 | F | 6 | 2525 | 2156 | 2686 | 192.7 | 14.61% | Pantores | 875 | M | 6 | 3103 | 2615 | 3545.5 | 302.1 | 15.72% | | | | |
| Nossis | 1123 | F | 14 | 2337 | 2170 | 2560 | 127.7 | 9.57% | Pericles | 476 | M | 6 | 2504 | 2361 | 2769 | 164.8 | 10.57% | | | | |
| Nysa | 820 | F | 9 | 3131 | 2688 | 3772.5 | 399.3 | 20.47% | Pheidippedes | 595 | M | 8 | 2545 | 2306 | 2893 | 165.7 | 13.66% | | | | |
| Phyllis | 961 | F | 5 | 2158 | 1761 | 2582.5 | 307.1 | 19.68% | Pindar | 427 | M | 7 | 2672 | 2424 | 2965 | 203.5 | 10.97% | | | | |
| Rima | 154 | F | 15 | 2695 | 2450 | 3016 | 178.9 | 11.90% | Remus | 117 | M | 9 | 3279 | 2769 | 3845 | 386.3 | 17.25% | | | | |
| Sappho | 374 | F | 13 | 2793 | 2306 | 3134 | 249.1 | 17.43% | Romulus | 78 | M | 30 | 3299 | 2600 | 4068 | 300.6 | 23.30% | | | | |
| Selene | 1069 | F | 13 | 2117 | 1902 | 2433 | 158.4 | 14.91% | Selauticus | 775 | M | 13 | 2907 | 2461 | 3490.5 | 251.2 | 20.05% | | | | |
| Thera | 555 | F | 11 | 3105 | 2726 | 3745.5 | 379.8 | 20.64% | Socrates | 1 | M | 11 | 3491 | 3042 | 3814 | 231.2 | 12.85% | | | | |
| Xantippe | 12 | F | 16 | 2456 | 2180 | 2906 | 178.1 | 18.31% | Sophocles | 434 | M | 8 | 3346 | 3032 | 3587 | 202.3 | 9.39% | | | | |
| Zenobia | 419 | F | 8 | 2416 | 2134 | 2960 | 278.6 | 22.54% | Thales | 517 | M | 9 | 2960 | 2560 | 3533 | 352.8 | 19.35% | | | | |
| | | | | | | | | | Xenophon | 471 | M | 5 | 2513 | 2388 | 2679 | 116.7 | 6.62% | | | | |

Table 5.3. Mean PBM (*i.e.*, estimated CTM) and observed range of PBM measurements for 63 *Lemur catta* (31 F, 32 M).

All measurements reported in grams. Max error is the maximum absolute value of percent difference for a single PBM measurement from the mean for that individual.

| Collection ID | Sex | Mass (g) | SSV1 (mm ³) | Collection ID | Sex | Mass (g) | SSV1 (mm ³) |
|---------------|-----|----------|-------------------------|---------------|-----|----------|-------------------------|
| AMNH-211614 | F | 562 | 162 | AMNH-211628 | M | 827 | 215 |
| AMNH-209933 | F | 642 | 157 | AMNH-211618 | M | 866 | 225 |
| AMNH-209928 | F | 647.5 | 158 | AMNH-211651 | M | 893 | 234 |
| AMNH-211609 | F | 670 | 181 | AMNH-211611 | M | 907 | 221 |
| AMNH-211630 | F | 673 | 167 | AMNH-211624 | M | 907 | 252 |
| AMNH-211631 | F | 708.9 | 162 | AMNH-209934 | M | 920 | 262 |
| AMNH-211606 | F | 735 | 200 | AMNH-211649 | M | 938 | 239 |
| AMNH-211591 | F | 751.8 | 164 | AMNH-211623 | M | 1020 | 244 |
| AMNH-211650 | F | 781 | 161 | AMNH-211601 | M | 1097 | 227 |
| AMNH-211653 | F | 782.5 | 166 | AMNH-211594 | M | 1170 | 224 |
| AMNH-211615 | F | 801 | 190 | AMNH-209930 | M | 1400 | 254 |
| AMNH-211616 | F | 816 | 194 | | | | |

Table 5.4. Body size variables for *Saimiri boliviensis boliviensis* sample.

| Regression | Data set | Figure | Data points | Regression type | Slope | 95% CI Slope | DF | P_{slope} | Reduced DF | P_{slope} (reduced) | Intercept | $P_{\text{intercept}}$ | r^2 |
|------------|----------------------------|--------|-------------|-----------------|-------|--------------|----|--------------------|------------|------------------------------|-----------|------------------------|-------|
| 1 | <i>Saimiri boliviensis</i> | 5.3 | I | U | 4.10 | 2.58 - 5.63 | 21 | < 0.001 | 3 | 0.011 | 17.3 | 0.910 | 0.599 |
| 2 | <i>Saimiri boliviensis</i> | 5.3 | I | C | 4.19 | 3.93 - 4.44 | 22 | < 0.001 | 4 | < 0.001 | 0 | - | 0.599 |
| 3 | full data set | 5.4 | M | U | 2.53 | 2.46 - 2.60 | 40 | < 0.001 | 6 | < 0.001 | 788 | 0.117 | 0.992 |
| 4 | full data set | 5.4 | M | C | 2.55 | 2.49 - 2.62 | 41 | < 0.001 | 7 | < 0.001 | 0 | - | 0.992 |
| 5 | hominoids | 5.5 | M | U | 2.57 | 2.33 - 2.80 | 8 | < 0.001 | 1 | 0.026 | -934 | 0.754 | 0.987 |
| 6 | hominoids | 5.5 | M | C | 2.54 | 2.40 - 2.68 | 9 | < 0.001 | 2 | < 0.001 | 0 | - | 0.987 |
| 7 | reduced hominoids | - | M | U | 2.71 | 1.94 - 3.47 | 4 | < 0.001 | 1 | 0.064 | -2600 | 0.662 | 0.960 |
| 8 | reduced hominoids | - | M | C | 2.58 | 2.40 - 2.76 | 5 | < 0.001 | 2 | < 0.001 | 0 | - | 0.958 |

Table 5.5. Parameters for regressions of PBM on SSV.

Abbreviations: CI, confidence interval; DF, degrees of freedom; I, individuals; M, sex-specific means; C, ordinary least squares with intercept constrained to zero; U, unconstrained ordinary least squares. "Figure" refers to the figure in which the regression is plotted. "Full data set" is the data set used to generate Figure 5.4 as explained in the text, "hominoids" is the data set used to generate Figure 5.5, and "reduced hominoids" is the same data set excluding *Hyllobates lar* and *Gorilla gorilla*. All slopes and intercepts are for regressions of PBM measured in grams against SSV1 measured in cubic millimeters. Confidence intervals for the slopes are calculated using the full degrees of freedom. Reduced degrees of freedom are calculated using Smith's (1994) technique. Hierarchical levels used in nested ANOVA for Smith's technique are as follows - regressions 1-2: sex; regressions 3-4: species, genus, family, infraorder, suborder; regressions 5-8: species, genus.

| Taxon | Mean Male Mass (g) | Mean Female Mass (g) | Mean Male SSV1 (mm ³) | Mean Female SSV1 (mm ³) |
|---|-----------------------|----------------------------|---|--|
| <i>Arctocebus calabarensis</i> | 312 | 306 | 59.1 | 61.1 |
| <i>Perodicticus potto</i> | 1250 | 1210 | 385 | 383 |
| <i>Euoticus elegantulus</i> | 287 | 261 | 77.4 | 73.6 |
| <i>Galagoides demidoff</i> | 63 | 60 | 12.9 | 12.7 |
| <i>Callithrix jacchus jacchus</i> | 362 | 381 | 58.9 | 57.3 |
| <i>Saguinus oedipus</i> | 418 | 404 | 110 | 108 |
| <i>Saimiri boliviensis boliviensis</i> | 911 | 711 | 236 | 172 |
| <i>Cebus albifrons</i> | 3180 | 2290 | 890 | 608 |
| <i>Cebus apella paraguayanus</i> | 3650 | 2520 | 924 | 649 |
| <i>Alouatta caraya</i> | 6420 | 4330 | 2280 | 1520 |
| <i>Aotus azarae boliviensis</i> | 1180 | 1230 | 308 | 296 |
| <i>Nasalis larvatus</i> | 20400 | 9820 | 6550 | 3350 |
| <i>Presbytis rubicunda</i> | 6290 | 6170 | 1750 | 1560 |
| <i>Trachypithecus cristata ultima</i> | 6610 | 5760 | 1810 | 1510 |
| <i>Macaca fascicularis fascicularis</i> | 5360 | 3590 | 1310 | 837 |
| <i>Papio cynocephalus anubis</i> | 25100 | 13300 | 7560 | 4060 |
| <i>Hylobates lar</i> | 5900 | 5340 | 2170 | 1990 |
| <i>Pongo pygmaeus</i> | 78500 | 35800 | 30100 | 13900 |
| <i>Pan paniscus</i> | 45000 | 33200 | 15700 | 15000 |
| <i>Pan troglodytes troglodytes</i> | 59700 | 45800 | 22500 | 18700 |
| <i>Gorilla gorilla gorilla</i> | 170400 | 71500 | 65100 | 33300 |

Table 5.6. Sex-specific mean body size variables for 21 primate taxa.

Mass means drawn from Smith and Jungers (1997).

| This study - SSV1 | | | | | | |
|-------------------|------------------------|-----------|-------|------------|-----------|-------|
| Regression | Ordinary Least Squares | | | Major Axis | | r |
| | Slope | Intercept | SEE | Slope | Intercept | |
| ln [HHMean] | 0.347 | 0.259 | 0.044 | 0.347 | 0.255 | 0.994 |
| ln [RHMaj] | 0.290* | 0.320 | 0.020 | 0.291* | 0.320 | 0.998 |
| ln [FHMean] | 0.333 | 0.236 | 0.019 | 0.333 | 0.235 | 0.999 |
| ln [TPMAP] | 0.322 | 0.430 | 0.020 | 0.322 | 0.429 | 0.999 |
| ln [TPLAP] | 0.275* | 0.711 | 0.051 | 0.275* | 0.706 | 0.988 |

| Jungers (1990) - PBM | | | | | | |
|----------------------|------------------------|-----------|-------|------------|-----------|-------|
| Regression | Ordinary Least Squares | | | Major Axis | | r |
| | Slope | Intercept | SEE | Slope | Intercept | |
| ln [HHMean] | 0.358 | 2.283 | 0.036 | 0.358 | 2.282 | 0.996 |
| ln [RHMaj] | 0.307 | 1.999 | 0.036 | 0.308 | 1.998 | 0.995 |
| ln [FHMean] | 0.343 | 2.183 | 0.028 | 0.343 | 2.182 | 0.997 |
| ln [TPMAP] | 0.345 | 2.222 | 0.046 | 0.345 | 2.221 | 0.993 |
| ln [TPLAP] | 0.296* | 2.254 | 0.036 | 0.296* | 2.253 | 0.994 |

Table 5.7. Regression statistics for interspecific hominoid analyses.

Abbreviations: *HHMean*, arithmetic mean of *HHMaj* and *HHMin*; *FHMean*, arithmetic mean of *FHMaj* and *FHMin*; SEE, standard error of estimate; *, differs significantly from isometry (0.333) at alpha = 0.05. In all cases the regression slopes calculated using SSV1 in this study do not differ significantly from the corresponding slopes calculated using PBM in Jungers (1990).

| Regression | Species | Ordinary Least Squares | | | Major Axis | | Correlation |
|-------------|------------------------|------------------------|-----------|-------|------------|-----------|-------------|
| | | Slope | Intercept | SEE | Slope | Intercept | |
| ln [HHMean] | <i>Gorilla gorilla</i> | 0.353* | 0.195 | 0.031 | 0.355* | 0.171 | 0.973 |
| | <i>Pongo pygmaeus</i> | 0.330 | 0.497 | 0.039 | 0.334 | 0.465 | 0.954 |
| | <i>Pan troglodytes</i> | 0.362 | 0.067 | 0.030 | 0.372* | -0.034 | 0.899 |
| | <i>Pan paniscus</i> | 0.331 | 0.374 | 0.024 | 0.345 | 0.241 | 0.843 |
| | <i>Hylobates lar</i> | 0.327 | 0.416 | 0.028 | 0.343 | 0.295 | 0.822 |
| ln [RHMaj] | <i>Gorilla gorilla</i> | 0.358* | -0.394 | 0.039 | 0.361* | -0.433 | 0.959 |
| | <i>Pongo pygmaeus</i> | 0.316 | 0.062 | 0.034 | 0.318 | 0.040 | 0.962 |
| | <i>Pan troglodytes</i> | 0.326 | -0.018 | 0.041 | 0.345 | -0.200 | 0.801 |
| | <i>Pan paniscus</i> | 0.542 | -2.116 | 0.046 | 0.617* | -2.840 | 0.802 |
| | <i>Hylobates lar</i> | 0.390* | -0.427 | 0.034 | 0.417* | -0.637 | 0.815 |
| ln [FHMean] | <i>Gorilla gorilla</i> | 0.317 | 0.421 | 0.037 | 0.320 | 0.390 | 0.954 |
| | <i>Pongo pygmaeus</i> | 0.313 | 0.458 | 0.025 | 0.314 | 0.446 | 0.978 |
| | <i>Pan troglodytes</i> | 0.338 | 0.166 | 0.032 | 0.349 | 0.053 | 0.870 |
| | <i>Pan paniscus</i> | 0.316 | 0.382 | 0.023 | 0.327 | 0.271 | 0.849 |
| | <i>Hylobates lar</i> | 0.296 | 0.520 | 0.026 | 0.309 | 0.422 | 0.811 |
| ln [TPMAP] | <i>Gorilla gorilla</i> | 0.350* | 0.148 | 0.036 | 0.353* | 0.116 | 0.963 |
| | <i>Pongo pygmaeus</i> | 0.335 | 0.311 | 0.051 | 0.341 | 0.258 | 0.929 |
| | <i>Pan troglodytes</i> | 0.327 | 0.364 | 0.041 | 0.345 | 0.185 | 0.804 |
| | <i>Pan paniscus</i> | 0.281 | 0.805 | 0.038 | 0.313 | 0.497 | 0.645 |
| | <i>Hylobates lar</i> | 0.208* | 1.312 | 0.046 | 0.241* | 1.059 | 0.481 |
| ln [TPLAP] | <i>Gorilla gorilla</i> | 0.364* | -0.237 | 0.057 | 0.372* | -0.321 | 0.920 |
| | <i>Pongo pygmaeus</i> | 0.321 | 0.320 | 0.044 | 0.325 | 0.281 | 0.940 |
| | <i>Pan troglodytes</i> | 0.291 | 0.505 | 0.058 | 0.326 | 0.162 | 0.649 |
| | <i>Pan paniscus</i> | 0.331 | 0.124 | 0.065 | 0.459 | -1.116 | 0.503 |
| | <i>Hylobates lar</i> | 0.264* | 0.812 | 0.036 | 0.287 | 0.636 | 0.668 |

Table 5.8. Regression statistics for intraspecific hominoid analyses.

Abbreviations are as for Table 5.7.

Chapter 6: Selection Pressures in the Evolution of Size and Dimorphism in *Pan* and the Hadar Hominids

INTRODUCTION

Many studies over the years have demonstrated relationships between sexual dimorphism (*i.e.*, sex differences in traits such as body size or canine size) and social variables in extant primates; these relationships have in turn been used to reconstruct social structure and behavior in fossil primates (*e.g.*, Plavcan, 2002) and numerous references therein). Unfortunately, reconstructed behaviors for extinct taxa are highly tenuous (Plavcan, 2002), in part due to the treatment of dimorphism as a property of populations in and of itself. As several authors have pointed out, dimorphism in any trait is a product of forces operating on males and females, and different forces may act on different sexes (Leigh, 1992; Martin *et al.*, 1994; 1995; Leigh & Shea, 1995; Plavcan *et al.*, 1995; Lindenfors, 2002). However, rigorous analyses of the forces affecting sex-specific size are few because of the difficulty in identifying and quantifying the source and relative strength of selective forces acting on each sex for any particular taxon. One potential method for identifying relative sex-specific selection intensities is to consider the predictions of quantitative genetics models in a phylogenetic comparative methods context.

Quantitative genetics models offer an opportunity to identify which sex is subject to more intense selection than the other. Lande (1980) developed a model that predicts how male and female mean size change in response to selection. In discussing the possible reasons why size dimorphism scales positively with body size in haplorhine primates (a relationship known as Rensch's rule, Rensch, 1959), Smith and Cheverud (2002) point out that Lande's model predicts the following: with a genetic correlation of

0.9 between sexes for a particular trait (*e.g.*, body mass or canine size), selection acting on male body size alone will produce positive scaling of size dimorphism and female body size with a slope nearly identical to that observed for haplorhine primates (Smith & Cheverud, 2002). Positive scaling results from the fact that body size in females is correlated to that of males, so large increases in male size produce smaller increases in females even when selection does not act on female body size.

The idea that Rensch's rule could result from correlated response to selection has been around for some time (Maynard Smith, 1977; Leutenegger, 1978; Zeng, 1988; Webster, 1992; Fairbairn & Preziosi, 1994), and a formal mathematical description of how correlated selection would work has been available since Lande published his model in 1980 (Lande, 1980). Lande himself thought that natural selection for female optimum body size would counteract the correlated response of female body size, in which case there would be no scaling of size and dimorphism once female size had returned to its optimum (Lande, 1980; Zeng, 1988; Emerson, 1994; Fairbairn, 1997). However, this makes a number of assumptions that may not be true. First, the scenario described by Lande requires that selection pressure operates only on male body size; in many circumstances selection may act on both sexes with greater selection pressure applied to one sex. Perhaps more importantly, Lande's scenario also assumes that constraints defining optimum body size for females remain stable long enough for a return to previous optimum body size at equilibrium, making no allowance for environmental change or the emergence of a new optimum in response to new conditions (Smith & Cheverud, 2002). For example, larger females may be able to move into new dietary niches with larger optimum body size; also, birthing constraints on delivering larger infants may select against small size in females, increasing optimum body size as male and female body size increases. Evidence for such correlated selection on female size in

response to selection on male size (distinct from correlated response in females to selection on males alone) has been found in birds and mammals (Ralls, 1976; Cabana *et al.*, 1982; Clutton-Brock *et al.*, 1988; Webster, 1992).

When an assumption of constant female optimum size and a necessary return to that optimum is *not* imposed, Lande's (1980) equations predict that body size dimorphism will scale positively with sex-specific body size whenever selection acts more intensely on males than females, and it will scale negatively whenever selection acts more intensely on females than males. These scaling relationships do not depend on direction of size change; *i.e.*, they are independent of whether selection acts to increase or decrease body size (Chapter 2). Agreement in model predictions and scaling patterns observed in a comparative analysis of major primate radiations indicates that Lande's model can be used to identify the sex that is the recipient of more intense selection pressures (Chapter 3). By using comparative methods that take into account ancestor-descendant relationships between taxa such as phylogenetically independent contrasts (Felsenstein, 1985) and phylogenetic generalized least squares reconstructions (Martins & Hansen, 1997), differential change in sex-specific body size and scaling of dimorphism can be identified between pairs of taxa, extant and/or extinct.

However, reconstructing the evolution of sex-specific body size is particularly difficult in fossil primates because of uncertain phylogenetic position, lack of body mass measurements, and general absence of simultaneous death assemblages containing large numbers of relatively complete and identifiable males and females. Fortunately for students of human evolution, fossil hominids offer some of the best-case scenarios for reconstructions of selection pressures on body size in extinct primates. Although phylogenetic relationships among fossil hominids (and indeed, the species designations of those fossils) are often debated (*e.g.*, Wolpoff, 1999; Wood & Collard, 1999;

Schwartz, 2003; White, 2003), the relationship of any single fossil hominid taxon to living taxa is well known. Body mass measurements may be unavailable, but relatively complete specimens (*e.g.*, A.L. 288-1 and KNM-WT-1500) exist which can be compared to living taxa on the basis of postcranial size. And one geologically simultaneous assemblage contains the remains of at least nine adult individuals (albeit incomplete specimens) in which two distinct size morphs can be identified (A.L. 333, McHenry, 1992; Harmon *et al.*, 2003).

Reconstructing the evolution of male and female body size in *Australopithecus afarensis* offers a challenge that is particularly complex and potentially quite rewarding. Several nearly-contemporaneous specimens of *A. afarensis* are available from the Denan Dora Member at Hadar: A.L. 288-1 and the A.L. 333 assemblage. The retention of postcranial morphologies in these specimens that appear adapted to arboreality (*e.g.*, Jungers & Stern, 1983; Stern & Susman, 1983; Rose, 1984; Susman *et al.*, 1984; Stern & Larson, 1993; Duncan *et al.*, 1994) suggests that comparisons of the evolution of size in *A. afarensis* and *Pan* are useful not only on the basis of phylogenetic similarity, but also due to potential overlap in habitat preference and use (although postcranial morphology in *A. afarensis* has also been argued to represent phylogenetic baggage that does not indicate any arboreality in these hominids, *e.g.*, Latimer & Lovejoy, 1989). *A. afarensis* also presents an interesting puzzle because this species has often been reconstructed as having high body size dimorphism, but low canine size dimorphism (McHenry, 1992; Hartwig-Scherer, 1993; Richmond & Jungers, 1995; Lockwood *et al.*, 1996; Plavcan & van Schaik, 1997a) This difference in dimorphism defies explanation by a simple model of intense male competition for mates (Wolpoff, 1976; Foley & Lee, 1989; McHenry, 1994a; 1994b) or monogamous pair-bonding (Lovejoy, 1981). Although the present study focuses primarily on the evolution of sex-specific body size in *Pan* and

Australopithecus afarensis, results will be considered in conjunction with results of previous studies of canine size dimorphism in these taxa.

As a final note, it has been argued that body size differences between fossils of *A. afarensis* found at different sites may primarily reflect ecogeographical or temporal variation rather than sexual dimorphism (Reno *et al.*, 2003). In a resampling analysis of dimorphism in estimated femoral head size at the simultaneous death assemblage A.L. 333, Reno *et al.* (2003) concluded that the level of dimorphism represented at A.L. 333 most closely resembles that of modern humans, and they reconstruct *A. afarensis* as a monogamous species. However, their estimation technique was based on an implicit untested assumption of isometric scaling between femoral head and all other linear dimensions, as well as an absence of inter-individual variability in the relationship between femoral head size and all other linear dimensions. These methodological errors act to overestimate femoral head size in some specimens and underestimate size in others, producing artificial measurements indicating a large number of specimens of intermediate size. Despite these flaws in methodology, Reno *et al.*'s point that differences in size between sites may primarily be due to differences in time and space is a valid one. To address that concern, this analysis is limited to specimens from the Denan Dora Member (*i.e.*, A.L. 288-1 and specimens from A.L. 333), which preserves several large and small adult specimens within a small geographic area and narrow time depth (Walter, 1994). In addition, at the end of this paper I will provide a brief interpretation of size differences in A.L. 288-1 and the A.L. 333 assemblage in the context of site differences.

SAMPLE AND METHODS

Sample

Postcranial measurements were collected for adult specimens of *Pan troglodytes troglodytes* (75 females and 34 males from the Cleveland Museum of Natural History and

the Powell-Cotton Museum in Kent, England), *P. t. schweinfurthii* (5 females and 6 males from the Royal Museum of Central Africa in Tervuren, Belgium), *P. paniscus* (9 females and 7 males from the Royal Museum of Central Africa), *Gorilla gorilla gorilla* (60 females and 62 males from the Cleveland Museum of Natural History and the Powell-Cotton Museum), and modern *Homo sapiens* (30 females and 70 males from the Cleveland Museum of Natural History). Adulthood was determined on the basis of postcranial epiphyseal fusion. In addition, body mass data and cause of death was available for all human specimens in this study.

The human sample is drawn from the Hamann-Todd Collection at the Cleveland Museum of Natural History, and is restricted to “wild-shot” specimens (e.g., Kappelman, 1996); i.e., individuals who died from causes other than illness. *P. paniscus* and *P. t. schweinfurthii* individuals are included despite small sample sizes in order to more completely represent postcranial size in *Pan* (as compared to a sample of *P. t. troglodytes* alone). *Australopithecus afarensis* is represented by the following specimens: A.L. 288-1, A.L. 333-3, A.L. 333x-26, A.L. 333-42, A.L. 333-107, and A.L. 333x-14. A.L. 333 specimens included here are all of the larger adult size morph identified at that site (McHenry, 1986), not due to a predetermined protocol of selecting only larger individuals, but because the elements available at A.L. 333 for the measurements used in this study all come from larger individuals. Although the A.L. 333x-14 radial head is from a subadult individual, it is from one of the largest fossil individuals at site A.L. 333 and is therefore included here. Fossil inclusion is restricted to Hadar’s Denan Dora Member in order to maximize the probability that specimens come from roughly contemporaneous individuals.

Methods

Proximal articular surfaces of the femur, tibia, humerus, and radius are represented by one linear dimension each for all specimens in the extant sample. Measurements correspond to McHenry's (1992) *Femhead*, *Humhead*, *Radv*, and the square root of *Proxtib* (converting it to a linear measure from a measure of area). Fossil measurements are taken from McHenry (1992). Sex-specific mean body mass is drawn from Smith and Jungers (1997) for the African apes, and is calculated based on museum records for the human sample.

Comparing Size

The most commonly cited body size estimate for male *A. afarensis*, 45 kg, is similar in size to that of adult chimpanzees (McHenry, 1992; Smith & Jungers, 1997). Because linear dimensions are likely to scale differently with overall body size in chimpanzees and australopithecines due to differences in locomotor adaptations, linear dimensions are compared between the larger Hadar hominids and male chimpanzees of *P. paniscus*, *P. t. troglodytes*, *P. t. schweinfurthii*. Comparisons are also made between A.L. 288-1 and female chimpanzees. Comparisons are conducted as the logarithm of chimpanzee size minus the logarithm of fossil size; this difference is equal to the logarithm of a ratio of chimpanzee size divided by fossil size and thus are measures of proportional or relative difference. Patterns of relative difference in linear dimensions are compared between males and females.

Because linear measures from different skeletal elements may not all scale with overall body size in the same way, comparisons between taxa based on single linear measurements can produce misleading results. However, geometric means of linear measurements produce robust size variables that can be used to demonstrate equivalence with, or deviation from, geometric similarity with body size (*i.e.*, isometry and allometry,

respectively) (Mosimann, 1970). This approach has been successfully used in developing regional size variables for primate morphometrics (*e.g.*, Falsetti *et al.*, 1993; Jungers *et al.*, 1995; Richmond & Jungers, 1995; Lague & Jungers, 1996; Ravosa, 1998) as well as an overall body size variable (*e.g.*, Jantz & Jantz, 1999).

In this study, a geometric mean of *Femhead*, *Proxtib*^{0.5}, *Humhead*, and *Radtv* is calculated for each extant specimen, and is referred to here as a skeletal size variable, or SSV. Because this variable equally represents proximal articular surfaces from the fore- and hindlimb, it is appropriate to consider SSV a measure of overall body size. However, it may or may not scale isometrically with body mass. Isometric scaling is desirable because proportional differences in one variable can be transformed into proportional differences in a second variable that scales isometrically with the first. Thus if SSV scales isometrically with body mass, proportional differences in SSV between taxa are equivalent to proportional differences in the cube root of body mass.

Log-transformed sex-specific mean body mass is regressed against log-transformed sex-specific mean SSV for the African ape sample to identify the scaling relationship between mass and SSV. Body mass data are taken from published sources that do not include body mass for all of the measured skeletal specimens; therefore, an extra source of error is introduced into body mass data used in this analysis. As a consequence, Model I regression is preferred to Model II so that the error is minimized along the Y-axis (logged mean body mass). Because SSV is a geometric mean of linear measurements, isometry corresponds to a slope of three. Humans are not included in this regression because some articular dimensions are known to scale differently in apes and humans (Jungers, 1990b). Instead, log-transformed sex-specific means of human body mass and SSV are compared against the African ape regression.

Resampling Analyses of Size and Dimorphism in Hadar Hominids

Measurements of SSV can be used to compare body size of Hadar hominids and extant taxa. All four linear dimensions that compose SSV are available for a single fossil specimen, A.L. 288-1. However, all four measurements are not available for any other single fossil individual, although all dimensions are represented separately by specimens of the larger size morph at A.L. 333 (right proximal femur, right and left proximal tibiae, right proximal humerus, and a radial head). These elements could conceivably have come from one individual, five individuals, or any number in between, although they most likely represent more than one individual. Thus an SSV calculated for these elements cannot be supposed to represent body size for a single individual, but it could be useful in size comparisons with extant taxa. Although comparisons between composite size in fossil specimens and individual size in extant specimens would be of dubious worth, resampling procedures such as exact randomization and bootstrapping can provide useful comparisons between composite size in fossil and extant taxa (Chernick, 1999). Resampling procedures have been used in various analyses of fossil hominids for over a decade (*e.g.*, Grine *et al.*, 1993; Kramer *et al.*, 1995; Richmond & Jungers, 1995; 1996; Lague & Jungers, 1996; Lockwood *et al.*, 1996; Arsuaga *et al.*, 1997; Thackeray, 1997; Lockwood, 1999; 2000; Richmond *et al.*, 2002; Reno *et al.*, 2003); in general, bootstrap techniques are more accurate than exact randomization and are preferred when feasible (*i.e.*, sample sizes are large enough) (Lockwood *et al.*, 1996; Aiello *et al.*, 2000).

Body size for a composite large-morph Hadar hominid is calculated as a geometric mean of (1) *Femhead* for A.L. 333-3, (2) arithmetic mean of *Proxtib*^{0.5} for A.L. 333x-26 and A.L. 333-42, (3) *Humhead* for A.L. 333-107, and (4) *Radtv* for A.L. 333x-14. Because the resulting SSV is a mean of measurements that most likely come from separate individuals, it probably not only falls within the range of individual SSV

for the larger Hadar hominids, but also probably lies closer to mean SSV for those hominids than a randomly selected individual SSV would be. This assertion can be demonstrated empirically by way of resampling procedures.

Composite extant “individuals” can be composed of the same combination of five linear measurements available in the A.L. 333 sample, drawn from one to five individuals for an extant taxon. For example, SSV for a composite male gorilla could be calculated using *Femhead* and *Proxtib*^{0.5} from one individual, *Humhead* and *Radtv* from a second individual, and *Proxtib*^{0.5} from a third individual. A finite number of composite individuals can be calculated for finite populations. For smaller populations it is feasible to calculate all possible composite SSV values and compare them to the range of SSV for actual individuals; *i.e.*, exact randomization. Bootstrap procedures can be used with larger samples, in which observed ranges of individual SSV are compared against a randomly selected subset of all possible composite individuals generated for that taxon.

Resampling procedures are used to determine whether SSV based on a composite male will fall within the observed range of SSV for all individual males within each extant taxon. Exact randomization comparisons are used to compare composite male SSV to individual SSV ranges for *P. paniscus* (7 males) and *P. t. schweinfurthii* (6 males). A total of 9604 and 4536 composite males can be calculated for each of these taxa, respectively. Bootstrap procedures are used for *P. t. troglodytes* (34 males), *G. gorilla* (62 males), and *H. sapiens* (70 males). Over 2.2×10^7 unique composite males can be calculated for the smallest of these samples (*P. t. troglodytes*). Thus calculation of 10,000 random composite males is unlikely to sample any particular composite male more than once.

Although comparison of size dimorphism in the Hadar hominids and extant taxa is not the primary goal of this paper, such a comparison is useful when discussing the

difference in size between A.L. 288-1 and the larger size morph at A.L. 333, regardless of whether those differences are attributed to sexual dimorphism, site differences, or a combination thereof. A ratio of SSV for the composite A.L. 333 hominid divided by SSV for A.L. 288-1 is calculated and compared to resampled ratios of one composite male divided by one female for each extant taxon. As above, exact randomization will be used to calculate ratios for *P. paniscus* and *P. t. schweinfurthii*, and bootstrapping will be used for *P. t. troglodytes*, *G. gorilla*, and *H. sapiens*.

It has been noted that A.L. 288-1 is smaller than all adult specimens at A.L. 333, and that the difference between A.L. 288-1 and the larger adult size morph at A.L. 333 may be due to ecomorphological or temporal variation rather than contemporaneous sex difference in a single population (Reno *et al.*, 2003). In order to mimic such differences in the extant sample, the fossil ratio is compared to a bootstrapped distribution for a ratio of SSV using one composite male from the chimp taxon with the largest body size in this study (*P. t. troglodytes*) divided by SSV for one female from the chimp taxa with the smallest body size (*P. paniscus* and *P. t. schweinfurthii*). All resampling procedures are performed using code written for the statistical programming language *R* (Ihaka & Gentleman, 1996) ([Appendix F](#)).

Phylogenetically Independent Contrasts Analyses

Whether or not size differences between A.L. 288-1 and the larger size morph at A.L. 333 are considered to be influenced by site differences, the A.L. 333 large adults are likely male based on the presence of two distinct size morphs at that site (McHenry, 1992). Extreme small size of A.L. 288-1 indicates that it is most probably female, an assessment that has been borne out by morphological analysis of the pelvis (Tague & Lovejoy, 1998). Therefore it is appropriate to conduct size contrasts analyses between chimpanzee males and the composite A.L. 333 hominid, and size contrasts analyses

between chimpanzee females and A.L. 288-1. Comparison of male and female *Pan–Australopithecus* contrasts are most appropriate if site differences are not considered to trump size differences. Implications of contrasts will be discussed for both scenarios.

Phylogenetically independent contrasts analyses allow identification of scaling patterns of size and dimorphism associated with phyletic divergences. Lande's (1980) quantitative genetics model predicts that dimorphism will scale positively with body size when selection acts primarily on males, and negatively with body size when selection acts primarily on females. Consider a bivariate plot in which positivized female contrasts of log [SSV] are plotted on the X-axis, and male contrasts are plotted on the Y-axis (Figure 6.1). A diagonal line with slope of one passing through the origin (*i.e.*, the line of identity) marks equal difference in male and female size. Any point plotting on that line indicates that the two taxa involved in that contrast are equally dimorphic, although the taxa are of different body size if the point is not sitting at the origin. Contrasts that plot above the line of equal change indicate that male body size differs between two taxa by a greater proportion than does female size, indicating that increased dimorphism is associated with greater proportional increase in male body size, and/or decreased dimorphism is associated with greater proportional decrease in male body size. In either case, body size and dimorphism are positively correlated, and body size has changed more for males than females. When contrasts plot below the line of identity, dimorphism scales negatively with size, and body size has changed more for females than males. Contrasts analyses will be used here to identify relative sex-specific selection intensities operating on the lineages leading to *Pan* and *Australopithecus* from their last common ancestor.

With only one female and one composite male available for *Australopithecus afarensis*, results of fossil contrasts analyses are decidedly tenuous. However,

resampling procedures can be used to assign probabilities to relative differences in size. In the case of female contrasts, the data set in this study allows 3375 possible sets of contrasts for one female *P. paniscus*, one female *P. t. troglodytes*, one female *P. t. schweinfurthii*, and A.L. 288-1. An exact randomization procedure is used to identify the range and 95% confidence limits for female contrasts of log [SSV]. A much larger number of unique contrasts are possible for one composite male each of the three *Pan* taxa and the A.L. 333 hominid due to the construction of composite males from up to five individuals. Therefore a bootstrap procedure is used to calculate range and 95% confidence limits for male contrasts.

An important element in any phylogenetic analysis is the phylogenetic tree imposed on the data. Branching sequence and branch lengths are based on a molecular reconstruction of divergence dates within *Pan* (Morin *et al.*, 1994) and a mean of 15 divergence dates for *Pan* and *Homo* (Purvis, 1995) (Figure 6.2). Garland *et al.* (1992) state that independent contrast analyses should only be performed with trees in which the absolute value of standardized contrasts are not significantly correlated with their standard deviations. Because of the large number of contrasts calculated in the resampling procedures used here, it is not feasible to meet this criterion for all contrasts. Correlation between standardized contrasts and their standard deviations is a concern when performing regressions on contrasts because standardized contrasts will become biased in their magnitude and act as leverage points on regressions. Fortunately, this study analyses male and female contrasts individually rather than performing regressions on contrasts. Since the same tree will be used for male and female contrasts, any bias due to branch length will scale magnitudes identically in contrasts for both sexes and thus will not affect their placement with respect to the line of identity shown in Figure 6.1.

Similarly, uncertainty regarding the divergence date of *Pan* and *Australopithecus* will not affect the relative placement of contrasts with respect to the line of identity and zero axes. The contrast between the Hadar hominids and the node at the base of *Pan* is first calculated as the difference in log [SSV] for the fossil and a phylogenetically-weighted mean of *Pan*. This weighted mean is a function of the values of log [SSV] in the three *Pan* taxa and of the branch lengths between them; it is *not* dependent on the branch lengths separating *Pan* from *Australopithecus*. The contrast is then standardized by the square root of the branch distance between *Pan* and *Australopithecus*. The standardization process does not affect the relative placement of the contrasts with respect to the line of identity and the zero axes because contrasts for both sexes are divided by the same positive number. Thus positive contrasts cannot become negative (and vice-versa), and ratios of male contrast to female contrast will remain constant so that data points cannot cross the line of identity.

RESULTS

Proximal Articulation Measurements

Means, ranges, and standard deviations for linear measures of long bone proximal articulations for African apes and humans are given in [Table 6.1](#). Comparison between A.L. 288-1 and females of three *Pan* taxa shows that linear dimensions of the hindlimb are slightly smaller in A.L. 288-1 than female means for *Pan*, and forelimb dimensions are considerably smaller in A.L. 288-1 than all *Pan* measurements ([Fig. 6.3](#)). Linear dimensions for the larger Hadar specimens tend to be larger than *Pan* male means in the hindlimb, but smaller in the forelimb. Linear dimensions in the larger Hadar hominids relative to male chimpanzees appear very similar to the pattern of relative size in A.L. 288-1 and female chimpanzees, translated downward along the Y-axis in [Figure 6.3](#).

This resemblance in pattern suggests that the larger Hadar material may come from individuals of roughly similar overall body size to each other.

Skeletal Size Variable

A geometric mean of the four linear variables, referred to here as a skeletal size variable (SSV), was calculated for all extant individuals and A.L. 288-1 (Table 6.2). A geometric mean was also calculated for *Femhead* of A.L. 333-3, the arithmetic mean of *Proxtib*^{0.5} of A.L. 333x-26 and A.L. 333-42, *Humhead* of A.L. 333-107, and *Radtv* of A.L. 333x-14. The resulting SSV represents body size in a “composite” Hadar hominid.

Composite Male Size Distributions

Bootstrap and exact randomization techniques were used to test the hypothesis that size for a composite individual would fall within the observed range of size from actual individuals for a particular taxon. In bootstrap analyses of the taxa with larger sample sizes (*G. gorilla*, *H. sapiens*, and *P. t. troglodytes*), SSV values for all composite males for a particular taxon were between minimum and maximum values of observed individual SSV (Table 6.2, Fig. 6.4). Exact randomization analyses of the smaller samples show that that 97.1% of composite male SSV values fall within observed limits for 7 *P. paniscus* males, and 96.0% of composite male SSV values are within observed limits for 6 *P. t. schweinfurthii* males (Table 6.2, Fig. 6.4). Note that in all five extant taxa, the probability of obtaining an SSV value close to the midpoint of the range for individual males is greater when selecting a composite male at random than when selecting an individual male at random (Fig. 6.4).

Size Dimorphism

Size dimorphism for SSV in the Hadar hominids is measured as a ratio of composite size of the larger specimens divided by size in A.L. 288-1. Size ratios of SSV for a composite male divided by one female are bootstrapped for the larger extant

samples and generated through exact randomization for the smaller extant samples (Table 6.3). The ratio of 1.36 observed in the Hadar hominids exceeds all ratios calculated for modern humans and separate chimpanzee taxa. The degree of dimorphism present in the Hadar hominids can be accommodated within gorillas and within a mixed ratio of different *Pan* taxa, but only 8% of bootstrapped gorilla ratios and 0.2% of bootstrapped mixed *Pan* ratios are more dimorphic (Table 6.3, Fig. 6.5).

Sex-Specific Size

Regression of log body mass against log SSV for African apes yields a significantly positive slope that does not differ significantly from isometry, where isometry is equal to a slope of 3 (d.f. = 6, slope = 2.99, $r^2 = .962$, $p < 0.001$; Fig. 6.6). Smith's (1994) reduced degrees of freedom method yields an effective sample size of 3 and a slope bordering on significance at $\alpha = 0.05$ (reduced d.f. = 1, $p = 0.052$). Human females plot within 0.3 standard error of the African ape regression line, while human males plot 2.7 standard errors below the line. Thus SSV overestimates body size (as measured by body mass) in human males when compared to African apes, although SSV does not appear to do so for human females. Mean SSV in human males must drop from 1.64 to 1.60 log units (a difference of 9.6%) in order to plot directly on the ape regression line.

Body size (as measured by SSV) in the composite Hadar hominid is smaller than all gorillas of either sex, all male humans, and all but the smallest of female humans (Table 6.2, Fig. 6.7). However, the composite hominid is larger than mean size in both sexes of *P. paniscus* and females of *P. troglodytes*, and only slightly smaller than mean male size in *P. troglodytes*. Composite Hadar hominid size falls within all 95% confidence intervals for each chimpanzee sex and taxon (Fig. 6.7). Adjusting SSV for the composite Hadar hominid downwards by the same proportion as SSV overestimates

body size in human males (*i.e.*, 0.04 log units) results in the same size as the mean for female *schweinfurthii* chimps, placing it in the body size range of female common chimpanzees and both sexes of bonobos but below the range of male common chimpanzees (see placement of mean female size for *P. t. schweinfurthii* in Fig. 6.7). A.L. 288-1 is considerably smaller than all extant individuals in this study, as well as all 95% confidence intervals (Table 6.2, Fig. 6.7). Further reduction to compensate for possible overestimation of size in A.L. 288-1 would increase this difference.

Phylogenetically Independent Contrasts Analysis

Phylogenetic independent contrasts for mean sex-specific size indicate that dimorphism in SSV scales positively with size in the relationship between *P. troglodytes* and *P. paniscus* (as shown by the position of those contrasts in Fig. 6.8 above the dashed line for equal difference in male and female contrasts). Dimorphism scales negatively with size between subspecies of *P. troglodytes* (contrasts plots below the dashed line in Fig. 6.8).

Phylogenetic independent contrasts were also calculated for mean female SSV in *Pan* and A.L. 288-1, and for mean male SSV in *Pan* and the composite large Hadar hominid. Exact randomization 95% confidence intervals do not include zero for the contrast between size of A.L. 288-1 and the phylogenetically-weighted mean of female size in *Pan* (Table 6.4, Fig. 6.8). In all cases, the phylogenetically-weighted mean of SSV for *Pan* females is greater than SSV in A.L. 288-1.

Exact randomization and bootstrap 95% confidence intervals both include zero for the contrast between size of the composite Hadar hominid and the phylogenetically-weighted mean of male size in *Pan* (Table 6.4, Fig. 6.8). SSV is larger in the composite Hadar hominid than in the phylogenetically-weighted mean of *Pan* males in 86.4% of exact randomization cases and 96.7% of bootstrap cases. If SSV is corrected downward

in the composite hominid by the same proportion that SSV overestimates body size in human males (*i.e.*, 0.04 log units or 9.6%), the composite Hadar hominid is smaller than the phylogenetically-weighted mean of male *Pan* in all cases (95% confidence intervals for independent contrasts: exact randomization individual males, 0.0054 to 0.0156; bootstrap composite males, 0.0071 to 0.0132). Confidence intervals for male and female contrasts of *Pan* and the Hadar hominids do not overlap, even if size is adjusted downward in the composite hominid but is not adjusted in A.L. 288-1 (*i.e.*, confidence intervals do not overlap the dashed diagonal line in Fig. 6.8). The lack of overlap indicates that A.L. 288-1 is smaller than female *Pan* by a greater proportion than the composite male is smaller than male *Pan*, even if size is overestimated in the composite hominid but not in A.L. 288-1.

DISCUSSION

Measuring Size in Hadar Hominids

Relative differences in linear dimensions between *Pan* females and A.L. 288-1, in which chimpanzees are slightly larger in hindlimb dimensions and considerably larger in forelimb dimensions, reflect the influence of habitual bipedality; *i.e.*, transmission of all or most of body weight through the hindlimb of Hadar hominids a greater percentage of the time than in extant chimpanzees. The same pattern of a shift between forelimb and hindlimb measurements is observed when linear dimensions of the larger hominid specimens of the Denan Dora Member are considered as a group. Thus those five specimens (A.L. 333-3 right proximal femur, A.L. 333x-26 right proximal tibia, A.L. 333-42 left proximal tibia, A.L. 333-107 right proximal humerus, and A.L. 333x-14 radial head) probably came from individuals roughly the same size as each other. Although the A.L. 333x-14 radial head is from a subadult individual, it is larger than all but one of the radial heads measured by McHenry (1992), who measured specimens

attributed to *A. afarensis*, *A. africanus*, robust australopithecines, and early *Homo*. Also, while the proportional difference between *Pan* and A.L. 288-1 is greater for *Radtv* than for *Humhead*, these differences are reversed in the larger Hadar specimens – indicating that the subadult radial head A.L. 333x-14 probably belonged to a larger individual than did the fully-fused humeral head of A.L. 333-107 (Fig. 6.3).

Calculating a geometric mean of the four linear measurements for A.L. 288-1 yields a size variable that equally represents proximal articulation size (and perhaps the weight-bearing contribution) of each major long bone of the appendicular skeleton. As bootstrap and exact randomization analyses depicted in Figure 6.4 demonstrate, the same size measure for a composite of multiple individuals will not only nearly always fall within the size range of actual individuals, but it will also have a higher probability of being closer to the mean of individual measures of SSV than does the SSV of a randomly selected individual. Even in the case of the smallest samples, seven male *P. paniscus* and six male *P. t. schweinfurthii*, more than 95% of all possible SSV values calculated for a composite male fall within the observed range. Assuming that the five fossil specimens belonged to a taxon containing at least six males in total, the measure of composite size calculated here is very likely to be within the size range exhibited in the population of living hominids from which these fossil samples were drawn.

Size Dimorphism and Sex-Specific Size

Results from bootstrap and exact randomization analyses of SSV ratios indicate that the level of dimorphism observed in the Hadar hominids can be accommodated within gorillas (at the high end of the bootstrap distribution), but it is greater than all bootstrap and exact randomization ratios of composite male size divided by individual female size in humans and chimpanzee taxa. The Hadar SSV ratio can just barely ($p = 0.002$) be accommodated within ratios for a “mixed assemblage” containing skeletal

elements from one to five *P. t. troglodytes* males and one *P. pansicus* or *P. t. schweinfurthii* female, indicating that size differences of the magnitude seen in the Hadar hominids could be produced by comparing across species or sub-species within *Pan*. Although the fossil specimens exhibit a high level of dimorphism, it is not so high as to preclude the possibility that all of the Hadar hominids of the Denan Dora Member belong to the same species on the basis of size alone. This finding agrees with previous resampling analyses of dimorphism in various postcranial elements of *A. afarensis* (Richmond & Jungers, 1995; Lockwood *et al.*, 1996).

When considering sex-specific size rather than ratios, SSV appears to be a good measure of overall body size in African apes and female humans. However, human males depart significantly from the African ape regression line (a difference of over three standard errors). This departure indicates that SSV substantially overestimates body size in male humans if body mass is used as a reference for overall size.

Despite the fact that the weight-bearing function of the forelimb has been transferred to the hindlimb in humans, we retain relatively large humeral heads. This is shown by the good fit of humans to non-human hominoid regressions of humeral head size against body mass, compared to the marked deviation of humans from non-human hominoid regressions of hindlimb dimensions against body mass (compare standard errors of estimate for living hominoid and non-human hominoid regressions in Jungers, 1990b). Thus hindlimb articular surfaces increased in size within the human lineage in conjunction with the greater proportion of body mass transmitted through the hindlimb, but the humeral head did not decrease in size in response to the removal of weight-bearing constraints on size. Overestimation of body size in human males by SSV is most likely due to the retention of relatively large humeral heads in conjunction with large

hindlimbs, although it is unclear why SSV does not similarly overestimate female human size.

Several anatomical features of *A. afarensis* indicate that these early hominids retained arboreal behavior in their locomotor repertoire: curved phalanges, cranially oriented glenoid fossae, *etc.* (Jungers & Stern, 1983; Stern & Susman, 1983; Rose, 1984; Susman *et al.*, 1984; Stern & Larson, 1993; Duncan *et al.*, 1994). Suspensory behaviors would probably have been used at least occasionally, during which time the humeral head would have played a weight-bearing role. Thus it is unclear whether SSV should be expected to overestimate body size in the Hadar hominids. All comparisons of body size as measured by SSV between Hadar hominids and other taxa in this study are undertaken with the caveat that SSV may overestimate body size in fossil hominids, particularly in males.

Body size in the larger Hadar hominids appears to be very similar to that of extant chimpanzees, even when uncertainty regarding the application of SSV to hominids is taken into account. However, A.L. 288-1 is considerably smaller than all other individuals in this analysis, regardless of whether SSV overestimates size in *A. afarensis*.

Size Change in *Pan* and the Hadar Hominids

Dimorphism in SSV scales positively with size in the contrast between *P. troglodytes* and *P. paniscus*, but negatively with size in the contrast between subspecies of *P. troglodytes*. Lande's (1980) quantitative genetics model predicts that dimorphism will scale positively with size when selection acts primarily on males, and negatively with size when selection acts primarily on females (Chapter 2, Smith & Cheverud, 2002). Sexual selection theory predicts that males should be the primary target of selection on body size when males can competitively exclude other males from reproductive opportunities (Andersson, 1994). Although dominance and mating success are positively

correlated in wild males of both *P. paniscus* (Kano, 1992) and *P. troglodytes* (Hasegawa & Hiraiwai-Hasegawa, 1990), consortships and mate-guarding behaviors have been observed in common chimpanzees, but not in bonobos (Tutin, 1979; Hasegawa & Hiraiwai-Hasegawa, 1990; Kano, 1992). Thus sexual selection on male size is expected to be more intense in common chimps, producing larger size and greater dimorphism in *P. troglodytes*. Examination of [Tables 6.2](#) and [6.3](#) shows that both subspecies of *P. troglodytes* are larger and more dimorphic than *P. paniscus* as measured by SSV.

Selection acting primarily on female size, indicated by the contrast between the two common chimpanzee subspecies, is expected under two scenarios. It may be the product of sexual selection acting on female size in polyandrous groups (Petrie, 1983; Gwynne, 1991; Andersson, 1994; Parker & Simmons, 1996; Cunningham & Birkhead, 1998), and/or it may result from female body size being more sensitive to resource pressure than male body size (Ralls, 1976; Emlen & Oring, 1977; Wrangham, 1980; van Schaik, 1989; Isbell, 1991; Mitchell *et al.*, 1991; van Hooff & van Schaik, 1992; Isbell & Pruett, 1998; Boinski *et al.*, 2002). For common chimpanzees, the probability of sexual selection operating on polyandrous groupings is extremely low. However, *P. troglodytes* is found in a variety of different habitats (Fleagle, 1999), so differences in body size between subspecies are probably due to differences in natural selection pressures on body size resulting from different ecological conditions.

When phylogenetically independent contrasts analyses are extended to the Hadar hominids using exact randomization and bootstrap techniques, SSV in A.L. 288-1 is shown to be smaller than all possible phylogenetic means of one female from each of the three chimpanzee taxa considered in this study. SSV for the composite Hadar hominid ranges from slightly larger to slightly smaller than phylogenetic means of one individual male or composite male from each of the three chimpanzee taxa.

A zero contrast between two observed taxa (as distinct from contrasts between internal nodes within a phylogeny) does not necessarily mean that no change has occurred since their last common ancestor (LCA). Rather, a zero contrast indicates that the same amount of change has occurred along both lineages, resulting in no difference in the descendant taxa. Non-zero contrasts indicate that different amounts of change have occurred along daughter lineages. When contrasts are calculated between an observed taxon and an internal node as in the case of contrasts between the Hadar hominids and the node at the base of *Pan* in this study, interpretation is slightly different. Internal nodes are phylogenetically-weighted means of observed taxa, and may or may not accurately represent the size of the LCA of the taxa included in that mean. Because there is considerable overlap in SSV between the composite Hadar hominid and chimpanzees of both sexes and all three subspecies, it is likely that the common ancestor of all chimpanzees was also similar in body size to living members of the genus *Pan*, in which case a phylogenetically-weighted mean of size in *Pan* is a reasonable approximation of body size for the common ancestor of *Pan*. More uncertain is body size in the LCA of *Pan* and *Australopithecus*.

There are no known fossil African apes documenting the time period between the divergence of the *Gorilla* and *Pan* lineages and the divergence of the *Pan* and *Australopithecus* lineages. However, there are fossil taxa that have been proposed as stem African apes: a middle Miocene genus from southern Africa (*Otavipithecus*, Pickford *et al.*, 1997), two late Miocene genera from Europe (*Dryopithecus*, Begun & Kordos, 1997 and *Ouranopithecus*, Andrews *et al.*, 1997), and a late Miocene genus from East Africa (*Samburupithecus*, Ishida & Pickford, 1997). Estimated body mass in these taxa ranges from 17.5 kg for *Otavipithecus* to 110 kg for *Ouranopithecus* (Fleagle, 1999); *i.e.*, from smaller than reconstructed body mass in A.L. 288-1 to larger than most female

gorillas (McHenry, 1992; Smith & Jungers, 1997). Of all of these taxa, only *Samburupithecus* and *Otavipithecus* are found in the same geographic regions as australopithecines. As the youngest of these taxa at 9.5 myr (Ishida & Pickford, 1997), *Samburupithecus* is closest in age to the probable divergence dates of *Gorilla*, *Pan*, and *Australopithecus*. Consisting of a single maxillary fragment (KNM SH 8531) with clear affinities to modern African apes (Ishida & Pickford, 1997), body size in *Samburupithecus* has been reconstructed on the basis of tooth size as approximately 60kg (Fleagle, 1999); *i.e.*, equal to mean body size in *P. t. troglodytes* males (Smith & Jungers, 1997). With only one fossil specimen, degree of dimorphism in *Samburupithecus* is unknown. However, body size for male *Samburupithecus* is unlikely to be significantly smaller than that of KNM SH 8531, and body size for female *Samburupithecus* is unlikely to be significantly larger.

Knowledge of body size in *Samburupithecus* does not place constraints on body size in the LCA of *Pan* and *Australopithecus*, even if *Samburupithecus* could be demonstrated to be the LCA of all African apes. However, considering that (1) KNM SH 8531, both sexes of *Pan*, and the larger Hadar hominids all converge on a narrow range of body size, and (2) body size in both sexes of *Gorilla* is even larger, it is unlikely that males of the LCA of *Pan* and *Australopithecus* were much smaller than the range of body size observed in living chimpanzees of both sexes. Change in male size from that ancestor to the Hadar hominids was probably somewhere between a slight increase to a moderate decrease in size, with a similar change in size occurring in the lineage leading to the common ancestor of extant *Pan* taxa.

Female body size in the LCA of *Pan* and *Australopithecus* is much more uncertain. If body size dimorphism approached that of gorillas, females may have been as small as A.L. 288-1. If that were the case, female size would have had to change at a

much higher rate than male size in the *Pan* lineage, while female and male size remained relatively stable in the lineage leading to the Hadar hominids. If body size dimorphism was closer to levels observed in *Pan* then changes in body size in the lineage leading to *Pan* would have been roughly similar in males and females. In that case, female body size in the hominid lineage would have been marked by a significant decrease, much greater than any possible decrease in male size. Thus size changes in males were approximately the same in both descendant lineages, regardless of starting condition, but female size changed in drastically different ways in the lineage leading to *Pan* and the lineage leading to the Hadar hominids. Understanding how body size dimorphism evolved in *A. afarensis* requires an understanding of why female body size evolved so differently in these two lineages when male body size evolution appears to have been quite similar.

Environmental Pressures, Sexual Selection, and Sex-Specific Body Size

It is difficult to identify the magnitude and direction of female body size change in the lineages leading to *Pan* (proto-chimps) and *Australopithecus* (proto-hominids) without a more extensive fossil record of late Miocene African apes. However, consideration of the biogeography of living apes and extinct hominids in conjunction with the selective forces likely to produce size change can help identify the more likely scenarios of change.

As discussed above, when female size changes proportionally more than male size, change usually results from sexual selection pressure acting on polyandrous females or from the greater sensitivity of females to resource pressures. The Hadar hominids and their direct ancestors were probably not polyandrous; extant African apes live in polygynous groups, and polyandry in living haplorhine primates is limited to the Callitrichidae (Dixson, 1998). A more likely source of selection pressure in this case is

resource limitation. Work on human dimorphism in Native Americans suggests that small body size is advantageous for mothers when resources are scarce during lactation (Hamilton, 1975 cited in Ralls, 1977). It has also been shown that smaller females breed more often than larger females in variable environments (Downhower, 1976), which could lead to greater lifetime reproductive success and thus select for small size in females.

Extant African apes are confined to narrow ecological and geographical boundaries: the tropical rainforests of equatorial Africa and nearby open woodlands, with gorillas and bonobos in particular limited to forested habitats. The ecological constraints placed on living African apes combined with postcranial features indicating an arboreal ancestry in *A. afarensis* suggest that the LCA of *Pan* and *Australopithecus* probably lived in similar environments. However, while the current geographic extent of chimpanzees suggests that the *Pan* lineage remained within the African continental forest, paleoenvironmental reconstructions of early hominid habitats indicate that the same cannot be said for the *Australopithecus* lineage.

Although the record of late Miocene Africa is not one of geographically uniform, monotonic increase in aridity (Kingston *et al.*, 1994; Griffin, 2002; Jacobs, 2002), it is characterized by an increase in open habitat mammals (Janis, 1993; Vrba *et al.*, 1995) and an increase in C₄ plants, most of which are subtropical grasses and sedges (Cerling *et al.*, 1993; Morgan *et al.*, 1994; 1997; 1998; Kingston *et al.*, 2002). Plio-Pleistocene East African habitats reflect these influences by preserving a diversity of open and closed habitats (Kappelman *et al.*, 1997). Thus the late Miocene in Africa likely saw forest fragmentation and habitat loss as a continent-spanning equatorial forest transitioned to a forest primarily located west of the Great Rift Valley (Pickford, 1991; Foley, 1994). In addition, early hominids habitats in the Middle Awash and Lukeino have been

reconstructed as relatively wet and wooded as compared to surrounding regions (WoldeGabriel *et al.*, 2001), suggesting that although early hominids had access to more open habitats, they may have preferred more forested environments.

A possible scenario for the evolution of hominids involves populations of proto-hominids living near forest edges that became reproductively isolated from core populations of proto-chimps by forest fragmentation. Restricted to islands of forest in seas of expanding grasslands, proto-hominids would have been limited to those food resources available in a relatively small area, and unable to move to more productive regions when resources were scarce. In these variable resource conditions, smaller females might have been able to breed earlier, improving their lifetime reproductive success and thus generating selection pressure for smaller female body size.

If such a scenario occurred in the lineage leading to the Hadar hominids, it would suggest that the difference in female body size between *Pan* and A.L. 288-1 is due primarily to female size reduction in the lineage leading to *A. afarensis* rather than size increase in the lineage leading to *Pan*. Rates of body size growth appear to decrease as ecological risk increases in African apes (Leigh & Shea, 1996), consistent with predictions that small female size should evolve in response to fluctuating environments. Retarded female growth rates in response to resource limitation within the proto-hominid lineage would have resulted in small adult females. But if resource pressures were so intense as to cause substantial size reductions in female body size, why would male body size not also have decreased?

A look at canine dimorphism in the Hadar hominids may help answer that question. As Plavcan *et al.* (1995) point out, although male primates compete primarily for mates and female primates compete primarily for resources, outcomes of those competitions should affect individual fitness regardless of the source of competition.

Thus canine size dimorphism should reflect relative competition levels present in both sexes. Canine size is mildly dimorphic in *A. afarensis*, similar in degree to that observed in *P. paniscus* (Plavcan & van Schaik, 1997a). If females in the Hadar lineage were highly competitive over limited resources, the mild dimorphism present in the Hadar hominids may reflect high competition levels between females over resources, and even higher competition levels between males over mates. At the very least, competition between males was probably at least as intense in *A. afarensis* as it is in *P. paniscus* (which, although low, is present, Kano, 1992), and that a social structure similar to that of bonobos or common chimpanzees is highly probable. Thus sexual selection would have acted to buoy up male size even as female size decreased.

Under this scenario of decreased female size in the proto-hominid lineage, selection pressures favoring small female size resulting from resource limitation would have been alleviated with (1) the evolution of more efficient bipedalism, allowing locomotion between widely separated forest fragments, and (2) the shift of later hominids into ecological niches utilizing resources available outside of forested areas. Dimorphism in later hominids would be expected to decrease as females grew larger in response to the lifting of selection pressures for small female size. Reconstructions of body mass and mass dimorphism in *A. afarensis* and later hominids suggest that this is exactly what happened (McHenry, 1992; Kappelman, 1996).

Site Differences versus Sex Differences

If size differences between A.L. 288-1 and the larger size morph at A.L. 333 are due to the combined effects of sex-difference and site-difference (akin to comparing males of one chimpanzee subspecies to females of another subspecies), direct comparison of sex-specific size contrasts in order to identify scaling relationships is not appropriate. However, it remains the case that A.L. 288-1 is much smaller than all of her extant and

extinct relatives. This small size requires an explanation. The scenario outlined above regarding selection intensities on female size resulting from environmental resource pressures is consistent with observations that female size is small in *A. afarensis* and becomes larger in later hominids that are presumably less dependent on contiguous forest habitats than their ancestors.

SUMMARY

This study finds a high degree of dimorphism in the Hadar hominids using a geometric mean of linear variables from the proximal articulations of the femur, tibia, humerus, and radius. When compared to dimorphism levels for extant African apes and humans, the degree of dimorphism observed in *Australopithecus afarensis* can only be accommodated within the range of dimorphism observed in gorillas, confirming previous findings of high body size dimorphism in *A. afarensis*. This study goes on to consider how that level of dimorphism evolved in the Hadar hominids as a product of differential change in female and male size.

There is significant overlap in body size among chimpanzees of both sexes (including *Pan paniscus*, *P. troglodytes troglodytes*, and *P. t. schweinfurthii*) and the larger Hadar hominids of the Denan Dora Member. Estimated size for *Samburupithecus kiptalami*, a late Miocene fossil African ape, falls within this same range of size. The convergence of body size among these taxa suggests that body size for the last common ancestor (LCA) of *Pan* and *Australopithecus* also fell within this range, at least for males. The presence of marked dimorphism in gorillas and the Hadar hominids raises the possibility that females of that LCA were considerably smaller, particularly since A.L. 288-1 is smaller than all extant apes and humans measured in this study. If the common ancestor of chimpanzees and hominids were only mildly dimorphic, female size would have remained fairly stable in the chimpanzee lineage and would have decreased

significantly in the hominid lineage. If the ancestor was highly dimorphic, female size would have remained fairly stable in the hominid lineage and would have increased significantly in the chimpanzee lineage.

Consideration of the biogeography of extant African apes and paleoreconstructions of Miocene African environments suggests the following: populations of proto-chimps living in deep-forest habitats were probably subject to relatively stable natural selection pressures in comparison with those affecting proto-hominids isolated in forest fragments separated from the continent-spanning forests of central Africa. Under these conditions, little to no change in proto-chimp female size and marked decrease in proto-hominid female size in response to resource limitation pressures is more likely than stable female size in proto-hominids and a marked increase in proto-chimps. Larger male size in the hominid lineage would have been maintained by at least mild competition among males for access to mates, as indicated by mild canine size dimorphism in the Hadar hominids. Female hominid body size later became less constrained with the evolution of more efficient bipedalism and reduced dependence on single forest fragments for all resources, resulting in larger females and reduced dimorphism in later hominids. Separate consideration of changes in male and female size is shown here to offer explanations regarding the evolution of size and dimorphism that are unavailable to analyses that consider dimorphism a property of populations rather than a function of both female and male size.

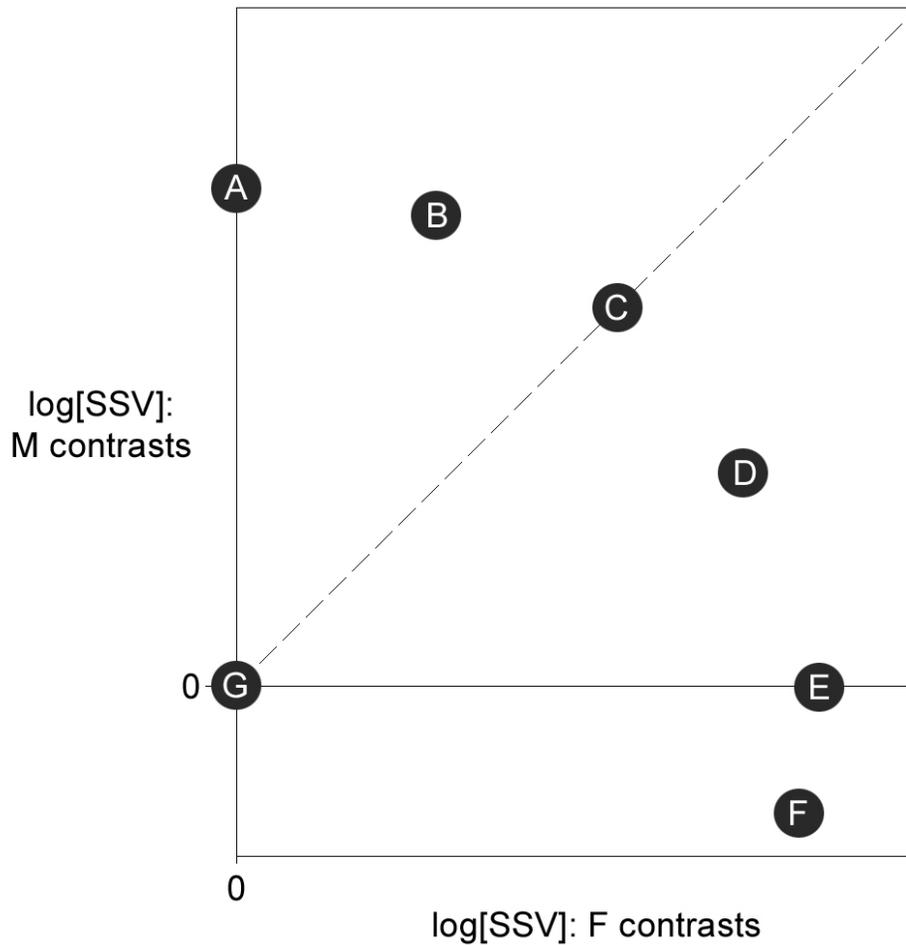


Figure 6.1. Possible relationships between male and female size contrasts between two taxa.

Zero axes indicate no difference in female size (Y-axis, point **A**) or male size (X-axis, point **E**). If there is no difference in size in either sex, contrasts will plot at the origin (point **G**). The dashed diagonal line marks a slope of 1 and indicates equal proportional difference in both sexes. Contrasts that plot on this line indicate that although size differs between two taxa, dimorphism is equal (point **C**). Any combination of non-zero contrasts that plot above this line (e.g., point **B**) indicate that male size differs proportionally more than female size, but changes are in the same direction (*i.e.*, one taxon is larger than the other for both sexes, but differences are greater for males). Contrasts that plot below the line of identity but above the X-axis indicate that female size differs proportionally more than male size, but changes are in the same direction (point **D**). Finally, contrasts that plot below the X-axis indicate that male and female size differ in opposite directions; *i.e.*, one taxon is larger in male size but smaller in female size than the other (point **F**).

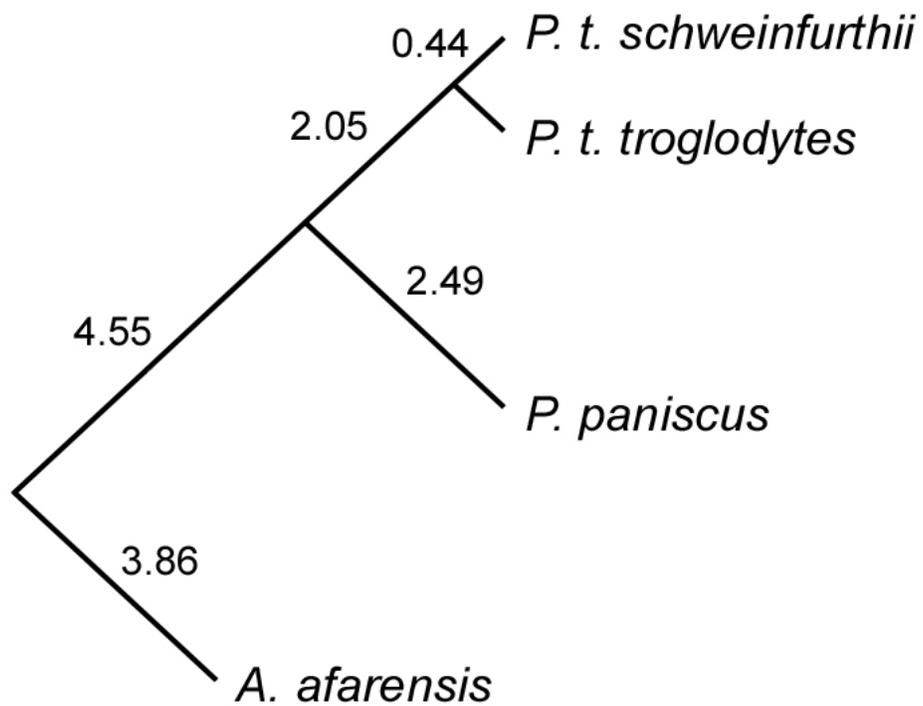


Figure 6.2. Phylogenetic relationships within *Pan* and *Australopithecus*.

Numbers indicate distance in millions of years along branches. Notice that the branch leading to *A. afarensis* terminates 3.18 million years before the present (Walter, 1994).

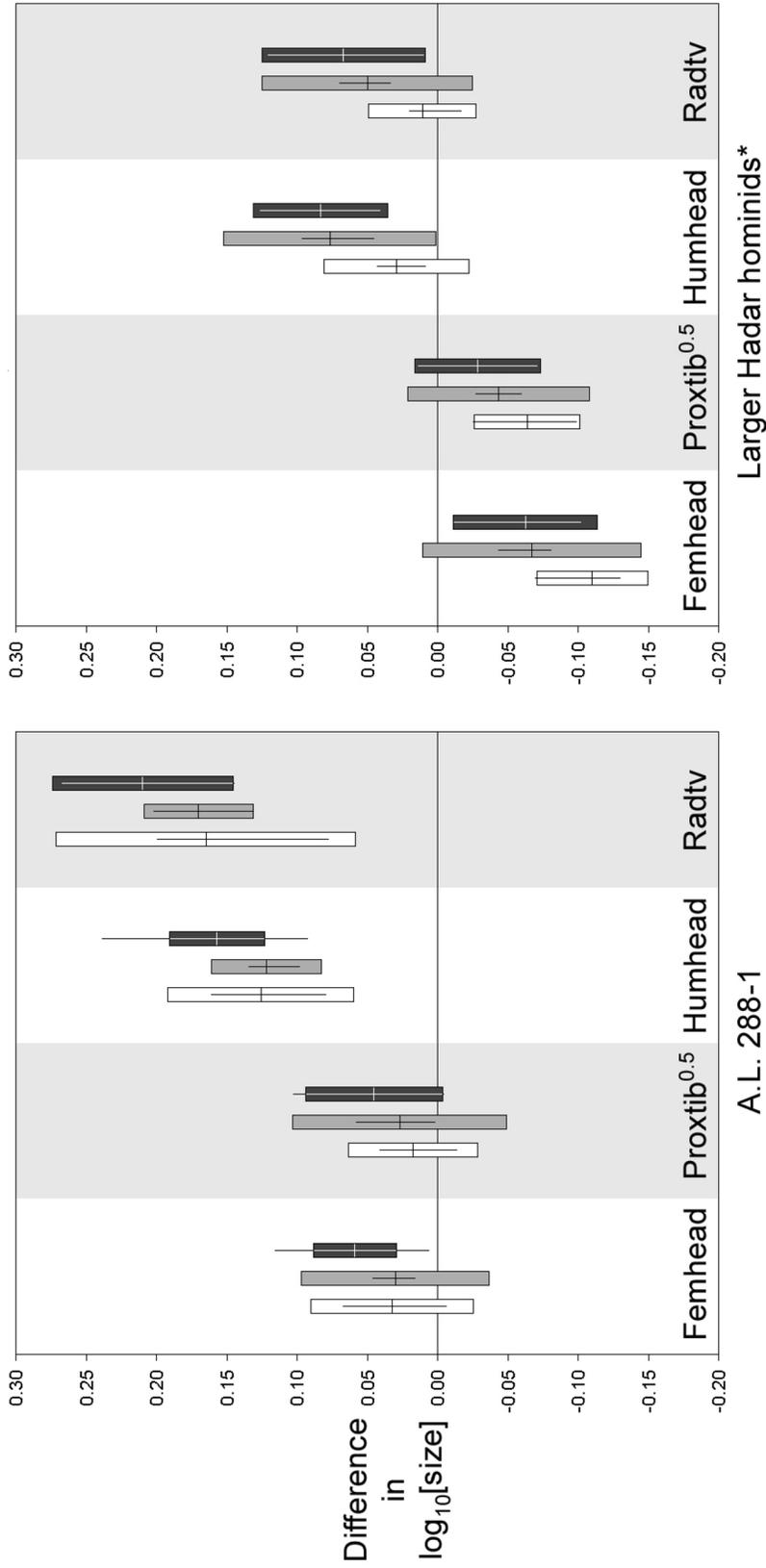


Figure 6.3. Proportional difference in linear dimensions between *Pan* and Hadar hominids.

Differences are calculated between female chimpanzees and A.L. 288-1 for the figure on the left and between male chimpanzees and larger Hadar hominids on the right. Zero line indicates no difference in linear dimension. *Pan* species are as follows: *P. paniscus*, white bars; *P. troglodytes schweinfurthii*, light gray bars; *P. t. troglodytes*, dark gray bars. Horizontal lines are mean difference, vertical lines are complete range of observed difference between all skeletal specimens and the fossil measurements, boxes indicate 95% confidence interval for differences between a single skeletal specimen and fossil measurements. * Measurements are from the following specimens: Femhead, A.L. 333x-26 and A.L. 333x-42; Proxtib, arithmetic mean of A.L. 333x-26 and A.L. 333-42; Humhead, A.L. 333-107; Radtv, A.L. 333x-14. All fossil measurements taken from McHenry (1992).

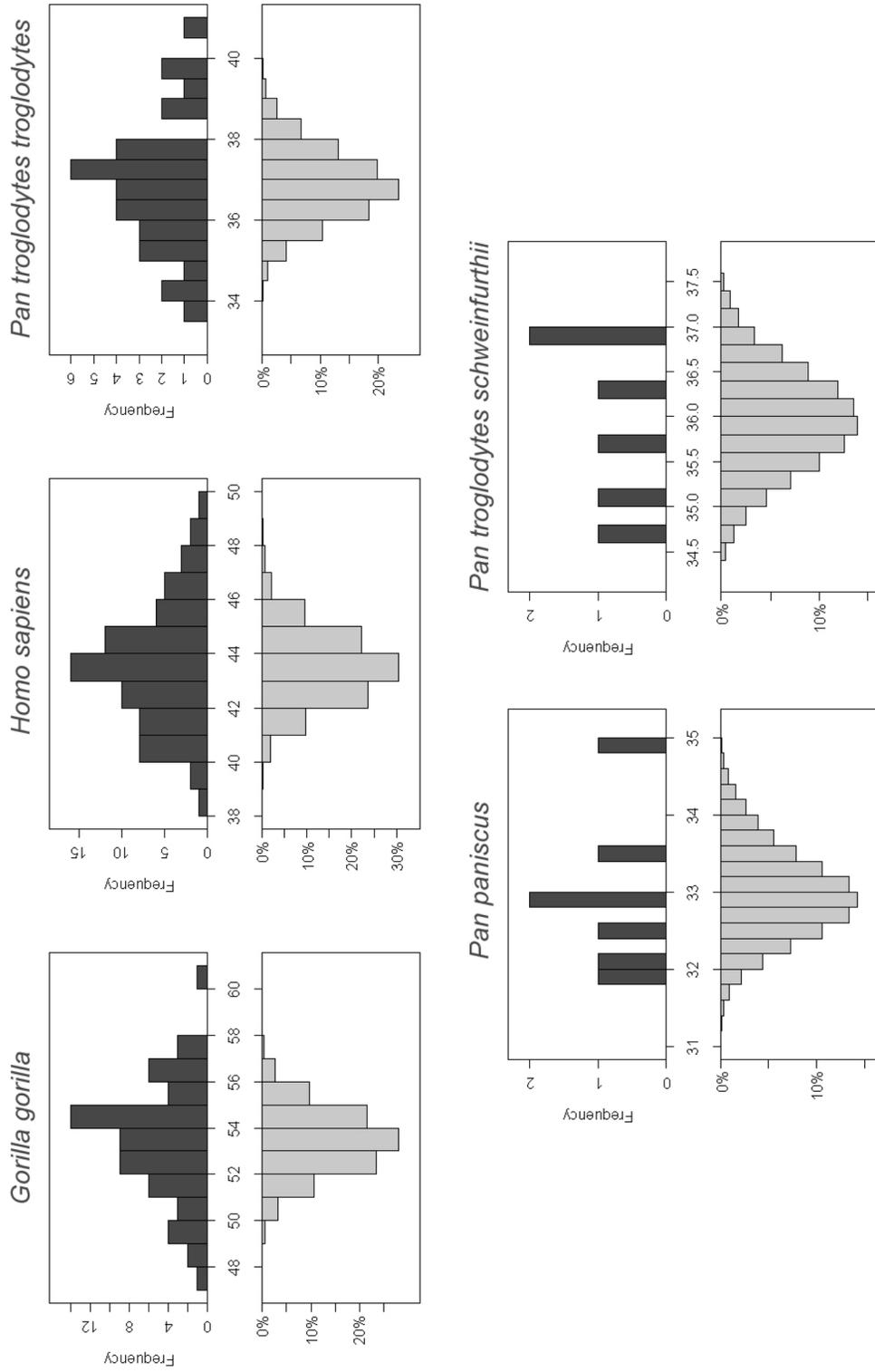


Figure 6.4. Comparison of individual and composite SSV distributions for male African apes and humans. Dark gray bars are observed values of male SSV, light gray bars are bootstrapped (top three taxa) or exact randomization SSV values (bottom two taxa) for composite males drawing measurements from up to five separate individuals. See text for details.

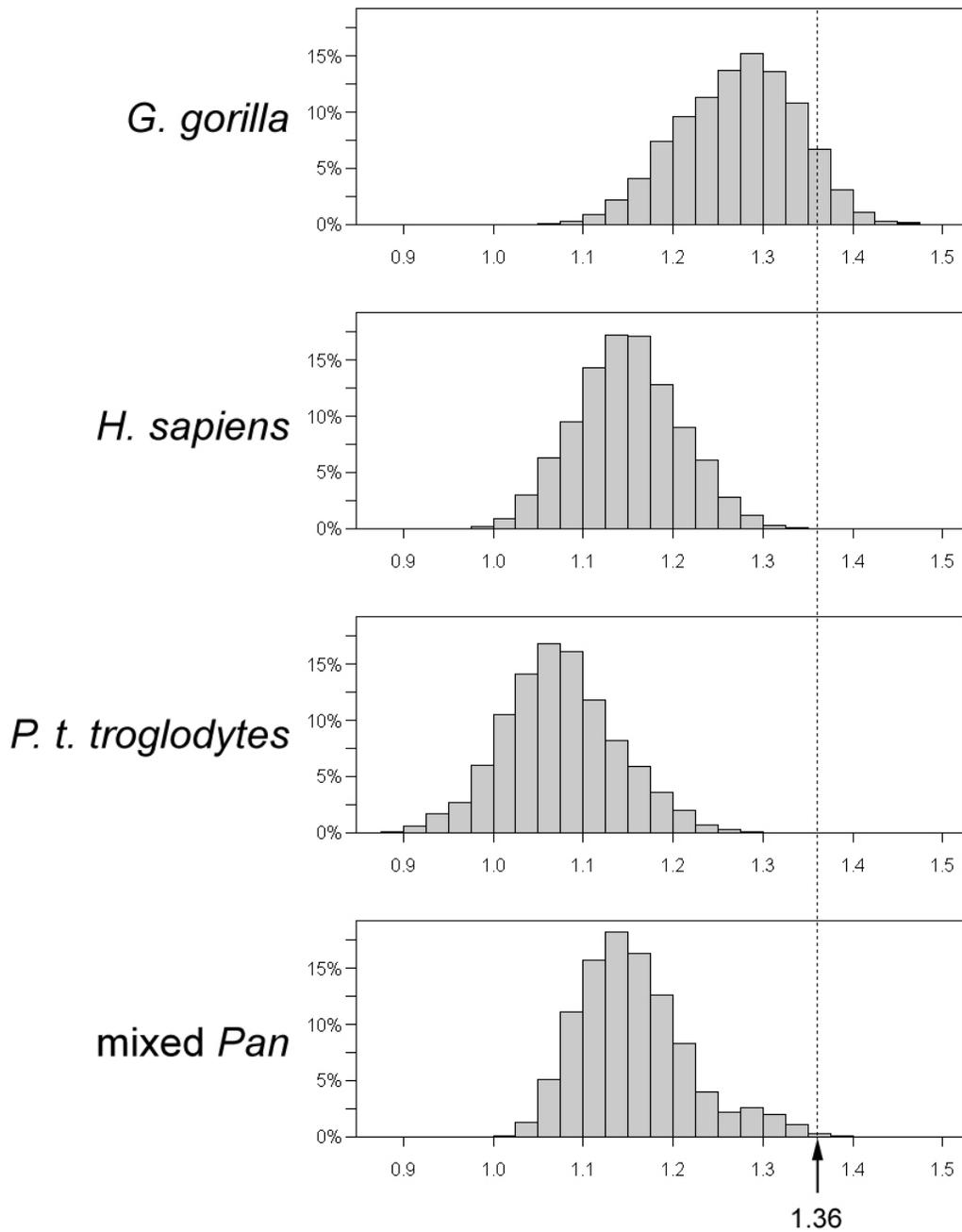


Figure 6.5. Relative frequency histograms of SSV ratios for African apes and humans.

Ratios are bootstrapped 10,000 times for each taxon. Male SSV is calculated as a composite of five males for extant taxa; female SSV is calculated for an individual female. The dotted vertical line indicates the SSV ratio for the Hadar hominids. Mixed *Pan* refers to bootstrapped ratios of SSV for one composite *P. t. troglodytes* male divided by SSV for one *P. paniscus* or *P. t. schweinfurthii* female.

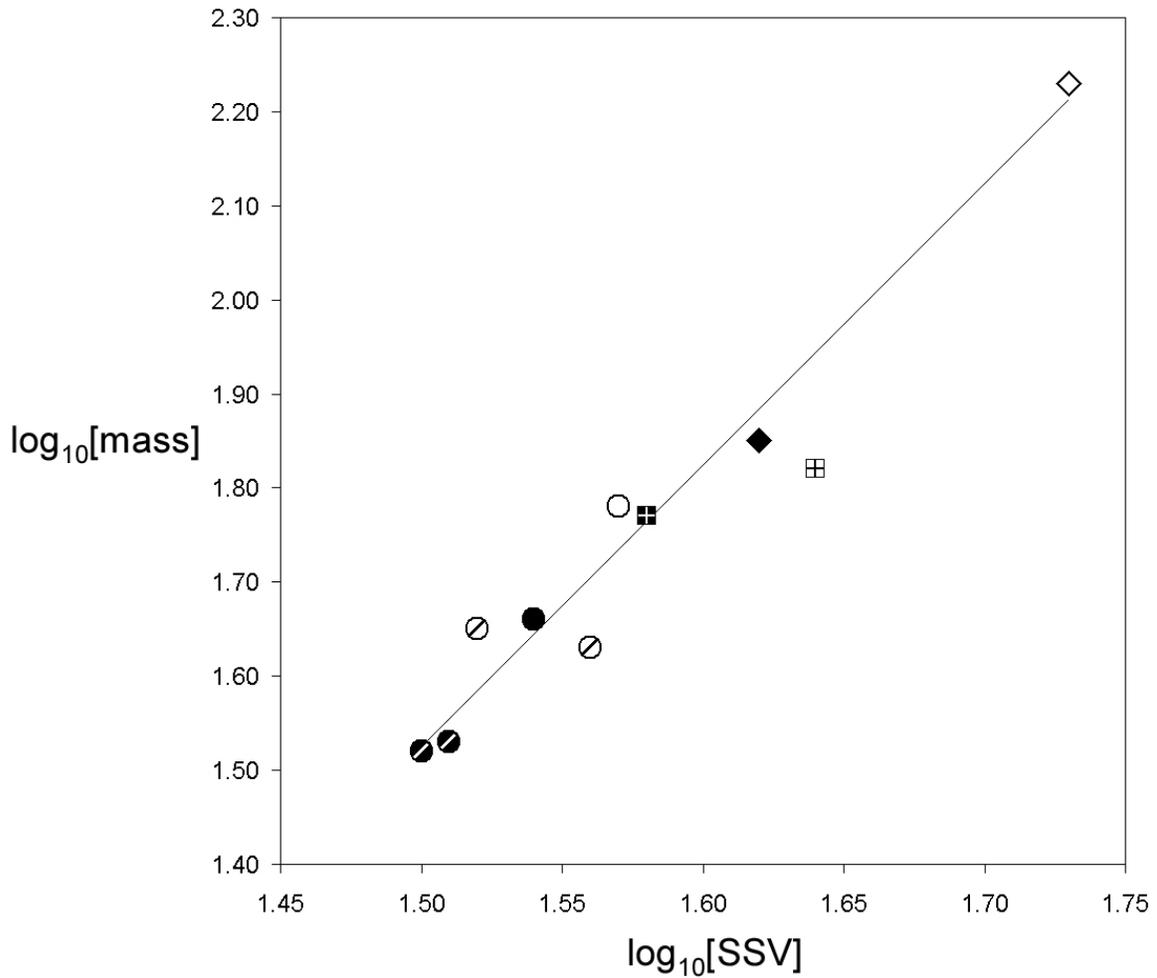


Figure 6.6. Regression of body mass against SSV in African apes.

Regression line does not include humans. Symbols are as follows: ●, *Pan*; ◆, *Gorilla*; ■, *Homo*. Closed symbols are females; open symbols are males. Diagonal slashes indicate small sex-specific sample sizes ($N < 10$). 95% confidence intervals for the slope include isometry (slope = 2.99, isometry = 3.00). Note that although female humans fall almost directly on the ape regression line, male humans have the highest displacement from the line along the Y-axis.

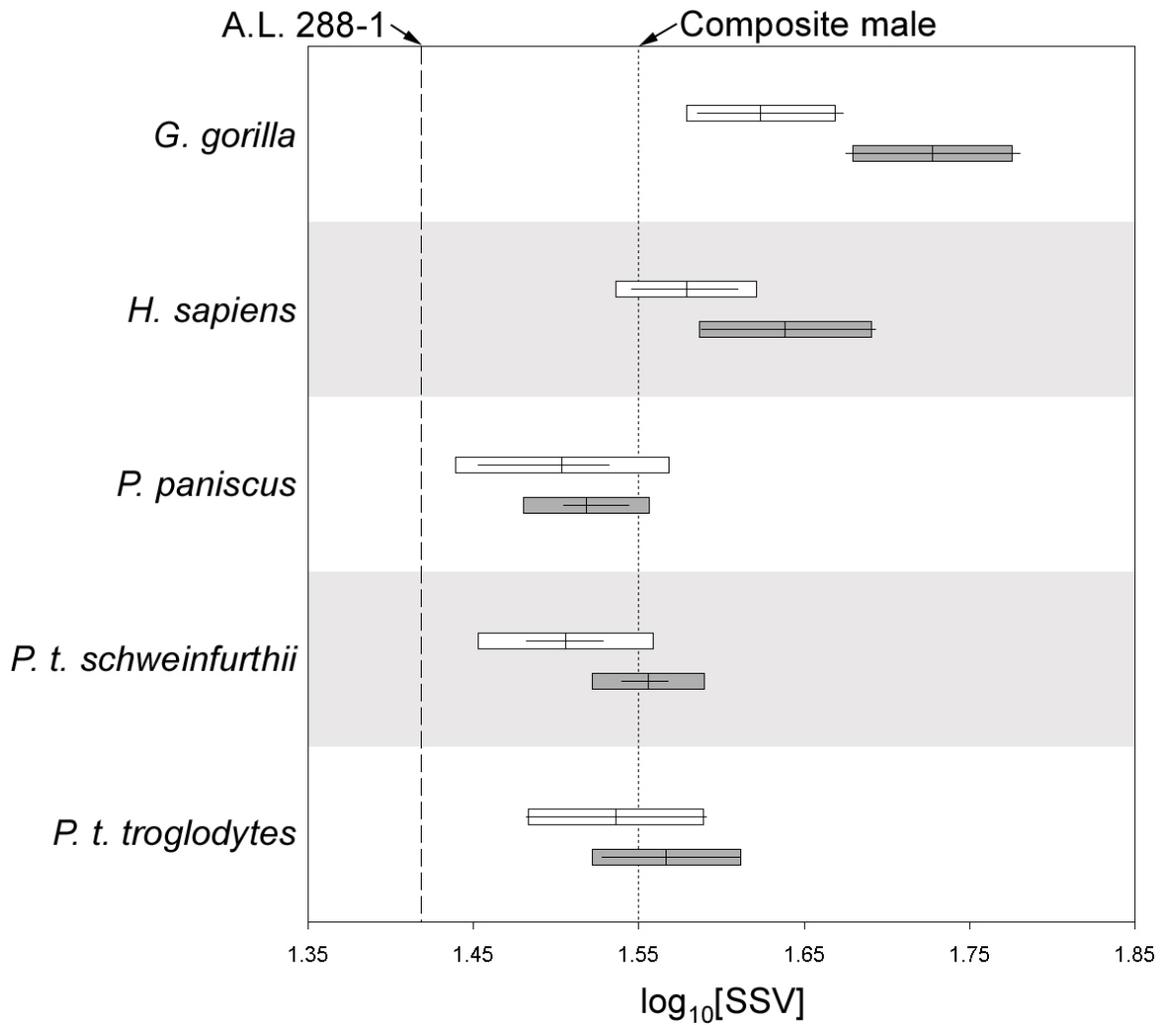


Figure 6.7. Sex-specific SSV in African apes, humans, and Hadar hominids.

White bars represent females, gray bars represent males. Short vertical lines are mean size, horizontal lines are complete range of observed size in this study, boxes indicate 95% confidence interval for size in the full sex-specific population. Long vertical dashed line shows size in A.L.288-1, dotted line shows size for a “composite male” using all measurements from the larger Hadar hominids of the Denan Dora Member.

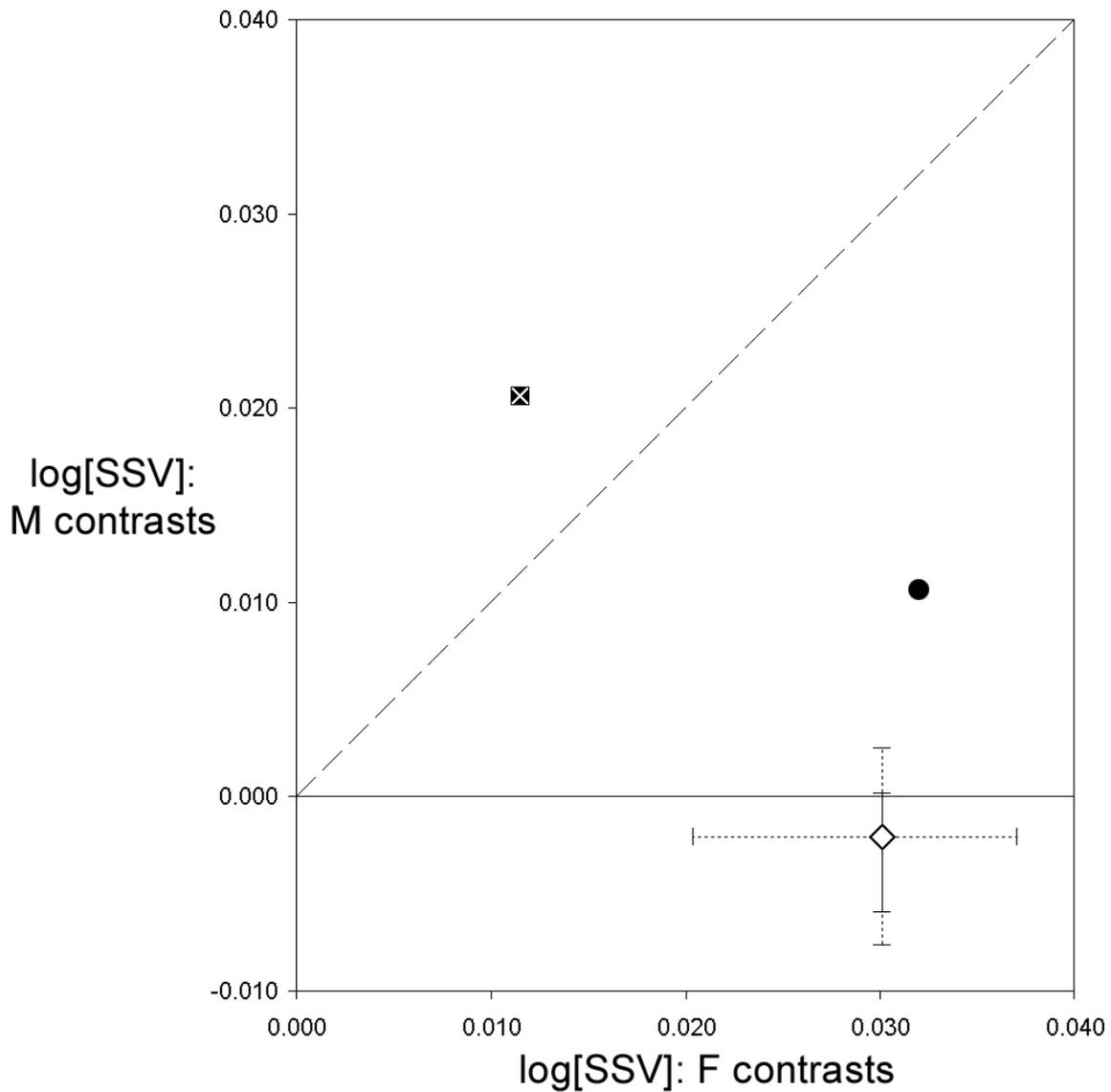


Figure 6.8. Phylogenetic independent contrasts of male and female $\log_{10}[\text{SSV}]$ for *Pan* and the Hadar hominids.

Diagonal dashed line indicates equality in male and female size contrasts. Symbols: ●, independent contrast between *Pan troglodytes troglodytes* and *P. t. schweinfurthii*; ■, independent contrast between *P. troglodytes* and *P. paniscus*; ◆, independent contrast between *Pan* and the Hadar hominids. Dotted error bars indicate 95% confidence intervals for contrasts based on SSV calculated for one individual from each taxon. Solid error bar indicates 95% confidence interval for contrasts based on a composite SSV calculated from five males for each taxon. Confidence intervals based on exact randomization and bootstrap analyses (see text for details).

| Group | Sex | N | Femhead | | | Proxib ^{0.5} | | | Humhead | | | Radtv | | | | | | |
|-----------------------------|-----|----|---------|-------|-------|-----------------------|-------|-------|---------|------|-------|-------|-------|------|-------|-------|-------|------|
| | | | Mean | Min | Max | SD | Mean | Min | Max | SD | Mean | Min | Max | SD | | | | |
| <i>G. gorilla</i> | F | 60 | 40.83 | 36.66 | 45.54 | 2.03 | 55.94 | 51.08 | 65.47 | 2.82 | 50.01 | 45.57 | 54.77 | 2.63 | 27.49 | 24.89 | 30.60 | 1.49 |
| | M | 62 | 50.81 | 45.89 | 57.40 | 2.63 | 70.47 | 60.08 | 80.65 | 3.73 | 64.59 | 56.04 | 72.95 | 3.43 | 35.34 | 30.02 | 39.67 | 2.15 |
| <i>H. sapiens</i> | F | 30 | 42.25 | 37.18 | 47.66 | 2.31 | 56.14 | 51.97 | 60.32 | 2.58 | 41.14 | 37.26 | 46.26 | 2.35 | 20.90 | 19.24 | 23.73 | 1.13 |
| | M | 70 | 48.72 | 43.38 | 54.42 | 2.60 | 63.50 | 55.64 | 70.65 | 3.36 | 47.81 | 41.20 | 56.08 | 2.74 | 24.46 | 20.65 | 29.56 | 1.68 |
| <i>P. t. troglodytes</i> | F | 75 | 32.82 | 28.95 | 37.37 | 2.07 | 44.79 | 39.87 | 51.09 | 2.35 | 39.25 | 33.75 | 47.38 | 2.43 | 24.36 | 20.9 | 27.67 | 1.48 |
| | M | 34 | 34.85 | 31.74 | 39.2 | 1.76 | 48.23 | 43.75 | 53.15 | 2.13 | 42.56 | 38.69 | 46.97 | 2.02 | 25.93 | 22.68 | 29.3 | 1.49 |
| <i>P. t. schweinfurthii</i> | F | 5 | 30.66 | 29.62 | 31.74 | 0.91 | 42.94 | 40.45 | 46.09 | 2.12 | 36.15 | 34.34 | 37.2 | 1.22 | 22.22 | 20.37 | 23.9 | 1.44 |
| | M | 6 | 34.45 | 33.35 | 36.35 | 1.16 | 46.53 | 44.92 | 48.29 | 1.47 | 41.91 | 38.99 | 43.84 | 1.78 | 24.92 | 23.94 | 26.03 | 0.8 |
| <i>P. paniscus</i> | F | 9 | 30.83 | 28.22 | 33.28 | 1.57 | 42 | 39.15 | 44.38 | 1.68 | 36.5 | 32.78 | 39.59 | 2.09 | 22.01 | 17.9 | 23.67 | 1.94 |
| | M | 7 | 31.22 | 29.8 | 34.3 | 1.56 | 44.47 | 40.98 | 48.6 | 2.48 | 37.54 | 35.77 | 38.82 | 1.07 | 22.76 | 21.43 | 23.28 | 0.63 |
| A.L. 288-1 | | | 28.6 | - | - | - | 40.31 | - | - | - | 27.3 | - | - | - | 15.0 | - | - | - |
| Larger Hadar hominids* | | | 40.2 | - | - | - | 51.42 | 50.60 | 52.25 | - | 35.1 | - | - | - | 22.2 | - | - | - |

Table 6.1. Long bone proximal articulation linear measurements for African apes, humans, and Hadar hominids.

All measurements are in millimeters. * Measurements are from the following specimens: Femhead, A.L. 333-3; Proxtib, A.L. 333x-26 and A.L.333-42; Humhead, A.L. 333-107; Radtv, A.L. 333x-14. All fossil measurements taken from McHenry (1992).

| Group | Sex | N | Mass (kg) | SSV | | | | Composite Male SSV | | | |
|-----------------------------|-----|----|--------------|-------|-------|-------|------|--------------------|-------|-------|----------|
| | | | | Mean | Min | Max | SD | Median | Min | Max | p |
| <i>G. gorilla</i> | F | 60 | 71.5 | 42.08 | 38.52 | 47.16 | 1.91 | 53.44 | 47.90 | 58.39 | < 0.0001 |
| | M | 62 | 170.4 | 53.45 | 47.35 | 60.34 | 2.57 | | | | |
| <i>H. sapiens</i> | F | 30 | 58.7 | 37.77 | 34.81 | 40.84 | 1.64 | 43.49 | 39.56 | 48.95 | < 0.0001 |
| | M | 70 | 65.8 | 43.60 | 38.69 | 49.30 | 2.21 | | | | |
| <i>P. t. troglodytes</i> | F | 75 | 45.8 | 34.42 | 30.33 | 38.97 | 1.84 | 36.84 | 34.06 | 40.13 | < 0.0001 |
| | M | 34 | 59.7 | 36.89 | 33.71 | 40.83 | 1.63 | | | | |
| <i>P. t. schweinfurthii</i> | F | 5 | 33.7 | 32.06 | 30.33 | 33.77 | 1.23 | 35.96 | 34.39 | 37.62 | 0.0399 |
| | M | 6 | 42.7 | 35.96 | 34.64 | 36.96 | 0.94 | | | | |
| <i>P. paniscus</i> | F | 9 | 33.2 | 31.92 | 28.38 | 34.03 | 1.72 | 32.95 | 31.11 | 35.03 | 0.0286 |
| | M | 7 | 45 | 32.99 | 31.96 | 34.98 | 1.03 | | | | |
| A.L. 288-1 | | | | 26.2 | | | | | | | |
| Hadar composite male | | | | | | | | 35.6 | | | |

Table 6.2. Sex-specific SSV and “composite male” SSV ranges for African apes, humans, and Hadar hominids.

Mean, minimum, maximum, and standard deviations of SSV are calculated based on individual extant specimens. Composite male SSV median, ranges, and p-values are generated using resampling procedures described in the text. Non-human body mass data taken from Smith and Jungers (1997). Human body mass data from records of the Cleveland Museum of Natural History.

| Group | Observed | Min | Max | 95% CI | p |
|-----------------------------|----------|-------|-------|---------------|----------|
| <i>G. gorilla</i> | 1.270 | 1.052 | 1.516 | 1.143 – 1.389 | 0.08 |
| <i>H. sapiens</i> | 1.149 | 0.969 | 1.361 | 1.042 – 1.262 | < 0.0001 |
| <i>P. t. troglodytes</i> | 1.072 | 0.882 | 1.289 | 0.954 – 1.202 | < 0.0001 |
| <i>P. t. schweinfurthii</i> | 1.122 | 1.069 | 1.128 | 1.082 – 1.127 | 0* |
| <i>P. paniscus</i> | 1.033 | 0.957 | 1.026 | 0.980 – 1.025 | 0* |
| mixed <i>Pan</i> | - | 1.013 | 1.395 | 1.058 – 1.306 | 0.002 |
| Hadar hominids | 1.36 | | | | |

Table 6.3. SSV ratios for African apes, humans, and Hadar hominids.

Observed value is mean male SSV divided by mean female SSV. Minimum ratios, maximum ratios, and 95% confidence intervals (CI) are calculated using a bootstrap procedure in the case of taxa with large sample sizes (*G. gorilla*, *H. sapiens*, *P. t. troglodytes*, and mixed *Pan*), and using an exact randomization procedure in the case of taxa with small sample sizes (*P. paniscus* and *P. t. schweinfurthii*). Mixed *Pan* refers to bootstrapped ratios of SSV for one composite *P. t. troglodytes* male divided by SSV for one *P. paniscus* or *P. t. schweinfurthii* female. P-values represent the probability of generating a ratio as high or higher than that observed in the Hadar hominids. * All possible ratios of one composite male and one female produce a ratio lower than that observed for the Hadar hominids.

| Females | | | | |
|--|----------|---------|--------|------------------|
| Contrast | Observed | Min | Max | 95% CI |
| <i>P.t.troglodytes</i> - <i>P.t.schweinfurthii</i> | 0.0320 | -0.0497 | 0.1160 | -0.0238 – 0.0891 |
| <i>P. troglodytes</i> - <i>P. paniscus</i> | 0.0115 | -0.0229 | 0.0489 | -0.0122 – 0.0359 |
| <i>Pan</i> - A.L. 288-1 | 0.0301 | 0.0156 | 0.0409 | 0.0204 – 0.0370 |

| Males | | | | |
|--|----------|---------|--------|------------------|
| Contrast | Observed | Min | Max | 95% CI |
| <i>P.t.troglodytes</i> - <i>P.t.schweinfurthii</i> | 0.0107 | -0.0426 | 0.0760 | -0.0327 – 0.0582 |
| <i>P. troglodytes</i> - <i>P. paniscus</i> | 0.0206 | -0.0047 | 0.0388 | 0.0033 – 0.0331 |
| <i>Pan</i> - composite Hadar male | -0.0021 | -0.0098 | 0.0057 | -0.0076 – 0.0026 |

| Composite Males | | | | |
|--|---------|---------|--------|------------------|
| Contrast | Median | Min | Max | 95% CI |
| <i>P.t.troglodytes</i> - <i>P.t.schweinfurthii</i> | 0.0115 | -0.0338 | 0.0586 | -0.0131 – 0.0369 |
| <i>P. troglodytes</i> - <i>P. paniscus</i> | 0.0197 | 0.0031 | 0.0345 | 0.0107 – 0.0282 |
| <i>Pan</i> - composite Hadar male | -0.0030 | -0.0084 | 0.0034 | -0.0059 – 0.0002 |

Table 6.4. Phylogenetic independent contrasts of $\log_{10}[\text{SSV}]$ for *Pan* and the Hadar hominids.

Observed contrasts are based on sex-specific mean SSV for extant taxa. Median, minimum, maximum, and 95% confidence intervals are based on resampling procedures.

Chapter 7: Conclusion

MECHANISMS UNDERLYING RENSCH'S RULE

Although Rensch's rule (positive scaling of body size with sexual size dimorphism) is present in many animal radiations, some radiations exhibit negative scaling or no relationship between size and dimorphism whatsoever. Lande's (1980) quantitative genetics model predicts (1) positive scaling (Rensch's rule) when selection acts more intensely on male body size than female body size, (2) no scaling when selection acts equally on both sexes, and (3) negative scaling when selection acts more intensely on female body size than male body size.

Described here is a combined response model which describes how sex-specific means (Lande, 1980) and relative variabilities (generalization of Bulmer, 1971) of continuous traits respond to sex-specific selection pressures. Observations among closely related primate populations provide examples consistent with predictions of the combined response model in which selection primarily acts to increase male size, primarily increase female size, and primarily decrease female size. Sexual selection theory predicts selection for larger size acting primarily on one sex will occur when members of that sex compete for access to mates, or when members of the second sex choose to mate with larger individuals of the first. Primate examples are consistent with these expectations. Natural selection can apply equal pressure to females and males in either direction (size increase or size decrease), but when natural selection pressures differ between sexes it is most likely due to resource pressures affecting females more intensely because of the energetic requirements of reproduction and lactation. In such cases, smaller females should be able to breed more often than larger females, generating selection for small size primarily on females. This pattern of selection also occurs in primates.

Thus positive scaling of sexual size dimorphism (SSD) and body size should occur when sexual selection acts to increase male size, usually within the context of male competition and female mate choice in polygynous groups within haplorhine primates. Negative scaling is expected when sexual selection acts to increase female size, usually within the context of female competition and male mate choice in polyandrous groups within platyrrhines; negative scaling is also expected when populations are subject to resource limitation, resulting in selection for smaller female size. No scaling pattern is expected when selection pressures on body size are equal between the sexes.

Although previous studies have identified the presence of Rensch's rule in living haplorhines, phylogenetic analyses performed in this study show that the modern scaling relationship is primarily the result of evolutionary relationships between higher-level haplorhine taxa (*i.e.*, above the generic level), and that more recent evolutionary patterns preserve a diversity of positive and negative scaling relationships. In the platyrrhines in particular, most recent (intra-generic) relationships are characterized by negative scaling of SSD and size, particularly within the facultatively-polyandrous Callitrichidae. Thus the presence of Rensch's rule in modern taxa probably results from a bias in preservation of positive scaling relationships at higher taxonomic levels. I argue that in the absence of polyandry (as is typical for most haplorhine primates), the most likely source of selection pressure acting primarily on females is resource limitation, and that resource limited populations are more likely to go extinct than sexually selected populations. Since higher level phylogenetic relationships only preserve information regarding the ancestry of living primates, not information about populations that have gone extinct without leaving living descendants, lineages preserved in phylogenetic relationships are likely to contain more sexually-selected populations than resource limited ones. In this context, Rensch's observation is not a rule, but merely the most likely scaling pattern in radiations

characterized by sexual selection on males. When sexual selection does not act on body size, the most likely patterns to be preserved are equal selection pressures acting on both sexes, resulting in no scaling of size and SSD (*e.g.*, in strepsirhine primates).

FORCES GENERATING SEX-SPECIFIC SELECTION PRESSURES IN PRIMATES

The causes of differences in sex-specific selection pressures on primate body size are important for a number of reasons. In terms of comparative studies of SSD, if large size causes changes in dimorphism then it may be appropriate to correct for the effect of size before conducting comparative analyses. However, this study demonstrates that there is no scaling between SSD and size once phylogeny and sexual selection has been taken into account. Thus not only is it unnecessary to “correct” for size in analyses of SSD, it is inappropriate because inevitably some of the informative variance in SSD will be corrected away.

In haplorhine primates, degree of dimorphism corresponds with mating system categories in a manner consistent with expectations of sexual selection theory, particularly when phylogenetic analyses are used to compare taxa. Mating systems do not correspond well to SSD in strepsirhine primates, indicating that sexual selection probably operates on traits other than body size in these primates. Although mating system and other proxies for intra-sexual competition account for the greatest proportion of variance in comparative studies of SSD in haplorhines, much variance remains unaccounted for. At least a portion of this variance could probably be accounted for by mate choice and ecological variables.

EVOLUTION OF SIZE DIMORPHISM IN SKELETAL BODY SIZE

Geometric means of skeletal measurements can be generated that (1) equally represent the major long bones of the primate appendicular skeleton, and (2) scale isometrically with body mass. Such variables, described here as Global Skeletal Size

Variables (GSV), may be preferred to body mass for some morphological studies because they should be more stable over time than body mass, and because individual measures of size are available for any relatively complete postcranial skeleton. Ratios of SSD will be identical for two variables that scale isometrically with each other, so GSV are useful for the study of dimorphism in animals for which no body mass data are available.

One such variable is used in a study of the evolution of sex-specific body size in *Pan* and *Australopithecus afarensis*. A geometric mean is calculated using measurements that are available for extant African apes, humans, and A.L. 288-1: one linear dimension each from the proximal femur, tibia, humerus, and radius. Resampling procedures (exact randomization and bootstrapping) demonstrate that geometric means of linear dimensions from different individuals will fall within the observed range of single-individual geometric means. This observation is used to justify the comparison of a GSV for a “composite male” Hadar hominid from A.L. 333 to “composite male” chimpanzees. Resampling procedures are then used to identify confidence limits on phylogenetically independent contrasts of sex-specific body size in *Pan troglodytes troglodytes*, *P. t. schweinfurthii*, *P. paniscus*, and *A. afarensis*. Male body size is reconstructed as having undergone similar amounts of change in the lineages leading to *Pan* and *Australopithecus* from their last common ancestor, ranging from a slight increase to a moderate decrease. In contrast, female body size probably experienced a similar amount of change as male body size in the lineage leading to *Pan*, but experienced a dramatic decrease in the lineage leading to *Australopithecus*. Based on reconstructions of environmental change and forest fragmentation in the late Miocene, a scenario is proposed here in which female body size in proto-hominids is subject to negative selection pressure due to resource limitation; male body size is maintained at a larger size by male competition for mates. With the adaptation of more efficient bipedalism and reduced reliance on isolated forest

fragment, selection pressures for small female size were lifted and dimorphism decreased as females grew larger.

SUMMARY

Quantitative genetics models can be powerful tools that generate explicit predictions regarding the evolution of sex-specific size and SSD. Identifying likely sources of different patterns for direction of selection and relative selection intensity applied to each sex allows us to interpret scaling patterns of SSD and size when they are observed in animal radiations. I hope that the work presented here has demonstrated that conceptual models based on quantitative genetic underpinnings can further our understanding of how sexual selection and natural selection operate to produce changes in sex-specific body size in extant and extinct taxa.

Appendix A: Derivation of the Generalized Bulmer Effect

Based on an analysis of Lande's quantitative genetic model for sexually dimorphic polygenic traits (Lande, 1980), Leutenegger and Cheverud (1982; 1985) present the expressions

$$\overline{\mathbf{R}}_M = \left(\frac{1}{2} \right) (h_M^2 s_M i_M + h_M h_F r_a s_M i_F) \quad [\text{A.1}]$$

and

$$\overline{\mathbf{R}}_F = \left(\frac{1}{2} \right) (h_F^2 s_F i_F + h_M h_F r_a s_F i_M), \quad [\text{A.2}]$$

where $\overline{\mathbf{R}}$ is the mean response of the trait to selection, h^2 is the heritability of the trait, s is the phenotypic standard deviation, i is the selection intensity, and r_a is genetic correlation between males and females for that trait. Subscripts indicate the sex to which the parameter refers (M, males; F, females). Heritability, selection intensity, and genetic correlation are all unitless values; thus the response to selection is measured in units of the standard deviation (*i.e.*, the units used to measure the phenotypic trait).

The response (\mathbf{R}) is the change in value of the continuous trait from one generation to the next; for example:

$$\mathbf{M}^* = \mathbf{M} + \mathbf{R}_M, \quad [\text{A.3}]$$

where \mathbf{M} is the variable for the continuous trait in the parental generation of males and \mathbf{M}^* is the variable for the trait in the offspring generation of males.

What follows is a derivation of the equations describing the sex-specific changes in variance between parental and offspring generations due to selection. Bulmer (1971) derived equations for the case when males and females do not differ in the expression of a continuous trait; here I derive a generalization that can be applied to all conditions ranging from absence of sex-linkage in the trait (*i.e.*, Bulmer's model, where $r_a = 1$) to

complete sex-linkage of a trait ($r_a = 0$). The male equation will be derived here; the female equation is obtained simply by replacing \mathbf{M} with \mathbf{F} every time it appears, and vice-versa.

The variable \mathbf{R}_M (distinct from the mean of this variable, $\overline{\mathbf{R}_M}$) is the sum of two independent variables: the change in males due to selection on males in the parental generation (\mathbf{R}_{Mm}), and the change in males due to selection on females in the parental generation (\mathbf{R}_{Mf}). Equation A.3 can be re-expressed as follows:

$$\mathbf{M}^* = \mathbf{M} + \mathbf{R}_{Mm} + \mathbf{R}_{Mf}, \quad [\text{A.4}]$$

where

$$\overline{\mathbf{R}_{Mm}} = \left(\frac{1}{2}\right)(h_M^2 s_M i_M) \quad [\text{A.5}]$$

and

$$\overline{\mathbf{R}_{Mf}} = \left(\frac{1}{2}\right)(h_M h_F r_a s_M i_F). \quad [\text{A.6}]$$

Next, I follow Bulmer in modeling selection as the truncation of a distribution at a particular value (Fig. A.1), which allows the post-selection distribution to be described as

$$\mathbf{M}' = \mathbf{M} + d\mathbf{M}, \quad [\text{A.7}]$$

where \mathbf{M}' is the variable for the trait in post-selection males. The other variable in equation A.7, $d\mathbf{M}$, describes the difference between pre- and post-selection parental distributions. It is independent of \mathbf{M} and has a mean of $\overline{d\mathbf{M}}$ and variance ds_M^2 , where

$$\overline{d\mathbf{M}} = \overline{\mathbf{M}'} - \overline{\mathbf{M}} \quad [\text{A.8}]$$

and

$$ds_M^2 = s'^2_M - s_M^2. \quad [\text{A.9}]$$

Selection intensity (i) is defined as the difference of the pre- and post-selection means, divided by the pre-selection standard deviation, so

$$i_M = \frac{\overline{dM}}{s_M} \quad [\text{A.10}]$$

and

$$i_F = \frac{\overline{dF}}{s_F}. \quad [\text{A.11}]$$

Replacing i_M and i_F in equations A.5 and A.6 yields

$$\overline{R_{Mm}} = \left(\frac{1}{2}\right) \left(h_M^2\right) \left(\overline{dM}\right) \quad [\text{A.12}]$$

and

$$\overline{R_{Mf}} = \left(\frac{1}{2}\right) \left(h_M h_F r_a \frac{s_M}{s_F}\right) \left(\overline{dF}\right). \quad [\text{A.13}]$$

The independent variables \mathbf{R}_{Mm} and \mathbf{R}_{Mf} can now be represented as

$$\mathbf{R}_{Mm} = \left(\frac{1}{2} h_M^2\right) dM \quad [\text{A.14}]$$

and

$$\mathbf{R}_{Mf} = \left(\frac{1}{2} h_M h_F r_a \frac{s_M}{s_F}\right) dF, \quad [\text{A.15}]$$

where \mathbf{R}_{Mm} and \mathbf{R}_{Mf} are expressed as linear transformations of the variables dM and dF , respectively. Their variances are as shown below:

$$\text{Var}[\mathbf{R}_{Mm}] = \left(\frac{1}{4} h_M^4\right) ds_M^2 \quad [\text{A.16}]$$

and

$$\text{Var}[\mathbf{R}_{Mf}] = \left(\frac{1}{4} h_M^2 h_F^2 r_a^2 \frac{s_M^2}{s_F^2}\right) ds_F^2. \quad [\text{A.17}]$$

Since the value of the continuous trait in the pre-selection parental males (\mathbf{M}) is independent of the responses due to selection in the parental males and females (dM and dF , respectively), variance in offspring males is expressed as

$$\text{Var}[\mathbf{M}^*] = \text{Var}[\mathbf{M}] + \text{Var}[\mathbf{R}_{Mm}] + \text{Var}[\mathbf{R}_{Mf}], \quad [\text{A.18}]$$

which expands to

$$s_M^{*2} = s_M^2 + \left(\frac{1}{4} h_M^4\right) ds_M^2 + \left(\frac{1}{4} h_M^2 h_F^2 r_a^2 \frac{s_M^2}{s_F^2}\right) ds_F^2, \quad [\text{A.19}]$$

where s_M^{*2} is the variance of \mathbf{M}^* . The equivalent expression for female offspring is as follows:

$$s_F^{*2} = s_F^2 + \left(\frac{1}{4} h_F^4\right) ds_F^2 + \left(\frac{1}{4} h_M^2 h_F^2 r_a^2 \frac{s_F^2}{s_M^2}\right) ds_M^2. \quad [\text{A.20}]$$

Equations A.19 and A.20 describe the change in variance for a continuous trait in male and female offspring due to selection on the parental generation. If there is no sex-linkage in the trait and selection acts equally on both sexes, then males and females form a single distribution. In that case, r_a equals one, and the subscripts can be removed from all other parameters in equations A.19 and A.20 since there is no distinction between female and male parameters. For such a situation, both equations reduce to

$$s^{*2} = s^2 + \left(\frac{1}{2} h^4\right) ds^2. \quad [\text{A.21}]$$

Equation A.21 is exactly the equation derived by Bulmer (1971) to describe the effect of selection on variance in a monomorphic population.

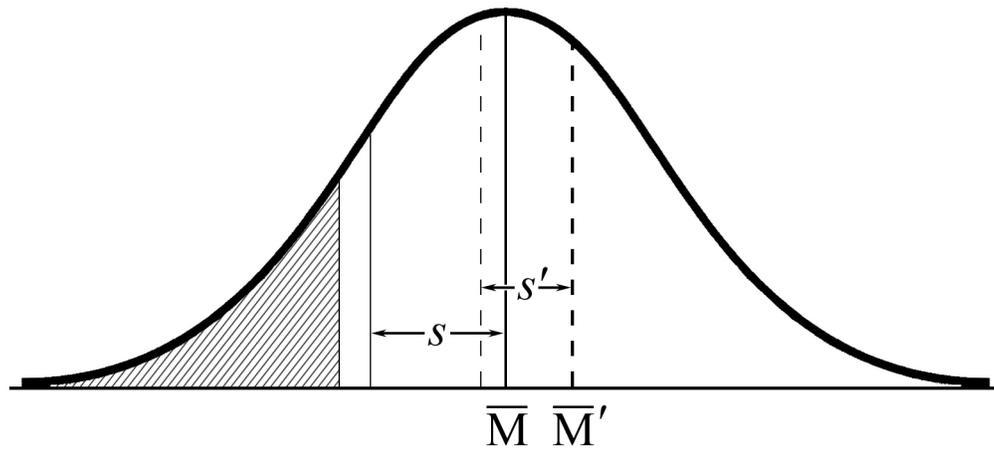


Figure A.1. Selection modeled as the truncation of a distribution following Bulmer (1971).

This figure represents the sex-specific distribution of body mass for a population of males. The pre-selection distribution fills the entire area under the heavy black curve with mean \bar{M} (heavy solid vertical line) and standard deviation s (light solid vertical line). Males that fall into the crosshatched portion of the distribution are selected against and do not reproduce. The post-selection distribution excludes the crosshatched area and has mean \bar{M}' (heavy dashed line) and standard deviation s' (light dashed line).

Appendix B: Relationship of Mean Responses to Raw Data

Data for a continuous trait such as body size can be log-transformed to produce scale-free variables, such that

$$M = \log[X_M] \quad [B.1]$$

and

$$F = \log[X_F], \quad [B.2]$$

where **M** and **F** are variables for male and female distributions as defined in [Appendix A](#), and **X** is the size variable as originally measured (*e.g.*, in kilograms). When the log transformation is performed, the mean sex-specific responses to selection (\overline{R}_M and \overline{R}_F from equations A.1 and A.2) can be rewritten as

$$\overline{R}_M = \overline{\log[X_M^*]} - \overline{\log[X_M]} \quad [B.3]$$

and

$$\overline{R}_F = \overline{\log[X_F^*]} - \overline{\log[X_F]}, \quad [B.4]$$

where the asterisk refers to the offspring generation. Equations B.3 and B.4 are equivalent to

$$\overline{R}_M = \log[GM_{XM}^*] - \log[GM_{XM}] \quad [B.5]$$

and

$$\overline{R}_F = \log[GM_{XF}^*] - \log[GM_{XF}], \quad [B.6]$$

where GM_{XM} and GM_{XF} are the geometric means of the raw size measurements for males and females, respectively. Using the log rules, equations B.5 and B.6 can also be expressed as

$$\overline{R}_M = \log\left[\frac{GM_{XM}^*}{GM_{XM}}\right] \quad [B.7]$$

and

$$\overline{R}_F = \log \left[\frac{GM_{XF}^*}{GM_{XF}} \right]. \quad [B.8]$$

In equations B.7 and B.8, \overline{R}_M and \overline{R}_F are shown to be the logarithms of ratios of offspring mean size divided by parent mean size. Replacing these ratios with the symbols p_{XM} and p_{XF} yields

$$\overline{R}_M = \log[p_{XM}] \quad [B.9]$$

and

$$\overline{R}_F = \log[p_{XF}] \quad [B.10]$$

where

$$GM_{XM}^* = GM_{XM} \times p_{XM} \quad [B.11]$$

and

$$GM_{XF}^* = GM_{XF} \times p_{XF}. \quad [B.12]$$

Thus the response variables \overline{R}_M and \overline{R}_F are shown to be the logarithms of scalars that describe the proportional change in sex-specific mean size between parent and offspring generations.

Leutenegger and Cheverud (1982; 1985) define the response of sexual dimorphism to sexual selection as the difference between the male and female responses, namely

$$\overline{R}_{SD} = \overline{R}_M - \overline{R}_F. \quad [B.13]$$

Substitution of equations B.7 and B.8 into B.13 yields

$$\overline{R}_{SD} = \log \left[\frac{GM_{XM}^*}{GM_{XM}} \right] - \log \left[\frac{GM_{XF}^*}{GM_{XF}} \right] \quad [B.14]$$

which can be shown to be equal to

$$\overline{R_{SD}} = \log \left[\frac{GM_{XM}^*}{GM_{XM}} / \frac{GM_{XF}^*}{GM_{XF}} \right] = \log \left[\frac{GM_{XM}^*}{GM_{XF}^*} / \frac{GM_{XM}}{GM_{XF}} \right]. \quad [B.15]$$

An index of sexual size dimorphism, \overline{SD} , can be calculated which is the ratio of mean male size divided by mean female size:

$$\overline{SD} = \frac{GM_{XM}}{GM_{XF}}, \quad [B.16]$$

which allows equation B.15 to be expressed as

$$\overline{R_{SD}} = \log \left[\frac{\overline{SD}^*}{\overline{SD}} \right]; \quad [B.17]$$

i.e., the logged ratio of sexual size dimorphism in the offspring generation divided by sexual size dimorphism in the parental generation. This ratio can be replaced with the symbol $p_{\overline{SD}}$, yielding

$$\overline{R_{SD}} = \log [p_{\overline{SD}}], \quad [B.18]$$

where

$$\overline{SD}^* = \overline{SD} \times p_{\overline{SD}}. \quad [B.19]$$

The response of sexual size dimorphism to selection ($\overline{R_{SD}}$) is therefore the logarithm of a scalar that describes the proportional change in sexual size dimorphism between parent and offspring generations,

$$\overline{SD}^* = \overline{SD} \times \text{antilog} [\overline{R_{SD}}]. \quad [B.20]$$

Appendix C: Derivation of the Combined Response Model

Equations A.1 and A.2 in [Appendix A](#) describe the mean responses to selection of male and female size ($\overline{\mathbf{R}}_M$ and $\overline{\mathbf{R}}_F$, respectively) in terms of the genetic correlation between the sexes, sex-specific heritabilities, sex-specific standard deviations, and sex specific selection intensities. Leutenegger and Cheverud (1982; 1985) use these equations to model the response of size dimorphism to conditions of pure sexual selection and pure variance dimorphism. Similarly, the change in sex-specific variance (as described in equations A.19 and A.20) can be used to model the response of differences in sex-specific variance (*i.e.*, variance dimorphism) to conditions of pure sexual selection and pure variance dimorphism. It can then be shown that these two sets of responses covary in predictable ways depending on the selective forces applied.

In [Appendix B](#), p_{XM} , p_{XF} , and p_{SD} were defined as offspring:parent ratios of arithmetic mean size of log-transformed data, which are shown to be equivalent to ratios of the geometric mean of raw data. Here I define analogous ratios for offspring and parent variances of log-transformed data:

$$p_{sM}^2 = \frac{S_M^{*2}}{S_M^2}, \quad [C.1]$$

$$p_{sF}^2 = \frac{S_F^{*2}}{S_F^2}, \quad [C.2]$$

and

$$p_{sSD}^2 = \frac{S_M^{*2}}{S_F^{*2}} \bigg/ \frac{S_M^2}{S_F^2} = \frac{S_M^{*2}}{S_M^2} \bigg/ \frac{S_F^{*2}}{S_F^2} = \frac{p_{sM}^2}{p_{sF}^2}, \quad [C.3]$$

where the asterisk refers to the offspring generation. (Note: the square roots of these three ratios are equal to the offspring:parent ratios of standard deviation rather than

variance.) Response variables may be defined as log-transformations of the three ratios as follows:

$$\mathbf{R}_{s^2M} = \log[p_{sM}^2] = \log\left[\frac{s_M^{*2}}{s_M^2}\right] = \log[s_M^{*2}] - \log[s_M^2], \quad [\text{C.4}]$$

$$\mathbf{R}_{s^2F} = \log[p_{sF}^2] = \log\left[\frac{s_F^{*2}}{s_F^2}\right] = \log[s_F^{*2}] - \log[s_F^2], \quad [\text{C.5}]$$

and

$$\mathbf{R}_{s^2SD} = \log\left[\frac{p_{sM}^2}{p_{sF}^2}\right] = \log[p_{sM}^2] - \log[p_{sF}^2] = \mathbf{R}_{s^2M} - \mathbf{R}_{s^2F}, \quad [\text{C.6}]$$

where \mathbf{R}_{s^2M} is the response of male variance to selection, \mathbf{R}_{s^2F} is the response of female variance to selection, and \mathbf{R}_{s^2SD} is the response of variance dimorphism to selection. As equation C.6 shows, these three response variables are related to each other in exactly the same way as the three response variables for the mean (equation B.13 in [Appendix B](#)).

The three variance ratios of equations C.1 through C.3 may be restated by substitution of equations A.19 and A.20:

$$p_{sM}^2 = \frac{s_M^2 + \left(\frac{1}{4}h_M^4\right)ds_M^2 + \left(\frac{1}{4}h_M^2h_F^2r_a^2\frac{s_M^2}{s_F^2}\right)ds_F^2}{s_M^2}, \quad [\text{C.7}]$$

$$p_{sF}^2 = \frac{s_F^2 + \left(\frac{1}{4}h_F^4\right)ds_F^2 + \left(\frac{1}{4}h_M^2h_F^2r_a^2\frac{s_F^2}{s_M^2}\right)ds_M^2}{s_F^2}, \quad [\text{C.8}]$$

and

$$p_{sM}^2 = \frac{s_M^2 + \left(\frac{1}{4}h_M^4\right)ds_M^2 + \left(\frac{1}{4}h_M^2h_F^2r_a^2\frac{s_M^2}{s_F^2}\right)ds_F^2}{s_F^2 + \left(\frac{1}{4}h_F^4\right)ds_F^2 + \left(\frac{1}{4}h_M^2h_F^2r_a^2\frac{s_F^2}{s_M^2}\right)ds_M^2} \times \frac{s_F^2}{s_M^2}. \quad [\text{C.9}]$$

Equation C.9 can also be expressed as

$$P_{sM}^2 = \frac{s_M^2 s_F^2 + \left(\frac{1}{4} h_M^4\right) s_F^2 ds_M^2 + \left(\frac{1}{4} h_M^2 h_F^2 r_a^2 \frac{s_M^2}{s_F^2}\right) s_F^2 ds_F^2}{s_M^2 s_F^2 + \left(\frac{1}{4} h_F^4\right) s_M^2 ds_F^2 + \left(\frac{1}{4} h_M^2 h_F^2 r_a^2 \frac{s_F^2}{s_M^2}\right) s_M^2 ds_M^2}. \quad [C.10]$$

Substituting equation C.10 into equation C.4 yields

$$R_{s^2SD} = \log \left[\frac{s_M^2 s_F^2 + \left(\frac{1}{4} h_M^4\right) s_F^2 ds_M^2 + \left(\frac{1}{4} h_M^2 h_F^2 r_a^2 \frac{s_M^2}{s_F^2}\right) s_F^2 ds_F^2}{s_M^2 s_F^2 + \left(\frac{1}{4} h_F^4\right) s_M^2 ds_F^2 + \left(\frac{1}{4} h_M^2 h_F^2 r_a^2 \frac{s_F^2}{s_M^2}\right) s_M^2 ds_M^2} \right], \quad [C.11]$$

a description of the response of relative variability ratio in the offspring generation to selection, expressed in terms of parameters drawn exclusively from the parental generation. A similar description of the response of mean sexual size dimorphism can be obtained by substituting equations A.1 and A.2 into B.13 (this equation appears in Leutenegger & Cheverud, 1982; 1985):

$$\overline{R_{SD}} = \left(\frac{1}{2}\right) \left[\left(h_M^2 s_M i_M - h_F^2 s_F i_F \right) + h_M h_F r_a (s_M i_F - s_F i_M) \right]. \quad [C.12]$$

Equations C.11 and C.12 jointly comprise the combined response model. Given the input parameters for these two equations, all of which are drawn only from the parental population, the response of male:female ratios of sex-specific mean size and sex-specific variance can be calculated for one or more generations. Constraining the input parameters to conditions consistent with various selective forces (*e.g.*, sexual selection with selection for increasing size in both sexes, variance dimorphism with selection for decreasing size in females and no selection on males, *etc.*) generates the set of possible responses of R_{s^2SD} and $\overline{R_{SD}}$ for those forces, which in turn allows for the identification of categories of outcomes which must correspond to particular selective forces.

Appendix D: Primate Phylogeny

When available, divergence dates are often used to set branch lengths for phylogenetic analyses. However, branch lengths are often not available or researchers may choose to use evolutionary models based on speciation events rather than divergence dates. In such cases it has been common for branch lengths to be set using a species-diversity based scaling technique (Grafen, 1989) or for branch lengths to all be set equal to represent equal expectation of change for every speciation event (*e.g.*, Mitani *et al.*, 1996; Plavcan & van Schaik, 1997b; Lindenfors & Tullberg, 1998; Smith & Cheverud, 2002). However, such algorithms for assigning branch lengths are only valid when the total number of speciation events are represented (Garland *et al.*, 1992); *i.e.*, when a phylogenetic tree includes all species ever descended from one common ancestor.

It is clearly impossible to accurately construct such a phylogeny, as many species that once existed will never appear in the fossil record, and the phylogenetic position of those that do will be difficult if not impossible to identify precisely. However, a next-best case scenario for speciation-based algorithms would assign branch lengths for trees that include all species present at a particular point in time. The resulting trees can then be “pruned” of those taxa that are not included in a particular analysis. Various authorities will differ on the number of taxa represented by the same group of animals, but an attempt to identify and include all known taxa in the construction of a phylogenetic tree is more appealing than simply throwing one’s hands up because the exact number of species in a particular clade is unknowable.

Because Grafen’s (1989) species-diversity based scaling technique is used in the present study when divergence dates are unavailable, it is important to construct a tree including all known extant primates which can later be pruned to include only those taxa

considered in this study. *Walker's Primates of the World* (Nowak, 1999) is used as the primary reference for primate taxa and is supplemented by various research articles identifying other primate species. In addition, subfossil lemurs are included here in order to represent the species diversity present in extant and “nearly extant” primates (*i.e.*, primates whose existence can be documented to within the past few thousand years). The inclusion of subfossil lemurs is particularly important given the large proportion of strepsirhine species that have recently gone extinct (16 of 62 species in the tree compiled here, or 25.8%). Although there are also subfossil haplorhines, they make up a much smaller percentage of extant and nearly extant haplorhines (Hartwig, 2002) and their phylogenetic positions are not well known. For example, the closest living relative of the Jamaican subfossil monkey *Xenothrix* has been variously proposed as a callitrichine (Ford, 1986; Ford, 1990), *Cebus* (Williams & Koopman, 1952), *Callicebus* (Horovitz & MacPhee, 1999; MacPhee & Horovitz, 2002), and *Aotus* (Rosenberger, 2002). Because of the low number of species and highly uncertain relationships of subfossil haplorhines, they have not been included in the supertree developed here.

The phylogenetic tree used in [Chapters 3 and 4](#) is based on Purvis' (1995; 1999) composite primate phylogeny, which is a “supertree” compiled from many published phylogenies for various primate taxa. The Purvis supertree is modified through a series of stages to produce the master set of trees used in this study. Supertree stages are as follows.

Stage 1. Extant species which are not included in the Purvis (1995; 1999) supertree are added. Branching sequence follows various published sources ([Table D.1](#)).

Stage 2. Some polytomies in the Stage 1 tree are resolved. In particular, intrageneric relationships within *Lepilemur* (Rumpler, 2002), *Alouatta* (Bonvicino *et al.*, 2001; Cortés-Ortiz *et al.*, 2003), and *Saimiri* (Boinski & Cropp, 1999) are modified.

Stage 3. Subfossil lemur taxa are added to the Stage 2 tree ([Table D.2](#)). Branching sequence follows Fleagle (1999). At this point, all species-level taxa have been added to the tree.

Stage 4. All remaining study taxa are added to the Stage 3 tree. These are subspecies which belong to species that are already represented in Stage 3. The Stage 4 supertree branching sequence is presented in [Figure D.1](#). Note that branching sequence within *Pan troglodytes* follows Morell (1994) and Morin *et al.* (1994). Two sets of trees are generated using this branching sequence: one using divergence dates and another using equal branch lengths (see [Chapters 3 and 4](#)). Divergence dates for the Stage 4 tree are presented in [Table D.3](#). All divergence dates that do not correspond to Purvis (1995) are explained in [Table D.4](#).

Stage 5. Trees are clipped for various analyses (full and reduced data sets for Primates, Strepsirhini, Haplorhini, Platyrrhini, and Catarrhini) and “best branches” are set as described in [Chapters 3 and 4](#).

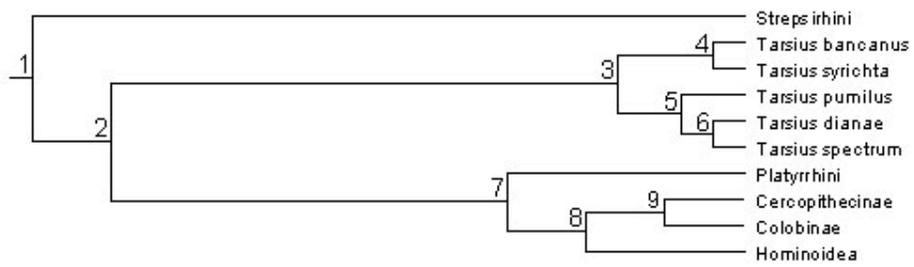


Figure D.1a. Branching sequences within *Tarsius* and among major radiations within the Primates.

Numbers correspond to Table D.3.

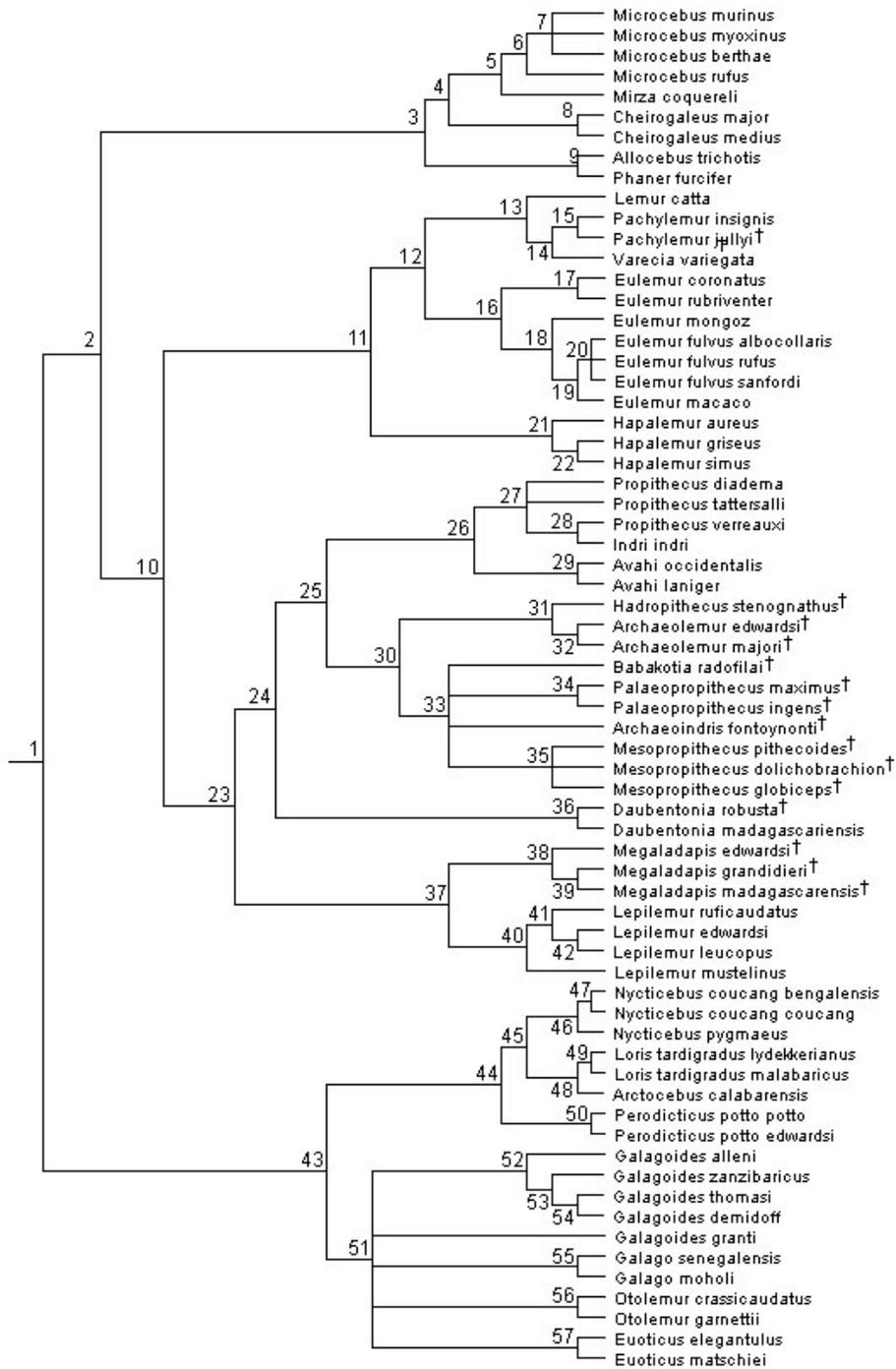


Figure D.1b. Branching sequences among the Strepsirhini.

Numbers correspond to Table D.3. † indicates extinct taxon.

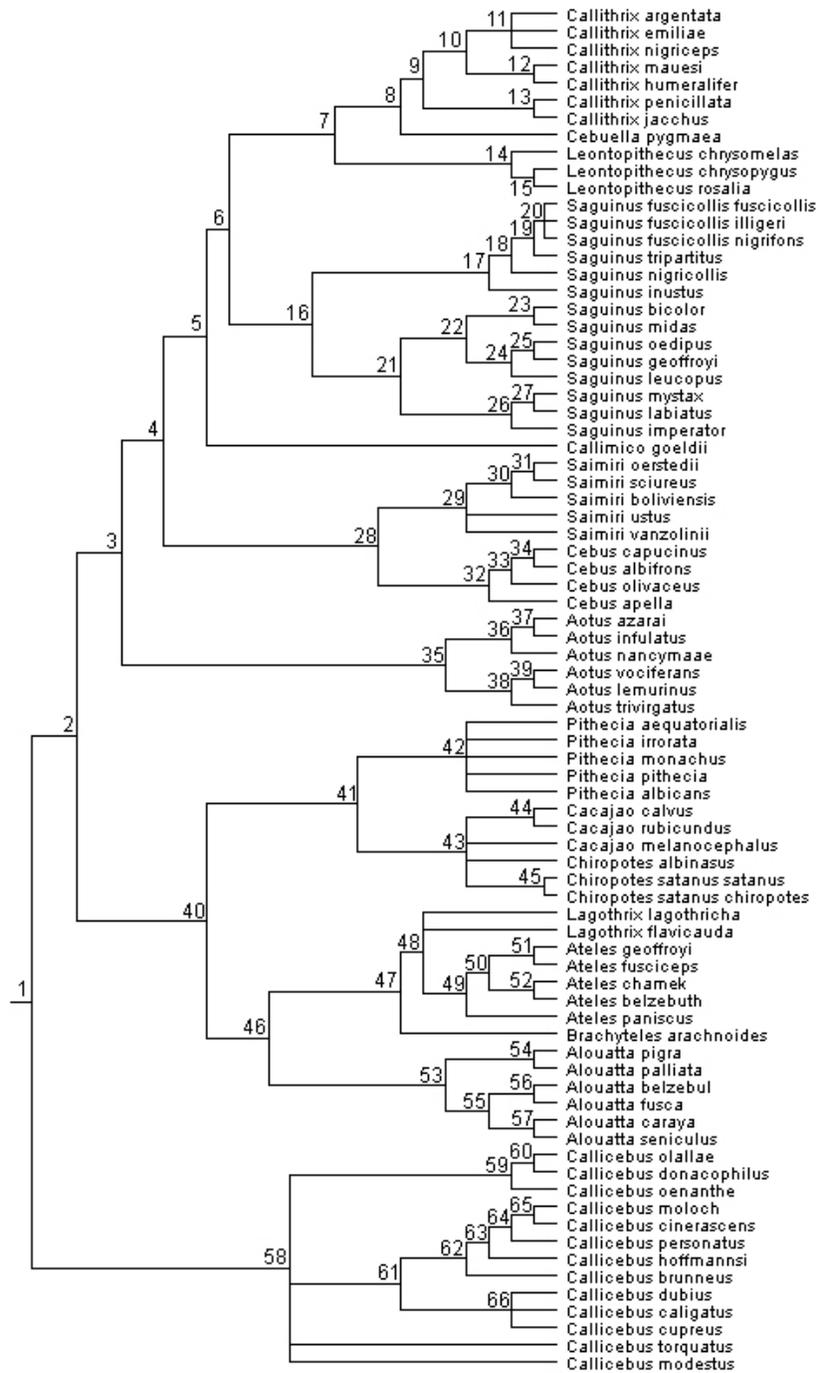


Figure D.1c. Branching sequences among the Platyrrhini.

Numbers correspond to Table D.3.

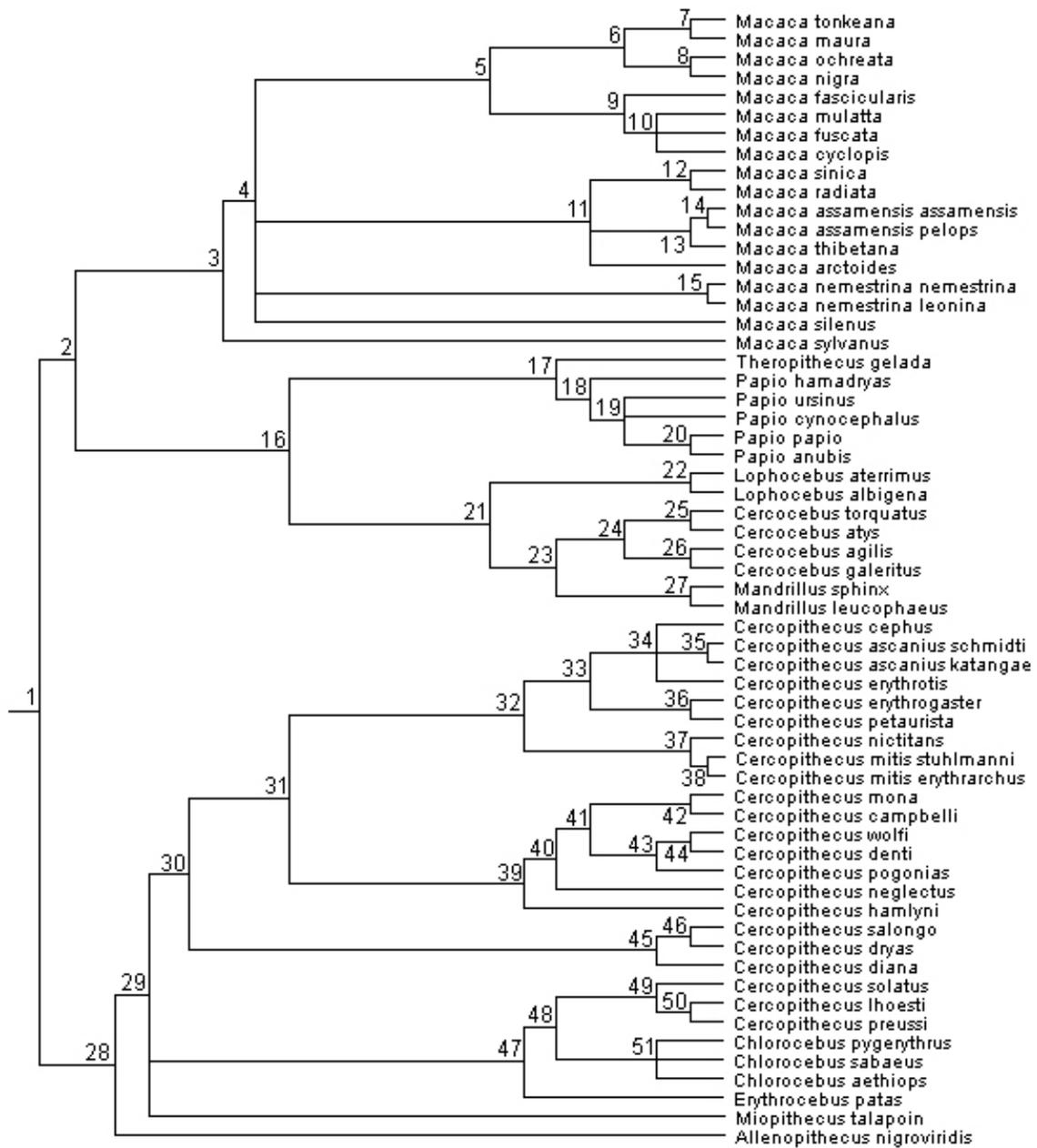


Figure D.1d. Branching sequences among the Cercopithecinae.

Numbers correspond to Table D.3.

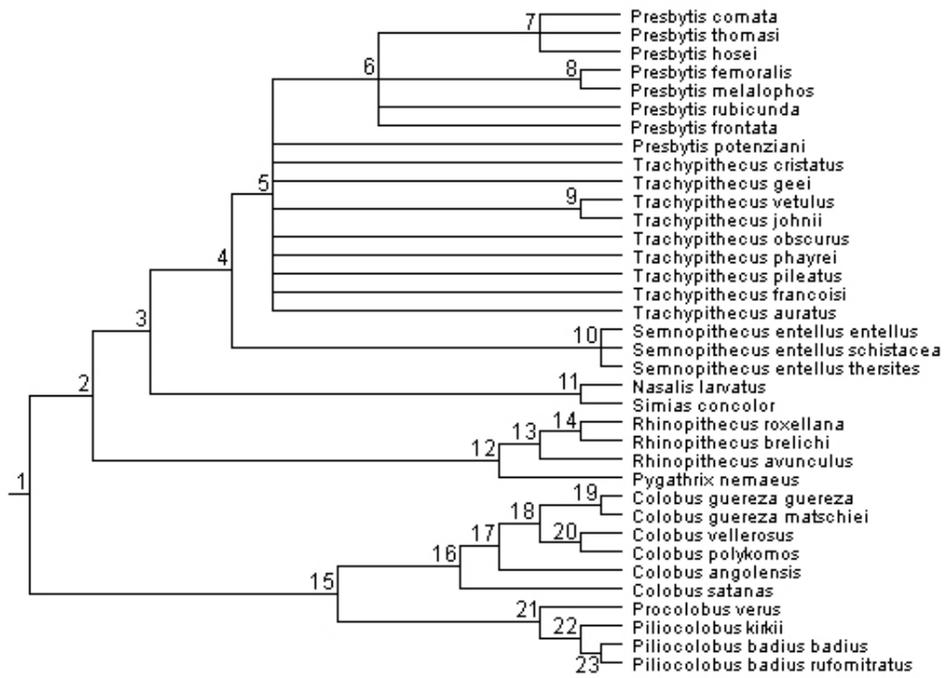


Figure D.1e. Branching sequences among the Colobinae.

Numbers correspond to Table D.3.

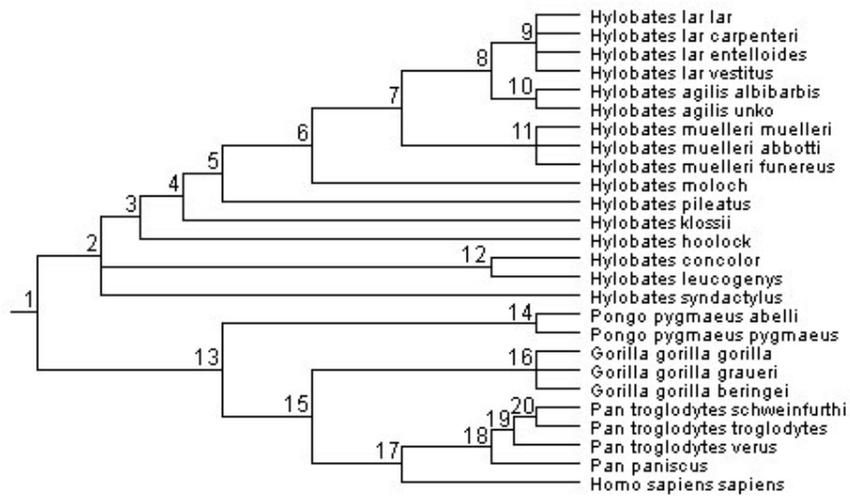


Figure D.1f. Branching sequences among the Hominoidea.

Numbers correspond to Table D.3.

| Species | Branching Sequence Note | References |
|-------------------------------|--|--|
| <i>Microcebus myoxinus</i> | polytomy: <i>M. berthae</i> , <i>M. murinus</i> , <i>M. myoxinus</i> | Rasoloarison <i>et al.</i> (2000) |
| <i>Microcebus berthae</i> | polytomy: <i>M. berthae</i> , <i>M. murinus</i> , <i>M. myoxinus</i> | Rasoloarison <i>et al.</i> (2000) |
| <i>Avahi occidentalis</i> | sister to <i>A. laniger</i> | Mittermier <i>et al.</i> (1994) |
| <i>Galagoides thomasi</i> | sister to <i>G. demidoff</i> | Nash <i>et al.</i> (1989) |
| <i>Tarsius ditaeae</i> | sister to <i>T. spectrum</i> | Niemitz <i>et al.</i> (1991), Groves (2003) |
| <i>Callithrix emiliae</i> | polytomy: <i>C. argentata</i> , <i>C. emiliae</i> , <i>C. nigriceps</i> following grouping of these taxa under <i>C. argentata</i> | Hershkovitz (1975), Groves in Wilson & Reeder (1993) |
| <i>Callithrix nigriceps</i> | polytomy: <i>C. argentata</i> , <i>C. emiliae</i> , <i>C. nigriceps</i> following grouping of these taxa under <i>C. argentata</i> | Hershkovitz (1975), Groves in Wilson & Reeder (1993) |
| <i>Callithrix mauesi</i> | sister to <i>C. humeralifera</i> following grouping of <i>C. mauesi</i> under <i>C. humeralifera</i> | Hershkovitz (1975) |
| <i>Callithrix penicillata</i> | sister to <i>C. jacchus</i> following grouping of <i>C. penicillata</i> under <i>C. jacchus</i> | Hershkovitz (1975) |
| <i>Saguinus Geoffroyi</i> | sister to <i>S. oedipus</i> | Natori (1988), Natori & Hanihara (1988, 1992) |
| <i>Aotus infulatus</i> | sister to <i>A. azarai</i> following grouping of <i>A. azarai</i> under <i>A. infulatus</i> | Ford (1994), Pieczarka <i>et al.</i> (1993) |
| <i>Aotus nancymaae</i> | sister to <i>A. azarai-A. infulatus</i> clade based on grouping in "red-neck species group" | Rylands <i>et al.</i> (1993) |
| <i>Aotus lemurinus</i> | sister to <i>A. vociferans</i> following grouping of <i>A. lemurinus</i> under <i>A. lemurinus-A. vociferans</i> clade placed sister to <i>A. trivirgatus</i> based on grouping in "gray-neck species group" | Ford (1994), Rylands <i>et al.</i> (1993) |
| <i>Aotus vociferans</i> | sister to <i>A. lemurinus</i> following grouping of <i>A. lemurinus</i> under <i>A. lemurinus-A. vociferans</i> clade placed sister to <i>A. trivirgatus</i> based on grouping in "gray-neck species group" | Ford (1994), Rylands <i>et al.</i> (1993) |
| <i>Ateles chamek</i> | sister to <i>A. belzebuth</i> | Froelich <i>et al.</i> (1991), Collins & Dubach (2000) |
| <i>Cercocebus agilis</i> | sister to <i>C. galeritus</i> | Groves (1989) |
| <i>Cercocebus atys</i> | sister to <i>C. torquatus</i> | Lee <i>et al.</i> (1988) |
| <i>Presbytis hosei</i> | polytomy: <i>P. comata</i> , <i>P. hosei</i> , <i>P. thomasi</i> following identification of <i>P. hosei</i> and <i>P. thomasi</i> as subspecies of <i>P. comata</i> | Brandon-Jones (1993) |
| <i>Presbytis thomasi</i> | polytomy: <i>P. comata</i> , <i>P. hosei</i> , <i>P. thomasi</i> following identification of <i>P. hosei</i> and <i>P. thomasi</i> as subspecies of <i>P. comata</i> | Brandon-Jones (1993) |
| <i>Presbytis femoralis</i> | sister to <i>P. melalophos</i> following grouping of <i>P. femoralis</i> under <i>P. melalophos</i> | Oates <i>et al.</i> (1994) |
| <i>Colobus vellerosus</i> | sister to <i>C. polykomos</i> following identification of <i>C. vellerosus</i> as a subspecies of <i>C. polykomos</i> | Groves in Wilson & Reeder (1993) |
| <i>Hylobates leucogenys</i> | sister to <i>H. concolor</i> | Geissmann (1993) |

Table D.1. Branching sequences for extant taxa not included in Purvis (1995, 1999).

| Species | Branching Sequence Note |
|---|--|
| <i>Pachylemur insignis</i> [†] | sister to <i>P. jullyi</i> ; genus is sister to <i>Varecia</i> |
| <i>Pachylemur jullyi</i> [†] | sister to <i>P. insignis</i> ; genus is sister to <i>Varecia</i> |
| <i>Megaladapis madagascarensis</i> [†] | sister to <i>M. grandidieri</i> |
| <i>Megaladapis grandidieri</i> [†] | sister to <i>M. madagascarensis</i> |
| <i>Megaladapis edwardsi</i> [†] | sister to clade of <i>M. grandidieri</i> and <i>M. madagascarensis</i> ; genus is sister to <i>Lepilemur</i> |
| <i>Mesopropithecus globiceps</i> [†] | polytomy: <i>M. globiceps</i> , <i>M. pithecoides</i> , <i>M. dolichobrachion</i> ; genus is in polytomy with <i>Mesopropithecus</i> , <i>Babakotia</i> , <i>Palaeopropithecus</i> , and <i>Archaeoindris</i> ; that clade is sister to the Indriinae (<i>Avahi</i> , <i>Propithecus</i> , <i>Indri</i>) |
| <i>Mesopropithecus pithecoides</i> [†] | polytomy: <i>M. globiceps</i> , <i>M. pithecoides</i> , <i>M. dolichobrachion</i> ; genus is in polytomy with <i>Mesopropithecus</i> , <i>Babakotia</i> , <i>Palaeopropithecus</i> , and <i>Archaeoindris</i> ; that clade is sister to the Indriinae (<i>Avahi</i> , <i>Propithecus</i> , <i>Indri</i>) |
| <i>Mesopropithecus dolichobrachion</i> [†] | polytomy: <i>M. globiceps</i> , <i>M. pithecoides</i> , <i>M. dolichobrachion</i> ; genus is in polytomy with <i>Mesopropithecus</i> , <i>Babakotia</i> , <i>Palaeopropithecus</i> , and <i>Archaeoindris</i> ; that clade is sister to the Indriinae (<i>Avahi</i> , <i>Propithecus</i> , <i>Indri</i>) |
| <i>Babakotia radofilai</i> [†] | genus is in polytomy with <i>Mesopropithecus</i> , <i>Babakotia</i> , <i>Palaeopropithecus</i> , and <i>Archaeoindris</i> ; that clade is sister to the Indriinae (<i>Avahi</i> , <i>Propithecus</i> , <i>Indri</i>) |
| <i>Palaeopropithecus ingens</i> [†] | sister to <i>P. maximus</i> ; genus is in polytomy with <i>Mesopropithecus</i> , <i>Babakotia</i> , <i>Palaeopropithecus</i> , and <i>Archaeoindris</i> ; that clade is sister to the Indriinae (<i>Avahi</i> , <i>Propithecus</i> , <i>Indri</i>) |
| <i>Palaeopropithecus maximus</i> [†] | sister to <i>P. ingens</i> ; genus is in polytomy with <i>Mesopropithecus</i> , <i>Babakotia</i> , <i>Palaeopropithecus</i> , and <i>Archaeoindris</i> ; that clade is sister to the Indriinae (<i>Avahi</i> , <i>Propithecus</i> , <i>Indri</i>) |
| <i>Archaeoindris fontoynonti</i> [†] | genus is in polytomy with <i>Mesopropithecus</i> , <i>Babakotia</i> , <i>Palaeopropithecus</i> , and <i>Archaeoindris</i> ; that clade is sister to the Indriinae (<i>Avahi</i> , <i>Propithecus</i> , <i>Indri</i>) |
| <i>Daubentonia robusta</i> [†] | sister to <i>D. madagascarensis</i> |
| <i>Archaeolemur majori</i> [†] | sister to <i>A. edwardsi</i> ; genus is sister to <i>Hadropithecus</i> ; that clade is sister to the Indriinae-Palaeopropithecinae clade |
| <i>Archaeolemur edwardsi</i> [†] | sister to <i>A. majori</i> ; genus is sister to <i>Hadropithecus</i> ; that clade is sister to the Indriinae-Palaeopropithecinae clade |
| <i>Hadropithecus stenognathus</i> [†] | genus is sister to <i>Archaeolemur</i> ; that clade is sister to the Indriinae-Palaeopropithecinae clade |

Table D.2. Branching sequences for subfossil lemurs.

[†] indicates extinct taxon.

| Divergence | |
|------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|
| Node | Date (mya) |
| A.1 | 57.17 | B.38 | 4.65* | C.27 | 0.25* | D.7 | 0.565* | E.2 | 4.60* |
| A.2 | 49.61 | B.39 | 2.325* | C.28 | 21.00 | D.8 | 0.565* | E.3 | 3.80* |
| A.3 | 10.00* | B.40 | 2.00* | C.29 | 10.50* | D.9 | 1.60 | E.4 | 3.40* |
| A.4 | 5.00* | B.41 | 1.50* | C.30 | 9.50* | D.10 | 1.16* | E.5 | 3.20* |
| A.5 | 5.00* | B.42 | 1.00* | C.31 | 8.50* | D.11 | 1.345* | E.6 | 1.20* |
| A.6 | 2.50* | B.43 | 22.11 | C.32 | 17.88 | D.12 | 0.67* | E.7 | 0.40* |
| A.7 | 39.88 | B.44 | 10.38 | C.33 | 8.94 | D.13 | 0.6725* | E.8 | 0.20* |
| A.8 | 27.50 | B.45 | 10.01* | C.34 | 4.47* | D.14 | 0.25* | E.9 | 0.20* |
| A.9 | 14.65 | B.46 | 2.70 | C.35 | 8.64 | D.15 | 0.25* | E.10 | 0.10* |
| | | B.47 | 0.25* | C.36 | 1.50* | D.16 | 6.80* | E.11 | 0.20* |
| B.1 | 41.79 | B.48 | 5.005* | C.37 | 1.00* | D.17 | 4.22 | E.12 | 0.60* |
| B.2 | 39.62 | B.49 | 0.25* | C.38 | 1.50* | D.18 | 1.36 | E.13 | 0.40* |
| B.3 | 30.68 | B.50 | 0.25* | C.39 | 1.00* | D.19 | 0.58 | E.14 | 0.20* |
| B.4 | 10.23 | B.51 | 1.86 | C.40 | 23.00 | D.20 | 0.49 | E.15 | 1.40* |
| B.5 | 5.115* | B.52 | 1.40* | C.41 | 9.45 | D.21 | 6.72 | E.16 | 0.80* |
| B.6 | 2.5575* | B.53 | 1.20* | C.42 | 4.725* | D.22 | 1.00* | E.17 | 0.60* |
| B.7 | 1.00* | B.54 | 1.00* | C.43 | 5.98 | D.23 | 3.19 | E.18 | 0.40* |
| B.8 | 8.23 | B.55 | 1.00* | C.44 | 2.99* | D.24 | 2.095* | E.19 | 0.10* |
| B.9 | 15.34 | B.56 | 1.00* | C.45 | 0.25* | D.25 | 1.00* | E.20 | 0.20* |
| B.10 | 20.00 | B.57 | 1.00* | C.46 | 16.00* | D.26 | 1.00* | E.21 | 0.40* |
| B.11 | 16.64 | | | C.47 | 14.12 | D.27 | 1.595* | E.22 | 0.20* |
| B.12 | 14.04 | C.1 | 33.71* | C.48 | 8.88 | D.28 | 5.20 | E.23 | 0.10* |
| B.13 | 10.92 | C.2 | 32.173* | C.49 | 5.105* | D.29 | 4.00 | | |
| B.14 | 5.46* | C.3 | 30.636* | C.50 | 1.33 | D.30 | 2.66* | F.1 | 17.58 |
| B.15 | 1.00* | C.4 | 29.10* | C.51 | 1.00* | D.31 | 2.16* | F.2 | 6.25 |
| B.16 | 10.43 | C.5 | 15.55 | C.52 | 1.00* | D.32 | 1.00* | F.3 | 4.164* |
| B.17 | 5.215* | C.6 | 13.51 | C.53 | 6.80* | D.33 | 0.66* | F.4 | 3.47* |
| B.18 | 8.51 | C.7 | 9.5 | C.54 | 3.00* | D.34 | 0.33* | F.5 | 2.776* |
| B.19 | 4.255* | C.8 | 7.22* | C.55 | 5.10* | D.35 | 0.165* | F.6 | 2.082* |
| B.20 | 0.25* | C.9 | 6.72 | C.56 | 4.00* | D.36 | 0.165* | F.7 | 1.388* |
| B.21 | 8.19 | C.10 | 2.65 | C.57 | 4.00* | D.37 | 0.165* | F.8 | 0.694* |
| B.22 | 7.19* | C.11 | 1.00* | C.58 | 7.30 | D.38 | 0.0825* | F.9 | 0.25* |
| B.23 | 18.60 | C.12 | 1.00* | C.59 | 3.65* | D.39 | 1.00* | F.10 | 0.25* |
| B.24 | 14.00 | C.13 | 1.00* | C.60 | 1.825* | D.40 | 0.835* | F.11 | 0.25* |
| B.25 | 7.00* | C.14 | 2.00* | C.61 | 3.65* | D.41 | 0.67* | F.12 | 0.694* |
| B.26 | 3.50* | C.15 | 1.00* | C.62 | 2.92* | D.42 | 0.165* | F.13 | 14.50 |
| B.27 | 1.75* | C.16 | 5.72 | C.63 | 2.19* | D.43 | 0.33* | F.14 | 0.25* |
| B.28 | 1.25* | C.17 | 3.432* | C.64 | 1.46* | D.44 | 0.165* | F.15 | 8.09 |
| B.29 | 1.00* | C.18 | 2.288* | C.65 | 0.73* | D.45 | 0.33* | F.16 | 0.25* |
| B.30 | 3.50* | C.19 | 1.144* | C.66 | 1.825* | D.46 | 0.165* | F.17 | 7.04 |
| B.31 | 1.75* | C.20 | 4.576* | | | D.47 | 1.00* | F.18 | 2.49 |
| B.32 | 1.00* | C.21 | 3.432* | D.1 | 9.62 | D.48 | 0.83* | F.19 | 1.58* |
| B.33 | 1.75* | C.22 | 1.144* | D.2 | 9.25 | D.49 | 0.33* | F.20 | 0.44* |
| B.34 | 1.00* | C.23 | 2.288* | D.3 | 5.00 | D.50 | 0.165* | | |
| B.35 | 1.00* | C.24 | 1.144* | D.4 | 2.54* | D.51 | 0.33* | | |
| B.36 | 7.00* | C.25 | 2.288* | D.5 | 2.07* | | | | |
| B.37 | 9.30* | C.26 | 1.144* | D.6 | 1.13 | E.1 | 9.27 | | |

Table D.3. Divergence dates for Stage 4 supertree.

Letters correspond to trees within Figure D.1; numbers correspond to nodes within those trees. * indicates a different date than given in Purvis (1995).

| Node | Clade | Divergence Date Note | Divergence Date (mya) |
|-------|---|--|-----------------------|
| A.3 | (<i>Tarsius bancanus-T. syrichta</i>)-other <i>Tarsius</i> | Although Eocene and Miocene fossils have been assigned to <i>Tarsius</i> (Beard <i>et al.</i> , 1994; Ginsburg & Mein, 1987), the genus probably does not extend back into the Eocene (Simons, 1997, 2003). Also, modern forms are limited to small geographic area. Arbitrary date of 10 mya set. | 10.00 |
| A.4 | <i>T. bancanus-T. syrichta</i> | halfway between previous divergence and the present | 5.00 |
| A.5 | <i>T. pumilus-(T. diana-T. spectrum)</i> | halfway between previous divergence and the present | 5.00 |
| A.6 | <i>T. diana-T. spectrum</i> | halfway between previous divergence and the present | 2.50 |
| B.5 | <i>Mirza-Microcebus</i> | halfway between previous divergence and the present | 5.115 |
| B.6 | <i>Microcebus rufus-Microcebus</i> polytomy | halfway between previous divergence and the present | 2.5575 |
| B.7 | <i>Microcebus</i> polytomy | presence of multiple species debated (Nowak, 1999) | 1.00 |
| B.8 | <i>Cheirogaleus major-C. medius</i> | unresolved to resolved (Purvis, 1999); 2 myr after previous | 8.23 |
| B.9 | <i>Phaner-Allocebus</i> | halfway between previous divergence and the present | 15.34 |
| B.14 | <i>Varecia-Pachylemur</i> [†] | halfway between previous divergence and the present | 5.46 |
| B.15 | <i>P. insignis</i> [†] - <i>P. jullyi</i> [†] | presence of multiple species debated (Nowak, 1999) | 1.00 |
| B.17 | <i>Eulemur coronatus-E. rubriventer</i> | halfway between previous divergence and the present | 5.215 |
| B.19 | <i>Eulemur fulvus-E. macaco</i> | halfway between previous divergence and the present | 4.255 |
| B.20 | <i>Eulemur fulvus</i> subspecies | subspecies divergences set to 0.25 mya | 0.25 |
| B.22 | <i>Haplemur griseus-H. simus</i> | unresolved to resolved (Purvis, 1999); 1 myr after previous | 7.19 |
| B.25 | Indriinae-(<i>Archaeolemurinae</i> [†] - <i>Palaeopropithecinae</i> [†]) | halfway between previous divergence and the present | 7.00 |
| B.26 | <i>Avahi-(Indri-Propithecus)</i> | halfway between previous divergence and the present | 3.50 |
| B.27 | <i>Indri-Propithecus</i> polytomy | halfway between previous divergence and the present | 1.75 |
| B.28 | <i>I. indri-P. verreauxi</i> | unresolved to resolved (Purvis, 1999); 0.5 myr after previous | 1.25 |
| B.29 | <i>A. laniger-A. occidentalis</i> | presence of multiple species debated (Nowak, 1999) | 1.00 |
| B.30 | <i>Archaeolemurinae</i> [†] - <i>Palaeopropithecinae</i> [†] | halfway between previous divergence and the present | 3.50 |
| B.31 | <i>Archaeolemur</i> [†] - <i>Hadropithecus</i> [†] | halfway between previous divergence and the present | 1.75 |
| B.32 | <i>A. edwardsi</i> [†] - <i>A. majori</i> [†] | half is less than 1 mya; imposed 1mya | 1.00 |
| B.33 | <i>Palaeopropithecinae</i> [†] polytomy | halfway between previous divergence and the present | 1.75 |
| B.34 | <i>Palaeopropithecus ingens</i> [†] - <i>P. maximus</i> [†] | presence of multiple species debated (Nowak, 1999) | 1.00 |
| B.35 | <i>Mesopropithecus</i> [†] polytomy | presence of more than two species debated (Nowak, 1999) | 1.00 |
| B.36 | <i>Daubentonia madagascarensis-D. robusta</i> [†] | halfway between previous divergence and the present | 7.00 |
| B.37 | <i>Lepilemur-Megaladapis</i> [†] | halfway between previous divergence and the present | 9.30 |
| B.38 | <i>Megaladapis</i> subgenus <i>Peloriadapis</i> [†] - <i>M.</i> subgenus <i>Megaladapis</i> [†] | halfway between previous divergence and the present | 4.65 |
| B.39 | <i>M. grandidieri</i> [†] - <i>M. madagascarensis</i> [†] | halfway between previous divergence and the present | 2.325 |
| B.41, | | | |
| B.42 | <i>Lepilemur</i> internal divergences | presence of multiple species debated (Nowak, 1999) | 2.00-1.00 |

| Node | Clade | Divergence Date Note | Divergence Date (mya) |
|-------------|---|---|------------------------------|
| B.45 | <i>Nycticebus</i> -(<i>Loris-Arctocebus</i>) | Purvis date older than previous divergence; used Purvis mean minus standard error | 10.01 |
| B.47 | <i>Nycticebus coucang</i> subspecies | subspecies divergences set to 0.25 mya | 0.25 |
| B.48 | <i>Loris-Arctocebus</i> | halfway between previous divergence and the present | 5.005 |
| B.49 | <i>Loris tardigradus</i> subspecies | subspecies divergences set to 0.25 mya | 0.25 |
| B.50 | <i>Perodicticus potto</i> subspecies | subspecies divergences set to 0.25 mya | 0.25 |
| B.52- | | | |
| B.54 | <i>Galagoidea</i> internal divergences | presence of multiple species debated (Nowak, 1999) | 1.40-1.00 |
| B.55 | <i>Galago senegalensis-G. moholi</i> | half is less than 1 mya; imposed 1mya | 1.00 |
| B.56 | <i>Otolemur crassicaudatus-O. garnettii</i> | half is less than 1 mya; imposed 1mya | 1.00 |
| B.57 | <i>Euticticus elegantulus-E. matschiei</i> | half is less than 1 mya; imposed 1mya | 1.00 |
| C.1 | <i>Callicebus</i> -other Platyrrhini | relationships revised drastically between Purvis (1995) and Purvis (1999); used Purvis mean plus standard error for first platyrrhine split | 33.71 |
| C.2, | (Atelinae-Pitheciinae)-(Aotus-[Cebinae- | | 32.173, |
| C.3 | Callitrichinae]); <i>Aotus</i> -(Cebinae-Callitrichinae) | divergence times split equally between divergences of C.1 and C.4 | 30.636 |
| C.4 | Cebinae-Callitrichinae | Purvis date older than earlier divergence; used Purvis mean minus standard error | 29.10 |
| C.8 | <i>Cebuella-Callithrix</i> | Purvis date younger than subsequent divergence; used subsequent divergence plus 0.5 myr | 7.22 |
| C.11 | <i>Callithrix argentata-C. emiliae-C.nigriceps</i> polytomy | presence of multiple species debated (Nowak, 1999) | 1.00 |
| C.12 | <i>C. mauesi-C. humeralifer</i> | presence of multiple species debated (Nowak, 1999) | 1.00 |
| C.13 | <i>C. jacchus-C. penicillata</i> | presence of multiple species debated (Nowak, 1999) | 1.00 |
| C.14, | <i>Leontopithecus chrysomelas</i> -(<i>L. chrysopygus</i> - <i>L.</i> | | |
| C.15 | <i>rosalia</i>); <i>L. chrysopygus</i> - <i>L. rosalia</i> | presence of multiple species debated (Nowak, 1999) | 2.00, 1.00 |
| C.16- | | Grafen (1989) method inconsistent with one internal date given by Purvis. | |
| C.26 | <i>Saguinus</i> internal divergences | Alternative method - time after first divergence at 5.72 mya split into five equal blocks of 1.144 myr; starting at tips, sister taxa separated by one block of time with additional blocks added to equal out branch lengths | 5.72-1.144 |
| C.27 | <i>Saguinus fuscicollis</i> subspecies | subspecies divergences set to 0.25 mya | 0.25 |
| C.29 | <i>Saimiri</i> basal polytomy | halfway between previous divergence and the present | 10.50 |
| C.30, | <i>S. boliviensis</i> -(<i>S. sciureus</i> - <i>S. oerstedii</i>); <i>S. sciureus</i> - <i>S.</i> | | |
| C.31 | <i>oerstedii</i> | unresolved to resolved (Purvis, 1999); 2 myr total after previous | 9.50, 8.50 |
| C.34 | <i>Cebus albifrons-C. capucinus</i> | halfway between previous divergence and the present | 4.47 |
| C.36, | <i>Aotus nancymae</i> -(<i>A. infulatus</i> - <i>A. azarai</i>); <i>A.</i> | | |
| C.37 | <i>infulatus</i> - <i>A. azarai</i> | presence of multiple species debated (Nowak, 1999) | 1.50, 1.00 |
| C.38, | <i>Aotus trivirgatus</i> -(<i>A. vociferans</i> - <i>A. lemurinus</i>); <i>A.</i> | | |
| C.39 | <i>vociferans</i> - <i>A. lemurinus</i> | presence of multiple species debated (Nowak, 1999) | 1.50, 1.00 |

| Node | Clade | Divergence Date Note | Divergence Date (mya) |
|-------------|--|--|------------------------------|
| C.42 | <i>Pithecia</i> polytomy | halfway between previous divergence and the present | 4.725 |
| C.44 | <i>Cacajao cabvus-C. rubicundus</i> | halfway between previous divergence and the present | 2.99 |
| C.45 | <i>Chirotopes satanus</i> subspecies | subspecies divergences set to 0.25 mya | 0.25 |
| C.46 | <i>Alouatta-(Brachyteles-[Ateles-Lagothrix])</i> | dating follows Cortés-Ortiz <i>et al.</i> (2003) | 16.00 |
| C.49 | <i>Ateles paniscus</i> -other <i>Ateles</i> | halfway between previous (8.88 mya) and subsequent (1.33 mya) divergences | 5.105 |
| C.51 | <i>Ateles Geoffroyi-A. fusciceps</i> | presence of multiple species debated (Nowak, 1999) | 1.00 |
| C.52 | <i>A. chamek-A. belzebuth</i> | presence of multiple species debated (Nowak, 1999) | 1.00 |
| C.53- | | | |
| C.57 | <i>Alouatta</i> internal divergences | dating follows Cortés-Ortiz <i>et al.</i> (2003) | 6.80-3.00 |
| C.59 | <i>Callicebus oenanthe-(C. olallae-C. donacophilus)</i> | halfway between previous divergence and the present | 3.65 |
| C.60 | <i>C. olallae-C. donacophilus</i> | halfway between previous divergence and the present | 1.825 |
| C.61 | <i>(C. caligatus-C. cupreus-C. dubius polytomy)</i> -five species <i>Callicebus</i> group | halfway between previous divergence and the present | 3.65 |
| C.62- | | | |
| C.65 | five species <i>Callicebus</i> group internal divergences | internal dating follows method of Grafen (1989) scaled to 3.65 myr; one Grafen unit = 0.73 myr | 2.92-0.73 |
| C.66 | <i>C. caligatus-C. cupreus-C. dubius</i> polytomy | halfway between previous divergence and the present | 1.825 |
| D.4 | <i>Macaca</i> polytomy (15 species) | resolved to unresolved (Purvis, 1999); weighted mean of four divergences now in polytomy | 2.54 |
| D.5 | <i>M. fascicularis</i> group-([<i>M. tonkeana-M. maura</i>]-[<i>M. ochreata-M. nigra</i>]) | halfway between previous (2.54 mya) and subsequent (1.60 mya) divergences | 2.07 |
| D.7 | <i>M. tonkeana-M. maura</i> | halfway between previous divergence and the present | 0.565 |
| D.8 | <i>M. ochreata-M. nigra</i> | halfway between previous divergence and the present | 0.565 |
| D.10 | <i>M. mulatta-M. fascicularis-M. cyclops</i> polytomy | resolved to unresolved (Purvis, 1999); weighted mean of two divergences now in polytomy | 1.16 |
| D.11 | <i>M. arctoides-sinica</i> group polytomy | resolved to unresolved (Purvis, 1999); weighted mean of two divergences now in polytomy | 1.345 |
| D.13 | <i>M. thibetana-M. assamensis</i> | halfway between previous divergence and the present | 0.6725 |
| D.14 | <i>M. assamensis</i> subspecies | subspecies divergences set to 0.25 mya | 0.25 |
| D.15 | <i>M. nemestrina</i> subspecies | subspecies divergences set to 0.25 mya | 0.25 |
| D.16 | baboons-(mangabeys-drills) | Purvis date younger than subsequent divergence; used Purvis mean plus standard error | 6.80 |
| D.22 | <i>Lophocebus albigena-L. aterrimus</i> | presence of multiple species debated (Nowak, 1999) | 1.00 |
| D.24 | <i>(Cercocebus torquatus-C. atys)-(C. agilis-C. galeritus)</i> | halfway between previous (3.19 mya) and subsequent (1.00 mya) divergences | 2.095 |
| D.25 | <i>C. torquatus-C. atys</i> | presence of multiple species debated (Nowak, 1999) | 1.00 |
| D.26 | <i>C. agilis-C. galeritus</i> | presence of multiple species debated (Nowak, 1999) | 1.00 |

| Node | Clade | Divergence Date Note | Divergence Date (mya) |
|-------------|---|---|------------------------------|
| D.27 | <i>Mandrillus sphinx</i> - <i>M. leucophaeus</i> | halfway between previous divergence and the present | 1.595 |
| D.29- | <i>Miopithecus-Erythrocebus-Chlorocebus-</i> | internal dating follows method of Grafen (1989) scaled to 4.00 myr; one | |
| D.51 | <i>Cercopithecus polytomy</i> | Grafen unit = 0.33 myr | 4.00-0.33 |
| D.35 | <i>Cercopithecus ascanius schmidti</i> - <i>C. a. katangae</i> | halfway between previous divergence and the present | 0.165 |
| D.38 | <i>C. mitis stuhlmani</i> - <i>C. m. erythrarchus</i> | halfway between previous divergence and the present | 0.0825 |
| E.2- | Clade containing <i>Pygathrix</i> , <i>Rhinopithecus</i> , <i>Simias</i> , | internal dating follows method of Grafen (1989) scaled to 4.60 myr; one | |
| E.13 | <i>Nasalis</i> , <i>Semnopithecus</i> , <i>Trachypithecus</i> , <i>Presbytis</i> | Grafen unit = 0.20 myr | 4.60-0.20 |
| E.10 | <i>Semnopithecus entellus</i> subspecies | half of one Grafen unit from above | 0.10 |
| E.15- | <i>Colobus</i> -(<i>Procolobus</i> - <i>Ptilocolobus</i>) internal | internal dating follows method of Grafen (1989) scaled to 1.40 myr; one | |
| E.23 | divergences | Grafen unit = 0.20 myr | 1.40-0.20 |
| E.19 | <i>C. guereza guereza</i> - <i>C. g. matschiei</i> | half of one Grafen unit from above | 0.10 |
| E.23 | <i>Ptilocolobus badius</i> - <i>P. b. rufomitratrus</i> | half of one Grafen unit from above | 0.10 |
| F.2- | | internal dating follows method of Grafen (1989) scaled to 6.25 myr; one | |
| F.12 | <i>Hylobates</i> internal divergences | Grafen unit = 0.694 myr | 6.25-0.694 |
| F.9 | <i>H. lar</i> subspecies | subspecies divergences set to 0.25 mya | 0.25 |
| F.10 | <i>H. agilis</i> subspecies | subspecies divergences set to 0.25 mya | 0.25 |
| F.11 | <i>H. muelleri</i> subspecies | subspecies divergences set to 0.25 mya | 0.25 |
| F.14 | <i>Pongo pygmaeus</i> subspecies | subspecies divergences set to 0.25 mya | 0.25 |
| F.16 | <i>Gorilla gorilla</i> subspecies | subspecies divergences set to 0.25 mya | 0.25 |
| F.19 | <i>Pan troglodytes verus</i> -(<i>P. t. troglodytes</i> - <i>P. t. schweinfurthi</i>) | dating follows Morin <i>et al.</i> (1994) | 1.58 |
| F.20 | <i>P. t. troglodytes</i> - <i>P. t. schweinfurthi</i> | dating follows Morin <i>et al.</i> (1994) | 0.44 |

Table D.4. Explanations for assigned dates in Table 3.D when divergence dates do not match Purvis (1995).

Node letters and numbers are as in Table D.3.

Appendix E: Newick Code for Primate Supertree

((((((((Microcebus murinus:1.0, Microcebus myoxinus:1.0, Microcebus berthae:1.0):1.5575, Microcebus rufus:2.5575):2.5575, Mirza coquereli:5.115):5.115, (Cheirogaleus major:8.23, Cheirogaleus medius:8.23):2.0):20.45, (Allocebus trichotis:15.34, Phaner furcifer:15.34):15.34):8.94, (((Lemur catta:10.92, Varecia variegata variegata:10.92):3.12, ((Eulemur coronatus:5.215, Eulemur rubriventer:5.215):5.215, (Eulemur mongoz:8.51, (Eulemur fulvus albocollaris:0.25, Eulemur fulvus rufus:0.25, Eulemur fulvus sanfordi:0.25):4.005, Eulemur macaco:4.255):4.255):1.92):3.61):2.6, (Hapalemur aureus:8.19, (Hapalemur griseus:7.19, Hapalemur simus:7.19):1.0):8.45):3.36, (((Propithecus diadema:1.75, Propithecus tattersalli:1.75, (Propithecus verreauxi verreauxi:1.25, Indri indri:1.25):0.5):1.75, (Avahi occidentalis:1.0, Avahi laniger laniger:1.0):2.5):10.5, Daubentonia madagascariensis:14.0):4.6, (Lepilemur ruficaudatus:1.5, (Lepilemur edwardsi:1.0, Lepilemur leucopus:1.0):0.5):17.1):1.4):19.62):2.17, (((((Nycticebus coucang bengalensis:0.25, Nycticebus coucang coucang:0.25):2.45, Nycticebus pygmaeus:2.7):7.31, ((Loris tardigradus lydekkerianus:0.25, Loris tardigradus malabaricus:0.25):4.755, Arctocebus calabarensis:5.005):5.005):0.37, (Perodicticus potto potto:0.25, Perodicticus potto edwardsi:0.25):10.13):11.73, ((Galagoides alleni:1.4, (Galagoides zanzibaricus:1.2, (Galagoides thomasi:1.0, Galagoides demidoff:1.0):0.2):0.2):0.46, (Galago senegalensis:1.0, Galago moholi:1.0):0.86, (Otolemur crassicaudatus:1.0, Otolemur garnettii:1.0):0.86, (Euoticus elegantulus:1.0, Euoticus matschiei:1.0):0.86):20.25):19.68):15.38, (((Tarsius bancanus:5.0, Tarsius syrichta:5.0):5.0, (Tarsius diana:2.5, Tarsius spectrum:2.5):7.5):39.61, (((((((((((Callithrix argentata:1.0, Callithrix emiliae:1.0, Callithrix nigriceps:1.0):1.65, (Callithrix mauesi:1.0, Callithrix humeralifer:1.0):1.65):4.07, (Callithrix penicillata:1.0, Callithrix jacchus:1.0):5.72):0.5, Cebuella pygmaea:7.22):2.28, (Leontopithecus chrysomelas:2.0, Leontopithecus rosalia:2.0):7.5):4.01, (((Saguinus fuscicollis fuscicollis:0.25, Saguinus fuscicollis illigeri:0.25, Saguinus fuscicollis nigrifrons:0.25):2.038, Saguinus nigricollis:2.288):3.432, (((Saguinus bicolor:1.144, Saguinus midas:1.144):2.288, ((Saguinus oedipus oedipus:1.144, Saguinus geoffroyi:1.144):1.144, Saguinus leucopus:2.288):1.144):1.144, (Saguinus mystax:1.144, Saguinus labiatus:1.144):3.432):1.144):7.79):15.59, (((Saimiri oerstedii:8.5, Saimiri sciureus:8.5):1.0, Saimiri boliviensis boliviensis:9.5):1.0, Saimiri ustus:10.5, Saimiri vanzolinii:10.5):10.5, (((Cebus capucinus:4.47, Cebus albifrons:4.47):4.47, Cebus olivaceus:8.94):8.94, Cebus apella:17.88):3.12):8.1):1.536, (((Aotus azarai:1.0, Aotus infulatus:1.0):0.5, Aotus nancymae:1.5):7.14, ((Aotus vociferans:1.0, Aotus lemurinus:1.0):0.5, Aotus trivirgatus:1.5):7.14):21.996):1.537, (((Pithecia irrorata:4.725, Pithecia monachus:4.725, Pithecia pithecia:4.725):4.725, (Cacajao calvus:5.98, Cacajao melanocephalus:5.98, Chiropotes albinasus:5.98, (Chiropotes satanus satanus:0.25, Chiropotes satanus chiropotes:0.25):5.73):3.47):13.55, (((Lagothrix lagothricha:8.88, (((Ateles geoffroyi:1.0, Ateles fusciceps:1.0):0.33, (Ateles chamek:1.0, Ateles belzebuth:1.0):0.33):3.775, Ateles paniscus:5.105):3.775):5.24, Brachyteles arachnoides:14.12):1.88, ((Alouatta pigra:3.0, Alouatta palliata:3.0):3.8, ((Alouatta belzebul:4.0, Alouatta fusca:4.0):1.1, (Alouatta caraya:4.0, Alouatta seniculus:4.0):1.1):1.7):9.2):7.0):9.173):1.537, (Callicebus donacophilus:7.3, (((Callicebus moloch:1.46, Callicebus personatus:1.46):0.73, Callicebus hoffmannsi:2.19):0.73, Callicebus brunneus:2.92):0.73, Callicebus cupreus:3.65):3.65, Callicebus torquatus:7.3):26.41):6.17,

(((((((Macaca tonkeana:0.565, Macaca maura:0.565):0.565, Macaca nigra:1.13):0.94,
 (Macaca fascicularis:1.6, (Macaca mulatta:1.16, Macaca fuscata:1.16, Macaca
 cyclopis:1.16):0.44):0.47):0.47, ((Macaca sinica:0.67, Macaca radiata radiata:0.67):0.675,
 (Macaca assamensis assamensis:0.25, Macaca assamensis pelops:0.25):1.095, Macaca
 arctoides:1.345):1.195, (Macaca nemestrina nemestrina:0.25, Macaca nemestrina
 leonina:0.25):2.29):6.71, ((Theropithecus gelada:4.22, (Papio hamadryas:1.36, (Papio
 ursinus:0.58, Papio cynocephalus:0.58, Papio anubis:0.58):0.78):2.86):2.58, ((Lophocebus
 aterrimus:1.0, Lophocebus albigena:1.0):5.72, (((Cercocebus torquatus:1.0, Cercocebus atys
 atys:1.0):1.095, (Cercocebus agilis:1.0, Cercocebus galeritus:1.0):1.095):1.095, Mandrillus
 sphinx:3.19):3.53):0.08):2.45):0.37, (((((((Cercopithecus cephus:0.33, (Cercopithecus
 ascanius schmidti:0.165, Cercopithecus ascanius katangae:0.165):0.165):0.33, Cercopithecus
 petaurista buettikoferi:0.66):0.34, (Cercopithecus nictitans:0.165, (Cercopithecus mitis
 stuhlmanni:0.0825, Cercopithecus mitis erythrarchus:0.0825):0.0825):0.835):1.16,
 (((Cercopithecus campbelli campbelli:0.67, ((Cercopithecus wolffi:0.165, Cercopithecus
 denti:0.165):0.165, Cercopithecus pogonias:0.33):0.34):0.165, Cercopithecus
 neglectus:0.835):0.165, Cercopithecus hamlyni hamlyni:1.0):1.16):0.5, Cercopithecus diana
 diana:2.66):1.34, ((Cercopithecus lhoesti:0.83, (Chlorocebus pygerythrus:0.33, Chlorocebus
 sabaeus:0.33, Chlorocebus aethiops:0.33):0.5):0.17, Erythrocebus patas:1.0):3.0, Miopithecus
 talapoin:4.0):1.2, Allenopithecus nigroviridis:5.2):4.42):5.03, (((((((Presbytis comata:0.4,
 Presbytis thomasi:0.4, Presbytis hosei:0.4):0.8, (Presbytis femoralis:0.2, Presbytis
 melalophos:0.2):1.0, Presbytis rubicunda:1.2):2.0, Presbytis potenzi:3.2, Trachypithecus
 cristatus ultima:3.2, Trachypithecus geei:3.2, (Trachypithecus vetulus:0.2, Trachypithecus
 johnii:0.2):3.0, Trachypithecus obscurus:3.2, Trachypithecus phayrei:3.2, Trachypithecus
 pileatus:3.2, Trachypithecus francoisi:3.2):0.2, (Semnopithecus entellus entellus group:0.1,
 Semnopithecus entellus schistacea group:0.1, Semnopithecus entellus thersites
 group:0.1):3.3):0.4, (Nasalis larvatus:0.2, Simias concolor:0.2):3.6):0.8, (Rhinopithecus
 roxellana:0.6, Pygathrix nemaus:0.6):4.0):4.67, (((((((Colobus guereza guereza:0.1, Colobus
 guereza matschiei:0.1):0.3, (Colobus vellerosus:0.2, Colobus polykomos
 polykomos:0.2):0.2):0.2, Colobus angolensis:0.6):0.2, Colobus satanas:0.8):0.6, (Procolobus
 verus:0.4, (Piliocolobus badius badius:0.1, Piliocolobus badius
 rufomitatus:0.1):0.3):1.0):7.87):5.38):12.85, (((((((((((Hylobates lar lar:0.25, Hylobates lar
 carpenteri:0.25, Hylobates lar entelloides:0.25, Hylobates lar vestitus:0.25):0.444, (Hylobates
 agilis albibarbis:0.25, Hylobates agilis unko:0.25):0.444):0.694, (Hylobates muelleri
 muelleri:0.25, Hylobates muelleri abbotti:0.25, Hylobates muelleri
 funereus:0.25):1.138):0.694, Hylobates moloch:2.082):0.694, Hylobates
 pileatus:2.776):0.694, Hylobates klossii:3.47):0.694, Hylobates hoolock:4.164):2.086,
 (Hylobates concolor:0.694, Hylobates leucogenys leucogenys:0.694):5.556, Hylobates
 syndactylus:6.25):11.33, ((Pongo pygmaeus abelli:0.25, Pongo pygmaeus
 pygmaeus:0.25):14.25, ((Gorilla gorilla gorilla:0.25, Gorilla gorilla graueri:0.25, Gorilla
 gorilla beringei:0.25):7.84, (((Pan troglodytes schweinfurthi:0.44, Pan troglodytes
 troglodytes:0.44):1.14, Pan troglodytes verus:1.58):0.91, Pan paniscus:2.49):4.55, Homo
 sapiens sapiens:7.04):1.05):6.41):3.08):9.92):12.38):9.73):7.56);

Appendix F: R Code

COVARIANCE MATRIX CONSTRUCTION AND PGLS RECONSTRUCTION CODE

```
pancest <- function(M, A, Tips, ErrorV=1, constrained="N", constraint=0, branches="b",
matrices="m"){

# Author: Adam Gordon, Dept. of Anthropology, Univ. of Texas at Austin
# This program reconstructs values of a continuous variable for all internal nodes within
# a phylogeny.
# Input variables:
# M: Connectance matrix. This is a square matrix. Identifiers are arranged
# such that all tips come first, followed by the base node, followed by
# the other nodes. Nodes that are not directly connected are represented
# by zeros, connected nodes are represented by a function of the branch
# length between them (see below).
# A: Ancestor vector. A column vector. Identifiers are arranged as in the
# connectance matrix. The entry for the base node is zero; for all other
# nodes it is the identifier of the node directly ancestral to it.
# Tips: Tip data vector. A column vector. Identifiers are the tips in the same
# order as in the connectance matrix. Entries are the observed value of
# the continuous character at the tips.
# constrained: Yes or no question - is the base node to be constrained to a specific
# value? If "N", uses GMM reconstructions. If "Y", sets the base node
# equal to a value entered by the user (AVM reconstruction).
# constraint: Value for the constrained base node. If "constrained" is equal to "N",
# then this value is ignored.
# branches: "b" if connectance matrix contains branch lengths, "i" if it contains
# inverse branch lengths.
# matrices: "m" if inputs are already in matrix form, "t" if they are text files to
# be read in.
#
# Output:
# A 2 column matrix containing reconstructed values of all internal nodes. The first
# column is generated through the standard model of PGLS (variance proportional to
# branch length); the second column is generated using an alternative model (standard
# deviation proportional to branch length).

#####
# Defining function to read in files
load.matrices <- function(Mmat="M.txt", Amat="A.txt", Tmat="Tips.txt") {
N <- read.table(Mmat)
M <<- matrix(0,length(N),length(N))
X <- 1
while (X <= length(N))
{
M[,X] <<- N[,X]
X <- X+1
}
N <- read.table(Amat)
A <<- matrix(0,dim(N)[1])
A[,1] <<- N[,1]
N <- read.table(Tmat)
Tips <<- matrix(0,dim(N)[1])
Tips[,1] <<- N[,1]
}

#####
# Defining functions to calculate constants
al <- function(Node, Connect=M, Ancestor=A){ # Input: Node, the identifier of a tip
or node; Connect, the connectance matrix; Ancestor, the ancestor vector
```

```

      (Connect[Node,Ancestor[Node]] +
Connect[Ancestor[Node],Ancestor[Ancestor[Node]])/Connect[Ancestor[Node],Ancestor[Ancesto
r[Node]]]
}
a2 <- function(Node, Connect=M, Ancestor=A){      # Input: Node, the identifier of a tip
or node; Connect, the connectance matrix; Ancestor, the ancestor vector
  -1*Connect[Node,Ancestor[Node]]/Connect[Ancestor[Node],Ancestor[Ancestor[Node]]]
}

#####
# If matrices are text files, load them
if (matrices=="t")
{
load.matrices(Mmat=M, Amat=A, Tmat=Tips)
}

#####
# Extracting information from input

ntips <- length(Tips)
ntotal <- length(M[,1])
nnodes <- ntotal - ntips
base <- max.col(-t(A))      # gets the identifier of the base node

#####
# Inverting branch lengths in M if they are inverse branch lengths
if (branches=="i")
{
  rowcounter <- 1
  while (rowcounter <= ntotal) {
    columncounter <- 1
    while (columncounter <= ntotal) {
      if (!(M[rowcounter,columncounter] == 0))
      {
        M[rowcounter,columncounter] <- 1/M[rowcounter,columncounter]
      }
      columncounter <- columncounter+1
    }
    rowcounter <- rowcounter+1
  }
}

#####
# Linear Model (equivalent to weighted square change parsimony)

LinearCov <- function(M,A,ntips,ntotal,nnodes,base) {      # generates the covariance
matrix using the linear model

COV <- matrix(0, ntotal, ntotal)      # This will become the matrix of coefficients for the
linear system
NodeType <- matrix(0, ntotal, 1)      # This will become a vector, the entry indicating the
number of nodes removed from the base node (0 for base, 1 for immediate descendants,
etc.)
rowcounter <- 1
while (rowcounter <= ntotal) {
  if (rowcounter == base)
  {
    NodeType[rowcounter] <- 0
  }
  else
  {
    level <- 1
    node <- rowcounter
    loopdone <- 0
    while (loopdone == 0) {
      if (A[node] == base)
      {

```

```

        NodeType[rowcounter] <- level
        loopdone <- 1
    }
    level <- level + 1
    node <- A[node]
} # end of while loop
} # end of else loop
rowcounter <- rowcounter + 1
}

INodeType <- matrix(0,nnodes-1,1) # column vector of the level of the internal nodes
rowcounter <- 1
while (rowcounter <= nnodes-1) {
    INodeType[rowcounter,] <- NodeType[rowcounter+ntips+1]
    rowcounter <- rowcounter + 1
}

COVorder <- t(t(order(INodeType))) # column vector of the order in which internal nodes
will have covariances calculated
Completed <- matrix(base,1) # column vector of the nodes which have had their
covariances calculated

# Procedure to fill in the covariance matrix for the internal nodes
rowcounter <- 1
while (rowcounter <= nnodes-1) {
    node <- COVorder[rowcounter]
    fullnode <- node+ntips+1
    length(Completed) <- rowcounter+1
    Completed[rowcounter+1] <- fullnode
    if (NodeType[fullnode] == 1)
    {
        COV[fullnode,fullnode] <<- M[fullnode,A[fullnode]]
    }
    else if (NodeType[fullnode] == 2)
    {
        CompletedCounter <- 1
        while (CompletedCounter <= length(Completed)) {
            othernode <- Completed[CompletedCounter]
            if (othernode == base)
            { # leaves covariance matrix entry set to zero
            }
            else if (othernode == fullnode)
            {
                COV[fullnode,fullnode] <<- COV[A[fullnode],A[fullnode]] + M[fullnode,A[fullnode]]
            }
            else
            {
                # set up if loop - calculates covariances differently if other node is level 0,
                # 1, or greater than 1
                if (NodeType[othernode] == 0)
                {
                    Covariance <- 0
                }
                else if ((NodeType[othernode] == 1) || (NodeType[othernode] == 2) || (A[fullnode]
                == othernode) || (A[A[fullnode]] == othernode))
                {
                    Covariance <- COV[A[fullnode],othernode]
                }
                else
                {
                    Covariance <- COV[A[fullnode],othernode]
                }
                COV[fullnode,othernode] <<- Covariance
                COV[othernode,fullnode] <<- Covariance
            }
            CompletedCounter <- CompletedCounter + 1
        } # end while loop
    }
}

```

```

    } # end else if loop
else # loop for level 3 and greater
{
  CompletedCounter <- 1
  while (CompletedCounter <= length(Completed)) {
    othernode <- Completed[CompletedCounter]
    if (othernode == base)
      { # leaves covariance matrix entry set to zero
      }
    else if (othernode == fullnode)
      {
        COV[fullnode,fullnode] <<- COV[A[fullnode],A[fullnode]] + M[fullnode,A[fullnode]]
      }
    else
      {
        # set up if loop - calculates covariances differently if other node is level 0,
1, or greater than 1
        if (NodeType[othernode] == 0)
          {
            Covariance <- 0
          }
        else if (NodeType[othernode] == 1)
          {
            Covariance <- COV[A[fullnode],othernode]
          }
        else if ((NodeType[othernode] == 1) || (NodeType[othernode] == 2) || (A[fullnode]
== othernode) || (A[A[fullnode]] ==othernode))
          {
            Covariance <- COV[A[fullnode],othernode]
          }
        else
          {
            Covariance <- COV[A[fullnode],othernode]
          }
        COV[fullnode,othernode] <<- Covariance
        COV[othernode,fullnode] <<- Covariance
      }
    CompletedCounter <- CompletedCounter + 1
  } # end while loop
} # end else if loop
rowcounter <- rowcounter + 1
}

# Procedure to fill in the rest of the covariance matrix

rowcounter <- 1
while (rowcounter <= ntips) {
  fullnode <- rowcounter
  length(Completed) <- length(Completed)+1
  Completed[nnodes+rowcounter] <- fullnode
  if (NodeType[fullnode] == 1)
    {
      COV[fullnode,fullnode] <<- M[fullnode,A[fullnode]]
    }
  else if (NodeType[fullnode] == 2)
    {
      CompletedCounter <- 1
      while (CompletedCounter <= length(Completed)) {
        othernode <- Completed[CompletedCounter]
        if (othernode == base)
          { # leaves covariance matrix entry set to zero
          }
        else if (othernode == fullnode)
          {
            COV[fullnode,fullnode] <<- COV[A[fullnode],A[fullnode]] + M[fullnode,A[fullnode]]
          }
        else

```

```

    {
      # set up if loop - calculates covariances differently if other node is level 0,
1, or greater than 1
      if (NodeType[othenode] == 0)
        {
          Covariance <- 0
        }
      else if ((NodeType[othenode] == 1) || (NodeType[othenode] == 2) || (A[fullnode]
== othenode) || (A[A[fullnode]] ==othenode))
        {
          Covariance <- COV[A[fullnode],othenode]
        }
      else
        {
          Covariance <- COV[A[fullnode],othenode]
        }
      COV[fullnode,othenode] <<- Covariance
      COV[othenode,fullnode] <<- Covariance
    }
    CompletedCounter <- CompletedCounter + 1
  } # end while loop
} # end else if loop
else # loop for level 3 and greater
{
  CompletedCounter <- 1
  while (CompletedCounter <= length(Completed)) {
    othenode <- Completed[CompletedCounter]
    if (othenode == base)
      { # leaves covariance matrix entry set to zero
      }
    else if (othenode == fullnode)
      {
        COV[fullnode,fullnode] <<- COV[A[fullnode],A[fullnode]] + M[fullnode,A[fullnode]]
      }
    else
      {
        # set up if loop - calculates covariances differently if other node is level 0,
1, or greater than 1
        if (NodeType[othenode] == 0)
          {
            Covariance <- 0
          }
        else if ((NodeType[othenode] == 1) || (NodeType[othenode] == 2) || (A[fullnode]
== othenode) || (A[A[fullnode]] ==othenode))
          {
            Covariance <- COV[A[fullnode],othenode]
          }
        else
          {
            Covariance <- COV[A[fullnode],othenode]
          }
        COV[fullnode,othenode] <<- Covariance
        COV[othenode,fullnode] <<- Covariance
      }
    CompletedCounter <- CompletedCounter + 1
  } # end while loop
} # end else if loop
rowcounter <- rowcounter + 1
}
COV
} # End of LinearCov function

#####
# Constant Rate Model

CRcov <- function(M,A,ErrorV,ntips,ntotal,nnodes,base) { # generates the covariance
matrix using the linear model

```

```

COV <- matrix(0, ntotal, ntotal) # This will become the matrix of coefficients for the
linear system
NodeType <- matrix(0, ntotal, 1) # This will become a vector, the entry indicating the
number of nodes removed from the base node (0 for base, 1 for immediate descendants,
etc.)
rowcounter <- 1
while (rowcounter <= ntotal) {
  if (rowcounter == base)
  {
    NodeType[rowcounter] <- 0
  }
  else
  {
    level <- 1
    node <- rowcounter
    loopdone <- 0
    while (loopdone == 0) {
      if (A[node] == base)
      {
        NodeType[rowcounter] <- level
        loopdone <- 1
      }
      level <- level + 1
      node <- A[node]
    } # end of while loop
  } # end of else loop
  rowcounter <- rowcounter + 1
}

INodeType <- matrix(0, nnodes-1, 1) # column vector of the level of the internal nodes
rowcounter <- 1
while (rowcounter <= nnodes-1) {
  INodeType[rowcounter,] <- NodeType[rowcounter+ntips+1]
  rowcounter <- rowcounter + 1
}

COVorder <- t(t(order(INodeType))) # column vector of the order in which internal nodes
will have covariances calculated
Completed <- matrix(base, 1) # column vector of the nodes which have had their
covariances calculated

# Procedure to fill in the covariance matrix for the internal nodes
rowcounter <- 1
while (rowcounter <= nnodes-1) {
  node <- COVorder[rowcounter]
  fullnode <- node+ntips+1
  length(Completed) <- rowcounter+1
  Completed[rowcounter+1] <- fullnode
  if (NodeType[fullnode] == 1)
  {
    COV[fullnode,fullnode] <- M[fullnode,A[fullnode]]^2*ErrorV
  }
  else if (NodeType[fullnode] == 2)
  {
    CompletedCounter <- 1
    while (CompletedCounter <= length(Completed)) {
      othernode <- Completed[CompletedCounter]
      if (othernode == base)
      { # leaves covariance matrix entry set to zero
      }
      else if (othernode == fullnode)
      {
        COV[fullnode,fullnode] <- COV[A[fullnode],A[fullnode]] +
M[fullnode,A[fullnode]]^2*ErrorV
      }
    }
  }
  else

```

```

    {
      # set up if loop - calculates covariances differently if other node is level 0,
1, or greater than 1
      if (NodeType[othernode] == 0)
        {
          Covariance <- 0
        }
      else if ((NodeType[othernode] == 1) || (NodeType[othernode] == 2) || (A[fullnode]
== othernode) || (A[A[fullnode]] ==othernode))
        {
          Covariance <- COV[A[fullnode],othernode]
        }
      else
        {
          Covariance <- COV[A[fullnode],othernode]
        }
      COV[fullnode,othernode] <<- Covariance
      COV[othernode,fullnode] <<- Covariance
    }
    CompletedCounter <- CompletedCounter + 1
  } # end while loop
} # end else if loop
else # loop for level 3 and greater
{
  CompletedCounter <- 1
  while (CompletedCounter <= length(Completed)) {
    othernode <- Completed[CompletedCounter]
    if (othernode == base)
      { # leaves covariance matrix entry set to zero
      }
    else if (othernode == fullnode)
      {
        COV[fullnode,fullnode] <<- COV[A[fullnode],A[fullnode]] +
M[fullnode,A[fullnode]]^2*ErrorV
      }
    else
      {
        # set up if loop - calculates covariances differently if other node is level 0,
1, or greater than 1
        if (NodeType[othernode] == 0)
          {
            Covariance <- 0
          }
        else if (NodeType[othernode] == 1)
          {
            Covariance <- COV[A[fullnode],othernode]
          }
        else if ((NodeType[othernode] == 1) || (NodeType[othernode] == 2) || (A[fullnode]
== othernode) || (A[A[fullnode]] ==othernode))
          {
            Covariance <- COV[A[fullnode],othernode]
          }
        else
          {
            Covariance <- COV[A[fullnode],othernode]
          }
        COV[fullnode,othernode] <<- Covariance
        COV[othernode,fullnode] <<- Covariance
      }
    CompletedCounter <- CompletedCounter + 1
  } # end while loop
} # end else if loop
rowcounter <- rowcounter + 1
}

# Procedure to fill in the rest of the covariance matrix

```

```

rowcounter <- 1
while (rowcounter <= ntips) {
  fullnode <- rowcounter
  length(Completed) <- length(Completed)+1
  Completed[nnodes+rowcounter] <- fullnode
  if (NodeType[fullnode] == 1)
  {
    COV[fullnode,fullnode] <<- M[fullnode,A[fullnode]]
  }
  else if (NodeType[fullnode] == 2)
  {
    CompletedCounter <- 1
    while (CompletedCounter <= length(Completed)) {
      othernode <- Completed[CompletedCounter]
      if (othernode == base)
        { # leaves covariance matrix entry set to zero
        }
      else if (othernode == fullnode)
        {
          COV[fullnode,fullnode] <<- COV[A[fullnode],A[fullnode]] +
M[fullnode,A[fullnode]]^2*ErrorV
        }
      else
        {
          # set up if loop - calculates covariances differently if other node is level 0,
1, or greater than 1
          if (NodeType[othernode] == 0)
            {
              Covariance <- 0
            }
          else if ((NodeType[othernode] == 1) || (NodeType[othernode] == 2) || (A[fullnode]
== othernode) || (A[A[fullnode]] ==othernode))
            {
              Covariance <- COV[A[fullnode],othernode]
            }
          else
            {
              Covariance <- COV[A[fullnode],othernode]
            }
          COV[fullnode,othernode] <<- Covariance
          COV[othernode,fullnode] <<- Covariance
        }
      CompletedCounter <- CompletedCounter + 1
    } # end while loop
  } # end else if loop
  else # loop for level 3 and greater
  {
    CompletedCounter <- 1
    while (CompletedCounter <= length(Completed)) {
      othernode <- Completed[CompletedCounter]
      if (othernode == base)
        { # leaves covariance matrix entry set to zero
        }
      else if (othernode == fullnode)
        {
          COV[fullnode,fullnode] <<- COV[A[fullnode],A[fullnode]] +
M[fullnode,A[fullnode]]^2*ErrorV
        }
      else
        {
          # set up if loop - calculates covariances differently if other node is level 0,
1, or greater than 1
          if (NodeType[othernode] == 0)
            {
              Covariance <- 0
            }

```

```

        else if ((NodeType[othernode] == 1) || (NodeType[othernode] == 2) || (A[fullnode]
== othernode) || (A[A[fullnode]] == othernode))
        {
            Covariance <- COV[A[fullnode],othernode]
        }
        else
        {
            Covariance <- COV[A[fullnode],othernode]
        }
        COV[fullnode,othernode] <<- Covariance
        COV[othernode,fullnode] <<- Covariance
    }
    CompletedCounter <- CompletedCounter + 1
} # end while loop
} # end else if loop
rowcounter <- rowcounter + 1
}
COV
} # End of CRcov function

#####
# Function to generate reconstructions

reconstruct <- function(COV,Tips,ntips,nnodes) { # generates the covariance matrix
using the inherited rate model

Sigma <<- matrix(0, ntips, ntips) # Tips covariance matrix
HO <<- matrix(0, nnodes, ntips) # Internal nodes and tips covariance matrix
HH <<- matrix(0, nnodes, nnodes) # Internal nodes covariance matrix
J <<- matrix(1, ntips, 1) # Column vector of ones
NodeStdError <<- matrix(0,nnodes,1) # Column vector of standard errors for nodes
Identity <<- matrix(0, ntips, ntips)
diag(Identity) <<- 1 # Identity matrix

columncounter <- 1
while (columncounter <= ntips) {
    rowcounter <- 1
    while (rowcounter <= ntips) {
        Sigma[rowcounter,columncounter] <<- COV[rowcounter,columncounter]
        rowcounter <- rowcounter + 1
    }
    rowcounter <- 1
    while (rowcounter <= nnodes) {
        HO[rowcounter,columncounter] <<- COV[rowcounter+ntips,columncounter]
        rowcounter <- rowcounter + 1
    }
    columncounter <- columncounter + 1
}

columncounter <- 1
while (columncounter <= nnodes) {
    rowcounter <- 1
    while (rowcounter <= nnodes) {
        HH[rowcounter,columncounter] <<- COV[rowcounter+ntips,columncounter+ntips]
        rowcounter <- rowcounter + 1
    }
    columncounter <- columncounter + 1
}

if (constrained == "N")
{
    Mg <<- solve(t(J)%*%solve(Sigma)%*%J)%*%t(J)%*%solve(Sigma)%*%Tips
}
else
{
    Mg <<- matrix(constraint, 1, 1)
}

```

```

}
YTips <- Tips - matrix(Mg[1], ntips, 1)
YhatNodes <- matrix(Mg[1], nnodes, 1) + HO%%solve(Sigma)%%(YTips)

w <- matrix(0,nnodes,ntips) # this the weights matrix from Rohlf's 2001 Evolution
paper - it can be used to calculate standard errors about the HTU values
counter<-1
while (counter <= nnodes)
{
  HOrrow <- HO[counter,]
  w[counter,] <- ((solve(t(J)%%solve(Sigma)%%J)[1]*t(J))+HOrrow%%(Identity-
solve(Sigma)%%J%%t(J)*(solve(t(J)%%solve(Sigma)%%J)[1]))%%solve(Sigma)
  counter <- counter+1
}

EvoRate <- (t(Tips - J %% Mg) %% solve(Sigma) %% (Tips - J %% Mg) / (ntips-1))[1] #
This function is from Garland and Ives, 2000 - it calculates the rate of evolution, aka
sigmaSquared
V <- Sigma * EvoRate
EstCovar <- w%%V%%t(w) # this function is from Rohlf's 2001
Evolution paper
NodeStdError <- t(sqrt(diag(EstCovar))) # Note: these errors don't match Martin's
errors, but they do match Mesquite's errors (at least for base node)

YhatNodes

} # End of reconstruct function

#####
# This constructs the solution vector

names <- matrix("Base node",nnodes,1)
counter <- 2
while (counter <= nnodes) {
  names[counter] <- paste("Node",counter-1)
  counter <- counter + 1
}

# ReconIR <- reconstruct(IRcov(M,A,ErrorV,ntips,ntotal,nnodes,base),Tips,ntips,nnodes)
# Error2 <- NodeStdError
# ReconIR2 <- reconstruct(IRcov2(M,A,ErrorV,ntips,ntotal,nnodes,base),Tips,ntips,nnodes)
# Error3 <- NodeStdError
# ReconIRLE <- reconstruct(IRLEcov(M,A,ntips,ntotal,nnodes,base),Tips,ntips,nnodes)
# Error4 <- NodeStdError
# ReconCRPLE <-
reconstruct(CRPLEcov(M,A,ErrorV,ntips,ntotal,nnodes,base),Tips,ntips,nnodes)
# Error6 <- NodeStdError

CI <- 0.95
Tcrit <- abs(qt((1-CI)/2,ntips-1))

ReconCR <- reconstruct(CRcov(M,A,ErrorV,ntips,ntotal,nnodes,base),Tips,ntips,nnodes)
Error5 <- NodeStdError
LLCI5 <- ReconCR - Error5 * Tcrit
ULCI5 <- ReconCR + Error5 * Tcrit
ReconLinear <- reconstruct(LinearCov(M,A,ntips,ntotal,nnodes,base),Tips,ntips,nnodes)
Error1 <- NodeStdError
LLCI1 <- ReconCR - Error1 * Tcrit
ULCI1 <- ReconCR + Error1 * Tcrit

# Solution <- data.frame(ReconLinear, Error1, ReconCR, Error5, ReconIR, Error2,
ReconIR2, Error3, ReconIRLE, Error4, ReconCRPLE, Error6, row.names = names)
# colnames(Solution) <- c("Linear", "Std Error", "Constant Rate", "Std Error",
"Gradualism", "Std Error", "Gradualism 2", "Std Error", "Gradualism w/linear error", "Std
Error", "Constant Rate plus Linear Error", "Std Error")

```

```

Solution <- data.frame(ReconLinear, Error1, LLCI1, ULCI1, ReconCR, Error5, LLCI5, ULCI5,
row.names = names)
colnames(Solution) <- c("Linear", "Std Error", "Lower CI", "Upper CI", "Constant Rate",
"Std Error", "Lower CI", "Upper CI")
Solution

#####
# This bracket ends the function "pancest"
}

```

PGLS REGRESSION CODE

```

PGLSreg <- function(X, Y, Sigma, AddIntercept="N", H=0, Special="N", CI=0.95) {
# X is a matrix holding independent variables for OTUs
# Y is a vector holding dependent variable for OTUs
# Sigma is the covariance matrix for the OTUs
# AddIntercept takes "N" or "Y"; specifies whether user would like the program to add in
# a column vector of ones to identify the intercept of the regression
# H is the null hypothesis slope
# Special takes "ANOVA", "ANCOVA", or "N" (N performs general linear analysis; user must
# provide all variables
# CI specifies confidence interval generated (i.e., 0.95 for a 95% confidence interval)

X <- t(t(X))
Y <- t(t(Y))

if (AddIntercept == "Y") {
X <- array(c(X, matrix(1,length(X[,1]),1)), c(length(X[,1]),length(X[,1])+1))
}

ntips <- length(X[,1])
nvars <- length(X[1,])
degfree <- ntips - nvars
Tcrit <- abs(qt((1-CI)/2,degfree))

# PGLS Regression
Beta <- solve(t(X)%*%solve(Sigma)%*%X)%*%t(X)%*%solve(Sigma)%*%Y
PredY <- X%*%Beta
V <- (t(Y-PredY)%*%solve(Sigma)%*(Y-PredY)/degfree)[1]*Sigma
BetaVar <- solve(t(X)%*%solve(V)%*%X)
BetaStdErr <- t(t(sqrt(diag(BetaVar))))
T <- (Beta - H)/BetaStdErr
P <- 2 * pt(-abs(T),matrix(degfree,length(T),1))
LLCI <- Beta - BetaStdErr * Tcrit
ULCI <- Beta + BetaStdErr * Tcrit
RSS <- t(Y-PredY)%*%solve(V)%*(Y-PredY)
Resid <- (Y-PredY)
StandResid <- solve(V)%*(Y-PredY)
# SSE <- sum(Resid^2)
SSE <- t(Resid)%*%solve(Sigma)%*%Resid

J <- matrix(1,ntips,1)
Mg <- solve(t(J)%*%solve(Sigma)%*%J)%*%t(J)%*%solve(Sigma)%*%Y
MeanResid <- Y - matrix(Mg[1], ntips, 1)
SSR <- t(MeanResid)%*%solve(Sigma)%*%MeanResid
Rsquare <- 1 - SSE/SSR

if (Special == "ANOVA") {
Betar <- solve(t(J)%*%solve(Sigma)%*%J)%*%t(J)%*%solve(Sigma)%*%Y
PredYr <- J%*%Betar
Residr <- (Y-PredYr)
# SSEr <- sum(Residr^2)
SSEr <- t(Residr)%*%solve(Sigma)%*%Residr
SST <- SSEr - SSE
dfN <- (nvars - 1)
dfD <- (ntips - nvars)
MST <- SST/dfN
}
}

```

```

MSE <- SSE/dfD
F <- MST/MSE
probF <- pf(F, dfN, dfD, lower.tail = FALSE)
P <-matrix(NaN, nvars, 1)
P[1,] <- probF
}

if (Special == "ANCOVA") { # generates 3 p-values: 1) Ho = common slope equal to zero,
# 2) Ho = slopes are equal, 3) Ho = intercepts are equal

# Calculate p-value for Ho = slopes are the same
TempX2 <- X[,1]*X
TempX3 <- matrix(0, ntips, (nvars-1)*2)
Counter <- 1
while (Counter <= nvars-1) {
  TempX3[,Counter] <- X[,Counter+1]
  Counter <- Counter + 1
}
Counter <- 1
while (Counter <= nvars-1) {
  TempX3[,Counter+nvars-1] <- TempX2[,Counter+1]
  Counter <- Counter + 1
}
rm(TempX2)

Betacom <- solve(t(TempX3)%*%solve(Sigma)%*%TempX3)%*%t(TempX3)%*%solve(Sigma)%*%Y
PredYcom <- TempX3%*%Betacom
Residcom <- (Y-PredYcom)
SSEcom <- t(Residcom)%*%solve(Sigma)%*%Residcom
SSTcom <- SSE - SSEcom
dfN <- (nvars-1)*2 - nvars
dfD <- ntips - (nvars-1)*2
MSTcom <- SSTcom/dfN
MSEcom <- SSEcom/dfD
Fcom <- MSTcom/MSEcom
probFcom <- pf(Fcom, dfN, dfD, lower.tail = FALSE)
P[2,] <- probFcom

# Calculate p-value for Ho = intercepts are the same
Counter <- 2
while (Counter <= length(T[,1])-1) {
  P[Counter+1,] <- NaN
  Counter <- Counter + 1
}
TempX <- matrix(1, ntips, 2)
TempX[,1] <- X[,1]
Betar <- solve(t(TempX)%*%solve(Sigma)%*%TempX)%*%t(TempX)%*%solve(Sigma)%*%Y
PredYr <- TempX%*%Betar
Residr <- (Y-PredYr)
# SSEr <- sum(Residr^2)
SSEr <- t(Residr)%*%solve(Sigma)%*%Residr
SST <- SSEr - SSE
dfN <- (nvars - 1)
dfD <- (ntips - nvars)
MST <- SST/dfN
MSE <- SSE/dfD
F <- MST/MSE
probF <- pf(F, dfN, dfD, lower.tail = FALSE)
P[3,] <- probF
} # closes the ANCOVA procedure

# Non-PGLS, OLS regression
SigmaIdent <- matrix(0, length(X[,1]), length(X[,1]))
diag(SigmaIdent) <- matrix(1, length(X[,1]), 1)
BetaOLS <- solve(t(X)%*%solve(SigmaIdent)%*%X)%*%t(X)%*%solve(SigmaIdent)%*%Y
PredYOLS <- X%*%BetaOLS

```

```

VOLS <- (t(Y-PredYOLS)%*%solve(SigmaIdent)%*(Y-PredYOLS)/degfree)[1]*SigmaIdent
BetaVarOLS <- solve(t(X)%*%solve(VOLS)%*%X)
BetaStdErrOLS <- t(t(sqrt(diag(BetaVarOLS))))
TOLS <- (BetaOLS - H)/BetaStdErrOLS
POLS <- 2 * pt(-(abs(TOLS)),matrix(degfree,length(TOLS),1))
LLCIOOLS <- BetaOLS - BetaStdErrOLS * Tcrit
ULCIOOLS <- BetaOLS + BetaStdErrOLS * Tcrit
ResidOLS <- (Y-PredYOLS)
StandResidOLS <- solve(VOLS)%*(Y-PredYOLS)
SSEOLS <- sum(ResidOLS^2)

MgOLS <- mean(Y)
MeanResidOLS <- Y - matrix(MgOLS, ntips, 1)
SSROLS <- sum(MeanResidOLS^2)
RsquareOLS <- 1 - SSEOLS/SSROLS

if (Special == "ANOVA") {
  BetaOLSr <- solve(t(J)%*%solve(SigmaIdent)%*%J)%*%t(J)%*%solve(SigmaIdent)%*%Y
  PredYOLSr <- J%*%BetaOLSr
  ResidOLSr <- (Y-PredYOLSr)
  SSErOLS <- sum(ResidOLSr^2)
  SSTOLS <- SSErOLS - SSEOLS
  MSTOLS <- SSTOLS/dfN
  MSEOLS <- SSEOLS/dfD
  FOLS <- MSTOLS/MSEOLS
  probFOLS <- pf(FOLS, dfN, dfD, lower.tail = FALSE)
  POLS <-matrix(NaN, nvars, 1)
  POLS[1,] <- probFOLS
}

if (Special == "ANCOVA") { # generates 3 p-values: 1) Ho = common slope equal to zero,
                          # 2) Ho = slopes are equal, 3) Ho = intercepts are equal

  # Calculate p-value for Ho = slopes are the same
  BetaOLScom <-
solve(t(TempX3)%*%solve(SigmaIdent)%*%TempX3)%*%t(TempX3)%*%solve(SigmaIdent)%*%Y
  PredYOLScom <- TempX3%*%BetaOLScom
  ResidOLScom <- (Y-PredYOLScom)
  SSEcomOLS <- sum(ResidOLScom^2)
  SSTcomOLS <- SSEOLS - SSEcomOLS
  dfN <- (nvars-1)*2 - nvars
  dfD <- ntips - (nvars-1)*2
  MSTcomOLS <- SSTcomOLS/dfN
  MSEcomOLS <- SSEcomOLS/dfD
  FcomOLS <- MSTcomOLS/MSEcomOLS
  probFcomOLS <- pf(FcomOLS, dfN, dfD, lower.tail = FALSE)
  POLS[2,] <- probFcomOLS

  # Calculate p-value for Ho = intercepts are the same
  Counter <- 2
  while (Counter <= length(T[,1])-1) {
    POLS[Counter+1,] <- NaN
    Counter <- Counter + 1
  }
  BetaOLSr <-
solve(t(TempX)%*%solve(SigmaIdent)%*%TempX)%*%t(TempX)%*%solve(SigmaIdent)%*%Y
  PredYOLSr <- TempX%*%BetaOLSr
  ResidOLSr <- (Y-PredYOLSr)
  SSErOLS <- sum(ResidOLSr^2)
  SSTOLS <- SSErOLS - SSEOLS
  dfN <- (nvars - 1)
  dfD <- (ntips - nvars)
  MSTOLS <- SSTOLS/dfN
  MSEOLS <- SSEOLS/dfD
  FOLS <- MSTOLS/MSEOLS
  probFOLS <- pf(FOLS, dfN, dfD, lower.tail = FALSE)

```

```

    POLS[3,] <- probFOLS
  }

RegSol <- data.frame(ntips, Beta, P, BetaStdErr, LLCI, ULCI, BetaOLS, POLS,
BetaStdErrOLS, LLCIOLS, ULCIOLS)
colnames(RegSol) <- c("n", "PGLS Beta", "p-value", "Std Error", "Lower CI", "Upper CI",
"OLS Beta", "p-value", "Std Error", "Lower CI", "Upper CI")
RegSol
} # This bracket ends the function "PGLSreg"

```

RESAMPLING CODE: COMPOSITE MALE SIZE DISTRIBUTION

```

CompMaleBoot <- function(MArray, nboots=2000, CI=95) {

BootArray <- matrix(0, nboots, 1)
ResultsTable <- matrix(0,5,1)
rownames(ResultsTable) <- c("Min", "CI LL", "Median", "CI UL", "Max")
FemurDraw <- sample(1:length(MArray[,1]), nboots, replace=TRUE)
TibiaDraw1 <- sample(1:length(MArray[,1]), nboots, replace=TRUE)
TibiaDraw2 <- sample(1:length(MArray[,1]), nboots, replace=TRUE)
HumerusDraw <- sample(1:length(MArray[,1]), nboots, replace=TRUE)
RadiusDraw <- sample(1:length(MArray[,1]), nboots, replace=TRUE)

Counter <- 1
while (Counter <= nboots) {
  BootArray[Counter] <- (MArray[FemurDraw[Counter],1] *
(MArray[TibiaDraw1[Counter],2]+MArray[TibiaDraw2[Counter],2])/2 *
MArray[HumerusDraw[Counter],3] * MArray[RadiusDraw[Counter],4])^(.25)
  Counter <- Counter +1
}

ndiscard <- ceiling((100-CI)/200 * (nboots+1))

BootArray <- sort(BootArray)
ResultsTable[1] <- BootArray[1]
ResultsTable[2] <- BootArray[ndiscard+1]
if (ceiling(nboots/2) > nboots/2) ResultsTable[3] <- (BootArray[ceiling(nboots/2)] +
BootArray[ceiling(nboots/2)-1])/2
else ResultsTable[3] <- BootArray[nboots/2]
ResultsTable[4] <- BootArray[nboots-ndiscard]
ResultsTable[5] <- BootArray[nboots]

BootArray <- BootArray
ResultsTable <- ResultsTable
hist(BootArray, freq=FALSE)

ResultsTable

} # end of CompMaleBoot function

# CompMaleBoot (PpM,1000)

```

```

CompMaleAllBoot <- function(MArray, CI=95) {

N <- length(MArray[,1])
nboots <- N^4 * (N-1)/2 + N

BootArray <- matrix(0, nboots, 1)
ResultsTable <- matrix(0,5,1)
rownames(ResultsTable) <- c("Min", "CI LL", "Median", "CI UL", "Max")
FemurCounter <- 1
TibiaCounter1 <- 1
TibiaCounter2 <- 1

```

```

HumerusCounter <- 1
RadiusCounter <- 1

Counter <- 1
while (FemurCounter <= N) {
  HumerusCounter <- 1
  while (HumerusCounter <= N) {
    RadiusCounter <- 1
    while (RadiusCounter <= N) {
      TibiaCounter1 <- 1
      while (TibiaCounter1 <= N) {
        TibiaCounter2 <- TibiaCounter1
        while (TibiaCounter2 <= N) {
          BootArray[Counter] <- (MArray[FemurCounter,1] *
(MArray[TibiaCounter1,2]+MArray[TibiaCounter2,2])/2 * MArray[HumerusCounter,3] *
MArray[RadiusCounter,4])^(.25)
          TibiaCounter2 <- TibiaCounter2 + 1
          Counter <- Counter + 1
        } # closes the TibiaCounter2 loop
        TibiaCounter1 <- TibiaCounter1 + 1
      } # closes the TibiaCounter1 loop
      RadiusCounter <- RadiusCounter + 1
    } # closes the RadiusCounter loop
    HumerusCounter <- HumerusCounter + 1
  } # closes the HumerusCounter loop
  FemurCounter <- FemurCounter + 1
} # closes the FemurCounter loop

ndiscard <- ceiling((100-CI)/200 * (nboots+1))

BootArray <- sort(BootArray)
ResultsTable[1] <- BootArray[1]
ResultsTable[2] <- BootArray[ndiscard+1]
if (ceiling(nboots/2) > nboots/2) ResultsTable[3] <- (BootArray[ceiling(nboots/2)] +
BootArray[ceiling(nboots/2)-1])/2
else ResultsTable[3] <- BootArray[nboots/2]
ResultsTable[4] <- BootArray[nboots-ndiscard]
ResultsTable[5] <- BootArray[nboots]

BootArray <<- BootArray
ResultsTable <<- ResultsTable
hist(BootArray, freq=FALSE)

ResultsTable

} # end of CompMaleAllBoot function

CompMaleAllBoot(PpM)
ResultsTable <- log(ResultsTable,10)
PpMarray <- BootArray
ResultsTable

CompMaleAllBoot(PtsM)
ResultsTable <- log(ResultsTable,10)
PtsMarray <- BootArray
ResultsTable

CompMaleBoot(HsM,10000)
HsMarray <- BootArray
ResultsTable <- log(ResultsTable,10)
ResultsTable

```

RESAMPLING CODE: DIMORPHISM RATIO DISTRIBUTION USING BOOTSTRAP

```

CompMaleBootRatio <- function(MArray, FArray, nboots=2000, CI=95) {
# This function calculates bootstrapped ratios of one composite male divided by one

```

```

# complete female for the extant sample and generates probability distributions.

BootArray <- matrix(0, nboots, 1)
ResultsTable <- matrix(0,5,1)
rownames(ResultsTable) <- c("Min", "CI LL", "Median", "CI UL", "Max")
FemurDraw <- sample(1:length(MArray[,1]), nboots, replace=TRUE)
TibiaDraw1 <- sample(1:length(MArray[,1]), nboots, replace=TRUE)
TibiaDraw2 <- sample(1:length(MArray[,1]), nboots, replace=TRUE)
HumerusDraw <- sample(1:length(MArray[,1]), nboots, replace=TRUE)
RadiusDraw <- sample(1:length(MArray[,1]), nboots, replace=TRUE)
FemaleDraw <- sample(1:length(FArray[,1]), nboots, replace=TRUE)

Counter <- 1
while (Counter <= nboots) {
  BootArray[Counter] <- ((MArray[FemurDraw[Counter],1] *
(MArray[TibiaDraw1[Counter],2]+MArray[TibiaDraw2[Counter],2])/2 *
MArray[HumerusDraw[Counter],3] * MArray[RadiusDraw[Counter],4])^(.25))/
FArray[FemaleDraw[Counter]]
  Counter <- Counter +1
}

ndiscard <- ceiling((100-CI)/200 * (nboots+1))

BootArray <- sort(BootArray)
ResultsTable[1] <- BootArray[1]
ResultsTable[2] <- BootArray[ndiscard+1]
if (ceiling(nboots/2) > nboots/2) ResultsTable[3] <- (BootArray[ceiling(nboots/2)] +
BootArray[ceiling(nboots/2)-1])/2
else ResultsTable[3] <- BootArray[nboots/2]
ResultsTable[4] <- BootArray[nboots-ndiscard]
ResultsTable[5] <- BootArray[nboots]

RatioArray <- BootArray
ResultsTable <- ResultsTable
hist(RatioArray, freq=FALSE)

ResultsTable

} # end of CompMaleBootRatio function

```

RESAMPLING CODE: DIMORPHISM RATIO DISTRIBUTION USING EXACT RANDOMIZATION

```

CompMaleAllBootRatio <- function(MArray, FArray, CI=95) {
# This function calculates exact randomization ratios of one composite male divided by
# one complete female for the extant sample and generates probability distributions.

N <- length(MArray[,1])
nboots <- N^4 * (N-1)/2 + N

BootArray <- matrix(0, nboots, 1)
ResultsTable <- matrix(0,5,1)
rownames(ResultsTable) <- c("Min", "CI LL", "Median", "CI UL", "Max")
FemurCounter <- 1
TibiaCounter1 <- 1
TibiaCounter2 <- 1
HumerusCounter <- 1
RadiusCounter <- 1

Counter <- 1
while (FemurCounter <= N) {
  HumerusCounter <- 1
  while (HumerusCounter <= N) {
    RadiusCounter <- 1
    while (RadiusCounter <= N) {
      TibiaCounter1 <- 1

```

```

while (TibiaCounter1 <= N) {
  TibiaCounter2 <- TibiaCounter1
  while (TibiaCounter2 <= N) {
    BootArray[Counter] <- (MArray[FemurCounter,1] *
(MArray[TibiaCounter1,2]+MArray[TibiaCounter2,2])/2 * MArray[HumerusCounter,3] *
MArray[RadiusCounter,4])^(.25)
    TibiaCounter2 <- TibiaCounter2 + 1
    Counter <- Counter + 1
  } # closes the TibiaCounter2 loop
  TibiaCounter1 <- TibiaCounter1 + 1
} # closes the TibiaCounter1 loop
RadiusCounter <- RadiusCounter + 1
} # closes the RadiusCounter loop
HumerusCounter <- HumerusCounter + 1
} # closes the HumerusCounter loop
FemurCounter <- FemurCounter + 1
} # closes the FemurCounter loop

ndiscard <- ceiling((100-CI)/200 * (nboots+1))

BootArray <- sort(BootArray)

Nfem <- length(FArray)

RatioArray <- matrix(0, Nfem*nboots,1)

Counter <- 1
FemaleCounter <- 1
while (FemaleCounter <= Nfem) {
  BootCounter <- 1
  while (BootCounter <= nboots) {
    RatioArray[Counter] <- BootArray[BootCounter]/FArray[FemaleCounter]
    BootCounter <- BootCounter + 1
    Counter <- Counter + 1
  } # close the BootCounter loop
  FemaleCounter <- FemaleCounter + 1
} # close the FemaleCounter loop

ResultsTable[1] <- RatioArray[1]
ResultsTable[2] <- RatioArray[ndiscard+1]
if (ceiling(nboots/2) > nboots/2) ResultsTable[3] <- (RatioArray[ceiling(nboots/2)] +
RatioArray[ceiling(nboots/2)-1])/2
else ResultsTable[3] <- RatioArray[nboots/2]
ResultsTable[4] <- RatioArray[nboots-ndiscard]
ResultsTable[5] <- RatioArray[nboots]

RatioArray <<- RatioArray
ResultsTable <<- ResultsTable
hist(RatioArray, freq=FALSE)

ResultsTable

} # end of CompMaleAllBootRatio function

```

RESAMPLING CODE: INDEPENDENT CONTRASTS USING EXACT RANDOMIZATION

```

ExactContrasts <- function(Group1, Group2, Group3, Fossil, BranchLengths) {
# This function calculates all possible sets of three contrasts based on the fossil and
# one measurement from each of the three groups. This function will later be used in
# another function which draws randomly from male and female contrasts to analyze
# scaling of size and SSD.

ThreeContrasts <- function(T1, T2, T3, T4, branchlengths) {
  b1 <- branchlengths[1]
  b2 <- branchlengths[2]

```

```

b3 <- branchlengths[3]
b4 <- branchlengths[4]
b5 <- branchlengths[5]
b6 <- branchlengths[6]
Contrast <- function(tip1, tip2, branch1, branch2) {
  (tip1 - tip2)/sqrt(branch1 + branch2)
} # end of Contrast function
Node <- function(tip1, tip2, branch1, branch2) {
  ((tip1/branch1) + (tip2/branch2)) / (1/branch1 + 1/branch2)
} # end of Node function
Vbranch <- function(branch1, branch2, newbranch) {
  newbranch + 1 / (1/branch1 + 1/branch2)
} # end of Vbranch function
C1 <<- Contrast(T1, T2, b1, b2)
N1 <<- Node(T1, T2, b1, b2)
V1 <<- Vbranch(b1, b2, b3)
C2 <<- Contrast(N1, T3, V1, b4)
N2 <<- Node(N1, T3, V1, b4)
V2 <<- Vbranch(V1, b4, b5)
C3 <<- Contrast(N2, T4, V2, b6)
} # end of ThreeContrasts function

Group1Length <- length(Group1)
Group2Length <- length(Group2)
Group3Length <- length(Group3)

ContrastArray <- matrix(0, Group1Length * Group2Length * Group3Length, 3)

TotalCounter <- 1

Group1Counter <- 1
while (Group1Counter <= Group1Length) {
  Group2Counter <- 1
  while (Group2Counter <= Group2Length) {
    Group3Counter <- 1
    while (Group3Counter <= Group3Length) {
      ThreeContrasts(Group1[Group1Counter], Group2[Group2Counter],
Group3[Group3Counter], Fossil, BranchLengths)
      ContrastArray[TotalCounter,1] <- C1
      ContrastArray[TotalCounter,2] <- C2
      ContrastArray[TotalCounter,3] <- C3
      Group3Counter <- Group3Counter + 1
      TotalCounter <- TotalCounter + 1
    }
    Group2Counter <- Group2Counter + 1
  }
  Group1Counter <- Group1Counter + 1
}

ContrastArray <<- ContrastArray

} # end of ExactContrasts function

```

RESAMPLING CODE: INDEPENDENT CONTRASTS USING BOOTSTRAP

```

BootContrasts <- function(Group1, Group2, Group3, Fossil, BranchLengths, nboots=2000,
CI=95) {
# This function calculates all possible sets of three contrasts based on the fossil and
# one measurement from each of the three groups. This function will later be used in
# another function which draws randomly from male and female contrasts to analyze
# scaling of size and SSD. Group2 MUST be Pan troglodytes troglodytes bootstraps.

ThreeContrasts <- function(T1, T2, T3, T4, branchlengths) {
  b1 <- branchlengths[1]
  b2 <- branchlengths[2]
  b3 <- branchlengths[3]
  b4 <- branchlengths[4]

```

```

b5 <- branchlengths[5]
b6 <- branchlengths[6]
Contrast <- function(tip1, tip2, branch1, branch2) {
  (tip1 - tip2)/sqrt(branch1 + branch2)
} # end of Contrast function
Node <- function(tip1, tip2, branch1, branch2) {
  ((tip1/branch1) + (tip2/branch2)) / (1/branch1 + 1/branch2)
} # end of Node function
Vbranch <- function(branch1, branch2, newbranch) {
  newbranch + 1 / (1/branch1 + 1/branch2)
} # end of Vbranch function
C1 <- Contrast(T1, T2, b1, b2)
N1 <- Node(T1, T2, b1, b2)
V1 <- Vbranch(b1, b2, b3)
C2 <- Contrast(N1, T3, V1, b4)
N2 <- Node(N1, T3, V1, b4)
V2 <- Vbranch(V1, b4, b5)
C3 <- Contrast(N2, T4, V2, b6)
} # end of ThreeContrasts function

Group1Length <- length(Group1)
Group2Length <- length(Group2)
Group3Length <- length(Group3)

Group1Draw <- sample(1:Group1Length, nboots, replace=TRUE)
Group2Draw <- sample(1:Group2Length, nboots, replace=FALSE)
Group3Draw <- sample(1:Group3Length, nboots, replace=TRUE)

ContrastArray <- matrix(0, nboots, 3)

TotalCounter <- 1

Counter <- 1
while (Counter <= nboots) {
  ThreeContrasts(Group1[Group1Draw[Counter]], Group2[Group2Draw[Counter]],
Group3[Group3Draw[Counter]], Fossil, BranchLengths)
  ContrastArray[Counter,1] <- C1
  ContrastArray[Counter,2] <- C2
  ContrastArray[Counter,3] <- C3
  Counter <- Counter +1
}

ContrastArray <- ContrastArray
SortedC3Array <- sort(ContrastArray[,3])

ResultsTable <- matrix(0,5,1)
rownames(ResultsTable) <- c("Min", "CI LL", "Median", "CI UL", "Max")
ndiscard <- ceiling((100-CI)/200 * (nboots+1))

ResultsTable[1] <- SortedC3Array[1]
ResultsTable[2] <- SortedC3Array[ndiscard+1]
if (ceiling(nboots/2) > nboots/2) ResultsTable[3] <- (SortedC3Array[ceiling(nboots/2)] +
SortedC3Array[ceiling(nboots/2)-1])/2
else ResultsTable[3] <- SortedC3Array[nboots/2]
ResultsTable[4] <- SortedC3Array[nboots-ndiscard]
ResultsTable[5] <- SortedC3Array[nboots]

ResultsTable <- ResultsTable

ResultsTable

} # end of ExactContrasts function

```

RESAMPLING CODE: INDEPENDENT CONTRASTS SUMMARY

```
RandResults <- function(FArray, MArray, nboots=2000, CI=95) {
```

```

ContrastsArray <- matrix(0, nboots, 9)
CountsTable <- matrix(0,3,9)
Fcontrasts <- sample(1:length(FArray[,1]), nboots, replace=TRUE)
Mcontrasts <- sample(1:length(MArray[,1]), nboots, replace=TRUE)

Counter <- 1
while (Counter <= nboots) {
  ContrastsArray[Counter,1] <- FArray[Fcontrasts[Counter],1] # C1 - females
  ContrastsArray[Counter,2] <- FArray[Fcontrasts[Counter],2] # C2 - females
  ContrastsArray[Counter,3] <- FArray[Fcontrasts[Counter],3] # C3 - females
  ContrastsArray[Counter,4] <- MArray[Mcontrasts[Counter],1] # C1 - males
  ContrastsArray[Counter,5] <- MArray[Mcontrasts[Counter],2] # C2 - males
  ContrastsArray[Counter,6] <- MArray[Mcontrasts[Counter],3] # C3 - males
  ContrastsArray[Counter,7] <- MArray[Mcontrasts[Counter],1] -
FArray[Fcontrasts[Counter],1] # C1 - SSD
  ContrastsArray[Counter,8] <- MArray[Mcontrasts[Counter],2] -
FArray[Fcontrasts[Counter],2] # C2 - SSD
  ContrastsArray[Counter,9] <- MArray[Mcontrasts[Counter],3] -
FArray[Fcontrasts[Counter],3] # C3 - SSD

  # C1 summaries
  if (ContrastsArray[Counter,1]*ContrastsArray[Counter,7] == 0) CountsTable[1,1] <-
CountsTable[1,1] + 1
  else if (ContrastsArray[Counter,1]*ContrastsArray[Counter,7] > 0) CountsTable[2,1] <-
CountsTable[2,1] + 1
  else CountsTable[3,1] <- CountsTable[3,1] + 1

  if (ContrastsArray[Counter,4]*ContrastsArray[Counter,7] == 0) CountsTable[1,2] <-
CountsTable[1,2] + 1
  else if (ContrastsArray[Counter,4]*ContrastsArray[Counter,7] > 0) CountsTable[2,2] <-
CountsTable[2,2] + 1
  else CountsTable[3,2] <- CountsTable[3,2] + 1

  if (ContrastsArray[Counter,1]*ContrastsArray[Counter,4] == 0) CountsTable[1,3] <-
CountsTable[1,3] + 1
  else if (ContrastsArray[Counter,1]*ContrastsArray[Counter,4] > 0) CountsTable[2,3] <-
CountsTable[2,3] + 1
  else CountsTable[3,3] <- CountsTable[3,3] + 1

  # C2 summaries
  if (ContrastsArray[Counter,2]*ContrastsArray[Counter,8] == 0) CountsTable[1,4] <-
CountsTable[1,4] + 1
  else if (ContrastsArray[Counter,2]*ContrastsArray[Counter,8] > 0) CountsTable[2,4] <-
CountsTable[2,4] + 1
  else CountsTable[3,4] <- CountsTable[3,4] + 1

  if (ContrastsArray[Counter,5]*ContrastsArray[Counter,8] == 0) CountsTable[1,5] <-
CountsTable[1,5] + 1
  else if (ContrastsArray[Counter,5]*ContrastsArray[Counter,8] > 0) CountsTable[2,5] <-
CountsTable[2,5] + 1
  else CountsTable[3,5] <- CountsTable[3,5] + 1

  if (ContrastsArray[Counter,2]*ContrastsArray[Counter,5] == 0) CountsTable[1,6] <-
CountsTable[1,6] + 1
  else if (ContrastsArray[Counter,2]*ContrastsArray[Counter,5] > 0) CountsTable[2,6] <-
CountsTable[2,6] + 1
  else CountsTable[3,6] <- CountsTable[3,6] + 1

  # C3 summaries
  if (ContrastsArray[Counter,3]*ContrastsArray[Counter,9] == 0) CountsTable[1,7] <-
CountsTable[1,7] + 1
  else if (ContrastsArray[Counter,3]*ContrastsArray[Counter,9] > 0) CountsTable[2,7] <-
CountsTable[2,7] + 1
  else CountsTable[3,7] <- CountsTable[3,7] + 1
}

```

```

    if (ContrastsArray[Counter,6]*ContrastsArray[Counter,9] == 0) CountsTable[1,8] <-
CountsTable[1,8] + 1
    else if (ContrastsArray[Counter,6]*ContrastsArray[Counter,9] > 0) CountsTable[2,8] <-
CountsTable[2,8] + 1
    else CountsTable[3,8] <- CountsTable[3,8] + 1

    if (ContrastsArray[Counter,3]*ContrastsArray[Counter,6] == 0) CountsTable[1,9] <-
CountsTable[1,9] + 1
    else if (ContrastsArray[Counter,3]*ContrastsArray[Counter,6] > 0) CountsTable[2,9] <-
CountsTable[2,9] + 1
    else CountsTable[3,9] <- CountsTable[3,9] + 1

    Counter <- Counter +1
}

CIArray <- matrix(0,5,9)
rownames(CIArray) <- c("Min", "95% LL", "Median", "95% UL", "Max")
colnames(CIArray) <- c("C1.F", "C2.F", "C3.F", "C1.M", "C2.M", "C3.M", "C1.SSD",
"C2.SSD", "C3.SSD")

ndiscard <- ceiling((100-CI)/200 * (nboots+1))

ColCounter <- 1
while (ColCounter <= 9) {
  TempArray <- sort(ContrastsArray[,ColCounter])
  CIArray[1,ColCounter] <- TempArray[1]
  CIArray[2,ColCounter] <- TempArray[ndiscard+1]
  if (ceiling(nboots/2) > nboots/2) CIArray[3,ColCounter] <-
(TempArray[ceiling(nboots/2)] + TempArray[ceiling(nboots/2)-1])/2
  else CIArray[3,ColCounter] <- TempArray[nboots/2]
  CIArray[4,ColCounter] <- TempArray[nboots-ndiscard]
  CIArray[5,ColCounter] <- TempArray[nboots]
  ColCounter <- ColCounter + 1
}

rownames(CountsTable) <- c("0", "+", "-")
colnames(CountsTable) <- c("C1.F.SSD", "C1.M.SSD", "C1.F.M", "C2.F.SSD", "C2.M.SSD",
"C2.F.M", "C3.F.SSD", "C3.M.SSD", "C3.F.M")

CountsTable <<- CountsTable
CIArray <<- CIArray
ContrastsArray <<- ContrastsArray

CountsTable

} # end of RandResults function

```

Appendix G: Comparison of Linear Models

Comparisons of linear models for the analysis in Chapter 4 are presented in the next several pages. Abbreviations are as follows: F, full sample; R, reduced sample; MS, mating system; Arb, arboreality; Ter, terrestriality. Cells above the diagonal are F scores for comparisons of complete (top row) and reduced (left column) linear models. Cells below the diagonal contain p-values for those same comparisons. In some cases no comparisons are made, either because the row variables are not a subset of the column variables, or because a particular variable has no values for that clade (*e.g.*, all platyrrhines are arboreal, so arboreality is not included in the platyrrhine analysis because it contains no additional information).

| Group | Reduced Model Variables | log F, MS, Arb, Ter | | | log F, MS, Arb, Ter | | | log F, MS, Arb, Ter | | | log F, MS, Arb, Ter | | | log F, MS, Arb, Ter | | |
|----------------|-------------------------|---------------------|---------------------|--------------|---------------------|---------------------|--------------|---------------------|--------------|---------------------|---------------------|---------------------|--------------|---------------------|--------------|--|
| | | MS, Arb, Ter | log F, MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | log F, MS, Arb, Ter | MS, Arb, Ter | log F, MS, Arb, Ter | MS, Arb, Ter | log F, MS, Arb, Ter | MS, Arb, Ter | log F, MS, Arb, Ter | MS, Arb, Ter | log F, MS, Arb, Ter | MS, Arb, Ter | |
| All Primates F | log F, MS, Arb, Ter | 5.3 | 1.3 | 4.3 | 7.1 | 6.0 | 5.7 | 0.9 | 2.9 | 0.9 | 5.8 | 2.9 | 4.9 | 4.6 | 4.3 | |
| All Primates F | log F, MS, Arb | 0.023 | | 3.2 | | 6.3 | | | 0.5 | | 5.9 | 1.6 | | 4.3 | | |
| All Primates F | log F, MS, Ter | 0.250 | | 7.2 | | | 7.9 | | | 0.6 | 7.3 | 3.6 | | | 5.3 | |
| All Primates F | log F, MS | 0.015 | | | | | | | | | 7.2 | 0.1 | | | | |
| All Primates F | log F, Arb, Ter | 0.001 | | | | 3.7 | 2.8 | | | | 4.3 | | 0.5 | 2.0 | 1.5 | |
| All Primates F | log F, Arb | 0.001 | | | 0.056 | | | | | | 4.8 | | | 0.2 | | |
| All Primates F | log F, Ter | 0.001 | 0.000 | | 0.096 | | | | | | 5.7 | | | | 0.1 | |
| All Primates F | MS, Arb, Ter | 0.342 | | | | | | | 4.9 | 1.0 | | 3.9 | 6.9 | 5.8 | 5.5 | |
| All Primates F | MS, Arb | 0.058 | | | | | | 0.029 | | | | 2.8 | | 6.2 | | |
| All Primates F | MS, Ter | 0.391 | 0.456 | | | | | 0.324 | | | | 6.7 | | | 7.7 | |
| All Primates F | log F | 0.000 | 0.001 | 0.001 | 0.015 | 0.029 | 0.018 | | | | | | | | | |
| All Primates F | MS | 0.037 | 0.197 | 0.763 | | | | 0.023 | 0.096 | 0.010 | | | | | | |
| All Primates F | Arb, Ter | 0.003 | | | 0.485 | | | 0.001 | | | | | | 3.5 | 2.5 | |
| All Primates F | Arb | 0.001 | | | 0.142 | 0.622 | | 0.001 | 0.002 | | | | 0.064 | | | |
| All Primates F | Ter | 0.002 | 0.001 | | 0.233 | | 0.710 | 0.001 | | 0.001 | | | 0.119 | | | |
| All Primates R | log F, MS, Arb, Ter | | 3.0 | 5.0 | 4.8 | 2.5 | 2.7 | 3.9 | 0.0 | 1.5 | 2.7 | 4.2 | 3.5 | 1.7 | 2.1 | |
| All Primates R | log F, MS, Arb | 0.088 | | | 6.6 | | 2.6 | | | 0.1 | | 4.5 | 3.7 | 1.8 | | |
| All Primates R | log F, MS, Ter | 0.026 | | | | | | 3.2 | | | 0.4 | 3.8 | 2.7 | | 2.5 | |
| All Primates R | log F, MS | 0.009 | 0.011 | 0.035 | | | | | | | | 3.4 | 0.8 | | | |
| All Primates R | log F, Arb, Ter | 0.085 | | | | | 3.1 | 6.5 | | | | 5.8 | | 0.2 | 1.7 | |
| All Primates R | log F, Arb | 0.046 | 0.079 | | 0.080 | | | | | | 8.3 | | | 0.3 | | |
| All Primates R | log F, Ter | 0.011 | 0.043 | | 0.012 | | | | | | 4.9 | | | | 1.0 | |
| All Primates R | MS, Arb, Ter | 0.934 | | | | | | | | | | 5.3 | 2.6 | 2.9 | 4.3 | |
| All Primates R | MS, Arb | 0.225 | 0.807 | | | | | | | 3.0 | 5.4 | | 7.5 | 2.7 | | |
| All Primates R | MS, Ter | 0.071 | 0.553 | | | | | | 0.084 | | | 5.0 | | | 3.6 | |
| All Primates R | log F | 0.003 | 0.004 | 0.011 | 0.037 | 0.004 | 0.005 | 0.029 | | | | | | | | |
| All Primates R | MS | 0.017 | 0.026 | 0.072 | 0.373 | | | | 0.006 | 0.007 | 0.026 | | | | | |
| All Primates R | Arb, Ter | 0.164 | | | 0.689 | | | | 0.077 | | | | | 3.3 | 7.4 | |
| All Primates R | Arb | 0.079 | 0.143 | | 0.182 | 0.561 | | | 0.039 | 0.068 | | | 0.071 | | | |
| All Primates R | Ter | 0.016 | 0.063 | | 0.025 | | 0.314 | 0.006 | | 0.030 | | | 0.007 | | | |

Table G.2. F- and p-values for comparisons of linear models: All primates, phylogenetic linear models (Best Branches).

| Group | Reduced Model Variables | log F, log F, log F, MS, Arb, MS, Ter | | | log F, log F, log F, MS, Arb, MS, Ter | | | log F, log F, log F, MS, Arb, MS, Ter | | | log F, log F, log F, MS, Arb, MS, Ter | | | | |
|----------------|-------------------------|---------------------------------------|----------------|----------------|---------------------------------------|----------------|----------------|---------------------------------------|----------------|----------------|---------------------------------------|----------------|----------------|-----|-----|
| | | log F, MS, Arb, Ter | log F, MS, Arb | log F, MS, Ter | log F, MS, Arb, Ter | log F, MS, Arb | log F, MS, Ter | log F, MS, Arb, Ter | log F, MS, Arb | log F, MS, Ter | log F, MS, Arb, Ter | log F, MS, Arb | log F, MS, Ter | | |
| Strepsirhini F | log F, MS, Arb, Ter | | | | | | | | | | | | | | |
| Strepsirhini F | log F, MS, Arb | | | 0.0 | | 0.2 | | | | 0.0 | | | | 0.1 | 0.0 |
| Strepsirhini F | log F, MS, Ter | | | 0.0 | | | 0.2 | | | 0.0 | | | | | 0.1 |
| Strepsirhini F | log F, MS | | | | | | | | | | | | | | |
| Strepsirhini F | log F, Arb, Ter | 0.912 | 0.912 | | | | | | | | | | | | |
| Strepsirhini F | log F, Arb | 0.837 | | | | | | | | | | | | 0.1 | |
| Strepsirhini F | log F, Ter | | 0.837 | | | | | | | 0.0 | | | | 0.1 | |
| Strepsirhini F | MS, Arb, Ter | | | | | | | | | | | | | | |
| Strepsirhini F | MS, Arb | 0.936 | | | | | | | | | | | | | |
| Strepsirhini F | MS, Ter | | 0.936 | | | | | | | | | | | 0.2 | |
| Strepsirhini F | log F | 0.940 | 0.940 | 0.822 | | 0.839 | 0.839 | | | | | | | | 0.2 |
| Strepsirhini F | MS | 0.991 | 0.991 | 0.940 | | | | | 0.914 | 0.914 | | | | | |
| Strepsirhini F | Arb, Ter | | | | | | | | | | | | | | |
| Strepsirhini F | Arb | 0.930 | | | | 0.765 | | | 0.800 | | | | | | |
| Strepsirhini F | Ter | | 0.930 | | | | 0.765 | | 0.800 | | | | | | |
| Strepsirhini R | log F, MS, Arb, Ter | | | | | | | | | | | | | | |
| Strepsirhini R | log F, MS, Arb | | | 0.0 | | 4.1 | | | 0.2 | | | | | 3.1 | |
| Strepsirhini R | log F, MS, Ter | | | 0.0 | | | 4.1 | | 0.2 | | | | | | 3.1 |
| Strepsirhini R | log F, MS | | | | | | | | | | | | | | |
| Strepsirhini R | log F, Arb, Ter | 0.914 | 0.914 | | | | | | | | | | | | |
| Strepsirhini R | log F, Arb | 0.028 | | | | | | | | | | | | 1.0 | |
| Strepsirhini R | log F, Ter | | 0.028 | | | | | | | 0.0 | | | | | 1.0 |
| Strepsirhini R | MS, Arb, Ter | | | | | | | | | | | | | | |
| Strepsirhini R | MS, Arb | 0.678 | | | | | | | | | | | | | |
| Strepsirhini R | MS, Ter | | 0.678 | | | | | | | | | | | | |
| Strepsirhini R | log F | 0.064 | 0.064 | 0.025 | | 0.947 | 0.947 | | | | | | | | |
| Strepsirhini R | MS | 0.909 | 0.909 | 0.669 | | | | | 0.901 | 0.901 | | | | | |
| Strepsirhini R | Arb, Ter | | | | | | | | | | | | | | |
| Strepsirhini R | Arb | 0.042 | | | | 0.325 | | | 0.017 | | | | | | |
| Strepsirhini R | Ter | | 0.042 | | | | 0.325 | | 0.017 | | | | | | |

Table G.3. F- and p-values for comparisons of linear models: Strepsirhini, traditional linear models.

| Group | Reduced Model Variables | log F, log F, log F, MS, Arb, MS, Ter | | | log F, log F, log F, MS, Arb, MS, Ter | | | log F, log F, log F, MS, Arb, MS, Ter | | | log F, log F, log F, MS, Arb, MS, Ter | | |
|----------------|-------------------------|---------------------------------------|----------------|----------------|---------------------------------------|----------------|----------------|---------------------------------------|----------------|----------------|---------------------------------------|----------------|----------------|
| | | log F, MS, Arb, Ter | log F, MS, Arb | log F, MS, Ter | log F, MS, Arb, Ter | log F, MS, Arb | log F, MS, Ter | log F, MS, Arb, Ter | log F, MS, Arb | log F, MS, Ter | log F, MS, Arb, Ter | log F, MS, Arb | log F, MS, Ter |
| Strepsirhini F | log F, MS, Arb, Ter | | | | | | | | | | | | |
| Strepsirhini F | log F, MS, Arb | | | 0.2 | | 0.6 | | | | 0.1 | | | 0.4 |
| Strepsirhini F | log F, MS, Ter | | | 0.2 | | 0.6 | | | | 0.1 | | | 0.4 |
| Strepsirhini F | log F, MS | | | | | | | | | | | | |
| Strepsirhini F | log F, Arb, Ter | 0.655 | 0.655 | | | | | | | | | | |
| Strepsirhini F | log F, Arb | 0.554 | | | | | | | | | | | |
| Strepsirhini F | log F, Ter | | 0.554 | | | | | | | 0.1 | | | 0.1 |
| Strepsirhini F | MS, Arb, Ter | | | | | | | | | | | | |
| Strepsirhini F | MS, Arb | 0.811 | | | | | | | | | | | |
| Strepsirhini F | MS, Ter | | 0.811 | | | | | | | | | | |
| Strepsirhini F | log F | 0.727 | 0.727 | 0.572 | | 0.731 | 0.731 | | | | | | |
| Strepsirhini F | MS | 0.873 | 0.873 | 0.791 | | | | | 0.643 | 0.643 | | | |
| Strepsirhini F | Arb, Ter | | | | | | | | | | | | |
| Strepsirhini F | Arb | 0.741 | | | | 0.811 | | | 0.548 | | | | |
| Strepsirhini F | Ter | | 0.741 | | | | 0.811 | | | 0.548 | | | |
| Strepsirhini R | log F, MS, Arb, Ter | | | | | | | | | | | | |
| Strepsirhini R | log F, MS, Arb | | | | 0.0 | | 2.0 | | 0.0 | | | | 1.4 |
| Strepsirhini R | log F, MS, Ter | | | | 0.0 | | | 2.0 | | 0.0 | | | 1.4 |
| Strepsirhini R | log F, MS | 0.875 | 0.875 | | | | | | | 2.1 | 0.0 | | |
| Strepsirhini R | log F, Arb, Ter | | | | | | | | | | | | |
| Strepsirhini R | log F, Arb | 0.153 | | | | | | | | 0.0 | | | 0.1 |
| Strepsirhini R | log F, Ter | | 0.153 | | | | | | | 0.0 | | | 0.1 |
| Strepsirhini R | MS, Arb, Ter | | | | | | | | | | | | |
| Strepsirhini R | MS, Arb | 0.862 | | | | | | | | | | | |
| Strepsirhini R | MS, Ter | | 0.862 | | | | | | | | | | |
| Strepsirhini R | log F | 0.280 | 0.280 | 0.144 | | 0.905 | 0.905 | | | | | | 2.1 |
| Strepsirhini R | MS | 0.973 | 0.973 | 0.863 | | | | | 0.876 | 0.876 | | | |
| Strepsirhini R | Arb, Ter | | | | | | | | | | | | |
| Strepsirhini R | Arb | 0.273 | | | | 0.773 | | | 0.140 | | | | |
| Strepsirhini R | Ter | | 0.273 | | | | 0.773 | | | 0.140 | | | |

Table G.4. F- and p-values for comparisons of linear models: Strepsirhini, phylogenetic linear models (Best Branches).

| Group | Reduced Model Variables | log F, MS, Arb, Ter | | | log F, MS, Arb, Ter | | |
|--------------|-------------------------|---------------------|--------------|--------------|---------------------|--------------|--------------|---------------------|--------------|--------------|---------------------|--------------|--------------|---------------------|--------------|--|
| | | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | |
| Haplorhini F | log F, MS, Arb, Ter | 14.9 | 13.0 | 26.1 | 30.5 | 29.1 | 23.7 | 0.0 | 7.8 | 6.8 | 31.0 | 20.0 | 28.3 | 33.5 | 25.2 | |
| Haplorhini F | log F, MS, Arb | 0.000 | | 34.4 | | 33.4 | | | 0.6 | | 33.6 | 20.8 | | 36.6 | | |
| Haplorhini F | log F, MS, Ter | 0.000 | | 36.6 | | | 27.0 | | | 0.5 | 34.5 | 21.9 | | | 27.3 | |
| Haplorhini F | log F, MS | 0.000 | 0.000 | | | | | | | | 27.6 | 5.9 | | | | |
| Haplorhini F | log F, Arb, Ter | 0.000 | | | | 19.5 | 7.3 | | | | 23.3 | | 17.6 | 27.0 | 14.7 | |
| Haplorhini F | log F, Arb | 0.000 | 0.000 | 0.000 | 0.000 | | | | | | 24.4 | | | 31.1 | | |
| Haplorhini F | log F, Ter | 0.000 | 0.000 | | 0.007 | | | | | | 37.8 | | | | 21.2 | |
| Haplorhini F | MS, Arb, Ter | 0.928 | | | | | | | 15.7 | 13.6 | | 30.1 | 42.6 | 44.9 | 33.8 | |
| Haplorhini F | MS, Arb | 0.001 | 0.421 | | | | | 0.000 | | | | 40.9 | | 54.8 | | |
| Haplorhini F | MS, Ter | 0.002 | 0.495 | | | | | 0.000 | | | | 43.4 | | | 40.8 | |
| Haplorhini F | log F | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | | | | | | | | | |
| Haplorhini F | MS | 0.000 | 0.000 | 0.016 | 0.000 | | | 0.000 | 0.000 | 0.000 | | | | | | |
| Haplorhini F | Arb, Ter | 0.000 | | | 0.000 | | | 0.000 | 0.000 | 0.000 | | | | 33.2 | 10.7 | |
| Haplorhini F | Arb | 0.000 | 0.000 | | 0.000 | 0.000 | | 0.000 | 0.000 | 0.000 | | | 0.000 | | | |
| Haplorhini F | Ter | 0.000 | 0.000 | | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | | | 0.001 | | | |
| Haplorhini R | log F, MS, Arb, Ter | | 11.2 | 10.3 | 18.6 | 22.9 | 18.0 | 0.1 | 5.7 | 5.2 | 22.4 | 13.8 | 19.2 | 23.0 | 17.4 | |
| Haplorhini R | log F, MS, Arb | 0.001 | | 23.9 | | 24.6 | | | 0.1 | | 24.1 | 13.8 | | 24.8 | | |
| Haplorhini R | log F, MS, Ter | 0.002 | | 24.9 | | | 20.3 | | | 0.1 | 24.5 | 14.4 | | | 18.3 | |
| Haplorhini R | log F, MS | 0.000 | 0.000 | | | | | | | | 20.3 | 3.2 | | | | |
| Haplorhini R | log F, Arb, Ter | 0.000 | | | | 13.7 | 5.9 | | | | 16.1 | | 8.6 | 16.9 | 8.6 | |
| Haplorhini R | log F, Arb | 0.000 | 0.000 | | 0.000 | | | | | | 16.6 | | | 18.2 | | |
| Haplorhini R | log F, Ter | 0.000 | 0.000 | | 0.016 | | | | | | 25.1 | | | | 10.9 | |
| Haplorhini R | MS, Arb, Ter | 0.736 | | | | | | | 11.4 | 10.3 | | 20.7 | 28.9 | 30.9 | 23.3 | |
| Haplorhini R | MS, Arb | 0.004 | 0.716 | | | | | 0.001 | | | | 27.7 | | 37.4 | | |
| Haplorhini R | MS, Ter | 0.007 | 0.813 | | | | | 0.002 | | | | 28.9 | | | 27.6 | |
| Haplorhini R | log F | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | | | | | | | | | |
| Haplorhini R | MS | 0.000 | 0.000 | 0.078 | | | | 0.000 | 0.000 | 0.000 | | | | | | |
| Haplorhini R | Arb, Ter | 0.000 | | | 0.004 | | | 0.000 | 0.000 | 0.000 | | | | 23.8 | 8.2 | |
| Haplorhini R | Arb | 0.000 | 0.000 | | 0.000 | 0.000 | | 0.000 | 0.000 | 0.000 | | | 0.000 | | | |
| Haplorhini R | Ter | 0.000 | 0.000 | | 0.000 | 0.000 | 0.001 | 0.000 | 0.000 | 0.000 | | | 0.005 | | | |

Table G.5. F- and p-values for comparisons of linear models: Haplorhini, traditional linear models.

| Group | Reduced Model Variables | log F, MS, Arb, Ter | | |
|--------------|-------------------------|---------------------|--------------|--------------|---------------------|--------------|--------------|---------------------|--------------|--------------|---------------------|--------------|--------------|---------------------|--------------|--------------|---------------------|--------------|--------------|
| | | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter |
| Haplorhini F | log F, MS, Arb, Ter | 5.1 | 1.7 | 4.2 | 6.4 | 5.5 | 5.3 | 1.3 | 2.9 | 1.2 | 5.3 | 2.8 | 4.4 | 4.2 | 4.0 | | | | |
| Haplorhini F | log F, MS, Arb | 0.026 | | 3.2 | | 5.6 | | | 0.6 | | 5.3 | 1.6 | | 3.8 | | | | | |
| Haplorhini F | log F, MS, Ter | 0.197 | | 6.6 | | | 7.1 | | | 0.6 | 6.5 | 3.3 | | | 4.7 | | | | |
| Haplorhini F | log F, MS | 0.017 | 0.011 | | | | | | | | 6.2 | 0.1 | | | | | | | |
| Haplorhini F | log F, Arb, Ter | 0.002 | | | | 3.5 | 2.9 | | | | 3.9 | | 0.4 | 1.8 | 1.5 | | | | |
| Haplorhini F | log F, Arb | 0.001 | 0.004 | | 0.065 | | | | | | 4.4 | | | 0.1 | | | | | |
| Haplorhini F | log F, Ter | 0.002 | 0.001 | | 0.090 | | | | | | 4.9 | | | | 0.0 | | | | |
| Haplorhini F | MS, Arb, Ter | 0.262 | | | | | | | 4.4 | 1.1 | | | 3.6 | 6.0 | 5.1 | 4.9 | | | |
| Haplorhini F | MS, Arb | 0.061 | 0.427 | | | | | 0.037 | | | | | 2.6 | | 5.3 | | | | |
| Haplorhini F | MS, Ter | 0.315 | 0.423 | | | | | 0.305 | | | | | 6.0 | | | 6.8 | | | |
| Haplorhini F | log F | 0.000 | 0.000 | 0.003 | 0.021 | 0.038 | 0.028 | | | | | | | | | | | | |
| Haplorhini F | MS | 0.042 | 0.200 | 0.038 | 0.800 | | | 0.031 | 0.107 | 0.015 | | | | | | | | | |
| Haplorhini F | Arb, Ter | 0.005 | | | 0.525 | | | 0.003 | | | | | | 3.2 | 2.5 | | | | |
| Haplorhini F | Arb | 0.003 | 0.012 | | 0.169 | 0.722 | | 0.002 | 0.006 | | | | 0.076 | | | | | | |
| Haplorhini F | Ter | 0.004 | 0.003 | | 0.233 | | 0.865 | 0.003 | | 0.001 | | | 0.113 | | | | | | |
| Haplorhini R | log F, MS, Arb, Ter | 2.8 | 5.2 | 4.5 | 2.3 | 2.5 | 3.6 | 0.1 | 1.4 | 2.7 | 3.7 | 3.2 | 1.5 | 1.9 | 3.0 | | | | |
| Haplorhini R | log F, MS, Arb | 0.096 | | 6.1 | | 2.4 | | | 0.0 | | 4.0 | 3.4 | | 1.6 | | | | | |
| Haplorhini R | log F, MS, Ter | 0.024 | | 3.7 | | | 2.7 | | | 0.2 | 3.1 | 2.2 | | | 2.1 | | | | |
| Haplorhini R | log F, MS | 0.013 | 0.015 | | | | | | | | 2.8 | 0.6 | | | | | | | |
| Haplorhini R | log F, Arb, Ter | 0.105 | | | | 3.0 | 6.1 | | | | 5.0 | | 0.0 | 1.6 | 3.6 | | | | |
| Haplorhini R | log F, Arb | 0.060 | 0.099 | | 0.088 | | | | | | 7.0 | | | 0.2 | | | | | |
| Haplorhini R | log F, Ter | 0.015 | 0.071 | | 0.015 | | | | | | 3.8 | | | | 1.0 | | | | |
| Haplorhini R | MS, Arb, Ter | 0.755 | | | | | | | | | | | 4.8 | 2.3 | 4.0 | | | | |
| Haplorhini R | MS, Arb | 0.248 | 0.936 | | | | | | 2.7 | 5.4 | | | 6.8 | 2.5 | | | | | |
| Haplorhini R | MS, Ter | 0.071 | 0.668 | | | | | 0.100 | | | | 4.1 | | | 3.1 | | | | |
| Haplorhini R | log F | 0.007 | 0.010 | 0.029 | 0.068 | 0.009 | 0.054 | | | | | | | | | | | | |
| Haplorhini R | MS | 0.025 | 0.037 | 0.121 | 0.430 | | | 0.010 | 0.010 | 0.044 | | | | | | | | | |
| Haplorhini R | Arb, Ter | 0.208 | | | 0.882 | | | 0.107 | | | | | | 3.1 | 7.2 | | | | |
| Haplorhini R | Arb | 0.107 | 0.185 | | 0.213 | 0.680 | | 0.057 | 0.089 | | | | 0.079 | | | | | | |
| Haplorhini R | Ter | 0.022 | 0.098 | | 0.031 | | 0.317 | 0.010 | | 0.047 | | | 0.008 | | | | | | |

Table G.6. F- and p-values for comparisons of linear models: Haplorhini, phylogenetic linear models (Best Branches).

| Group | Reduced Model Variables | log F, log F, log F, MS, Arb, MS, Ter | | | log F, log F, log F, MS, Arb, MS, Ter | | | log F, log F, log F, MS, Arb, MS, Ter | | | log F, log F, log F, MS, Arb, MS, Ter | | |
|--------------|-------------------------|---------------------------------------|--------------|--------------|---------------------------------------|--------------|--------------|---------------------------------------|--------------|--------------|---------------------------------------|--------------|--|
| | | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | |
| Platyrhini F | log F, MS, Arb, Ter | | | | | | | | | | | | |
| Platyrhini F | log F, MS, Arb | | | | | | | | | | | | |
| Platyrhini F | log F, MS, Ter | | | 1.6 | | | | 0.5 | | 12.2 | 1.2 | 20.5 | |
| Platyrhini F | log F, MS | | | 0.212 | | | | | | 17.3 | 0.8 | | |
| Platyrhini F | log F, Arb, Ter | | | | | | | | | | | | |
| Platyrhini F | log F, Arb | | | | | | | | | | | | |
| Platyrhini F | log F, Ter | | | 0.000 | | | | | | 1.6 | | 18.0 | |
| Platyrhini F | MS, Arb, Ter | | | | | | | | | | | | |
| Platyrhini F | MS, Arb | | | | | | | | | | | | |
| Platyrhini F | MS, Ter | | | 0.503 | | | | | | | 1.9 | 30.8 | |
| Platyrhini F | log F | | | 0.000 | | | 0.207 | | | | | | |
| Platyrhini F | MS | | | 0.315 | | | | 0.171 | | | | | |
| Platyrhini F | Arb, Ter | | | | | | | | | | | | |
| Platyrhini F | Arb | | | | | | | | | | | | |
| Platyrhini F | Ter | | | 0.000 | | | 0.000 | | | | | | |
| Platyrhini R | log F, MS, Arb, Ter | | | | | | | | | | | | |
| Platyrhini R | log F, MS, Arb | | | | | | | | | | | | |
| Platyrhini R | log F, MS, Ter | | | | | 1.5 | | 0.8 | | 8.6 | 1.4 | 12.6 | |
| Platyrhini R | log F, MS | | | 0.233 | | | | | | 12.0 | 1.3 | | |
| Platyrhini R | log F, Arb, Ter | | | | | | | | | | | | |
| Platyrhini R | log F, Arb | | | | | | | | | | | | |
| Platyrhini R | log F, Ter | | | 0.000 | | | | | | 1.3 | | 9.5 | |
| Platyrhini R | MS, Arb, Ter | | | | | | | | | | | | |
| Platyrhini R | MS, Arb | | | | | | | | | | | | |
| Platyrhini R | MS, Ter | | | 0.363 | | | | | | | 1.9 | 18.5 | |
| Platyrhini R | log F | | | 0.000 | | | 0.253 | | | | | | |
| Platyrhini R | MS | | | 0.261 | | | | 0.171 | | | | | |
| Platyrhini R | Arb, Ter | | | | | | | | | | | | |
| Platyrhini R | Arb | | | | | | | | | | | | |
| Platyrhini R | Ter | | | 0.000 | | | 0.004 | | | | | | |

Table G.7. F- and p-values for comparisons of linear models: Platyrhini, traditional linear models.

| Group | Reduced Model Variables | log F, log F, log F, MS, Arb, MS, Ter | | | log F, log F, log F, MS, Arb, MS, Ter | | | log F, log F, log F, MS, Arb, MS, Ter | | | log F, log F, log F, MS, Arb, MS, Ter | | |
|--------------|-------------------------|---------------------------------------|--------------|--------------|---------------------------------------|--------------|--------------|---------------------------------------|--------------|--------------|---------------------------------------|--------------|--|
| | | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | |
| Platyrhini F | log F, MS, Arb, Ter | | | | | | | | | | | | |
| Platyrhini F | log F, MS, Arb | | | | | | | | | | | | |
| Platyrhini F | log F, MS, Ter | | | 0.5 | | | | | 0.7 | | | | |
| Platyrhini F | log F, MS | | | 0.470 | | | 4.3 | | 3.1 | | 0.6 | | |
| Platyrhini F | log F, Arb, Ter | | | | | | | | 4.4 | | 0.7 | | |
| Platyrhini F | log F, Arb | | | | | | | | | | | | |
| Platyrhini F | log F, Ter | | | 0.018 | | | | | 0.5 | | | 0.2 | |
| Platyrhini F | MS, Arb, Ter | | | | | | | | | | | | |
| Platyrhini F | MS, Arb | | | | | | | | | | | | |
| Platyrhini F | MS, Ter | | | 0.419 | | | | | | | 0.6 | | |
| Platyrhini F | log F | | | 0.034 | | | 0.470 | | | | | | |
| Platyrhini F | MS | | | 0.535 | | | | | 0.439 | | | | |
| Platyrhini F | Arb, Ter | | | | | | | | | | | | |
| Platyrhini F | Arb | | | | | | | | | | | | |
| Platyrhini F | Ter | | | 0.039 | | | 0.645 | | | | | | |
| Platyrhini R | log F, MS, Arb, Ter | | | | | | | | | | | | |
| Platyrhini R | log F, MS, Arb | | | | | | | | | | | | |
| Platyrhini R | log F, MS, Ter | | | | | 0.8 | | 2.2 | 0.1 | 1.7 | 0.5 | 1.6 | |
| Platyrhini R | log F, MS | | | 0.384 | | | | | 2.2 | 0.2 | | | |
| Platyrhini R | log F, Arb, Ter | | | | | | | | | | | | |
| Platyrhini R | log F, Arb | | | | | | | | | | | | |
| Platyrhini R | log F, Ter | | | 0.124 | | | | | | 0.7 | | 0.5 | |
| Platyrhini R | MS, Arb, Ter | | | | | | | | | | | | |
| Platyrhini R | MS, Arb | | | | | | | | | | | | |
| Platyrhini R | MS, Ter | | | 0.702 | | | | | | | 0.9 | 2.4 | |
| Platyrhini R | log F | | | 0.182 | | 0.127 | 0.417 | | | | | | |
| Platyrhini R | MS | | | 0.612 | | 0.641 | | | 0.358 | | | | |
| Platyrhini R | Arb, Ter | | | | | | | | | | | | |
| Platyrhini R | Arb | | | | | | | | | | | | |
| Platyrhini R | Ter | | | 0.198 | | | 0.496 | | 0.102 | | | | |

Table G.8. F- and p-values for comparisons of linear models: Platyrhini, phylogenetic linear models (Best Branches).

| Group | Reduced Model Variables | log F, MS, Arb, Ter | | | log F, MS, Arb, Ter | | |
|--------------|-------------------------|---------------------|--------------|--------------|---------------------|--------------|--------------|---------------------|--------------|--------------|---------------------|--------------|--------------|---------------------|--------------|--|
| | | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | |
| Catarrhini F | log F, MS, Arb, Ter | 6.9 | 10.6 | 14.8 | 13.8 | 16.1 | 13.0 | 0.4 | 3.5 | 5.4 | 11.3 | 9.4 | 12.1 | 9.8 | | |
| Catarrhini F | log F, MS, Arb | 0.010 | | 21.4 | | 19.6 | | | 0.1 | | 23.5 | 12.7 | 13.0 | | | |
| Catarrhini F | log F, MS, Ter | 0.002 | | 17.3 | | 12.9 | | | | 0.2 | 21.6 | 10.6 | | 8.7 | | |
| Catarrhini F | log F, MS | 0.000 | 0.000 | | | | | | | | 20.4 | 3.3 | | | | |
| Catarrhini F | log F, Arb, Ter | 0.000 | | | | 16.4 | 9.0 | | | | 21.5 | 0.5 | 8.2 | 4.6 | | |
| Catarrhini F | log F, Arb | 0.000 | 0.000 | 0.000 | 0.000 | | | | | | 23.0 | | 0.0 | | | |
| Catarrhini F | log F, Ter | 0.000 | 0.000 | 0.003 | | | | | | | 31.4 | | | 0.1 | | |
| Catarrhini F | MS, Arb, Ter | 0.506 | | | | | | | 6.5 | 10.4 | 16.8 | 14.0 | 16.0 | 13.0 | | |
| Catarrhini F | MS, Arb | 0.035 | 0.815 | | | | | 0.012 | | | 25.6 | | 19.7 | | | |
| Catarrhini F | MS, Ter | 0.006 | 0.691 | | | | | 0.002 | | | 21.1 | | | 13.0 | | |
| Catarrhini F | log F | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | | | | | | | | | |
| Catarrhini F | MS | 0.000 | 0.000 | 0.072 | | | | 0.000 | 0.000 | 0.000 | | | | | | |
| Catarrhini F | Arb, Ter | 0.000 | | | 0.497 | | | 0.000 | | | | | 16.1 | 8.7 | | |
| Catarrhini F | Arb | 0.000 | 0.000 | | 0.000 | 0.917 | | 0.000 | 0.000 | | | 0.000 | | | | |
| Catarrhini F | Ter | 0.000 | 0.000 | | 0.013 | 0.724 | | 0.000 | 0.000 | 0.000 | | 0.004 | | | | |
| Catarrhini R | log F, MS, Arb, Ter | | 5.7 | 8.7 | 11.1 | 8.3 | 10.2 | 9.0 | 1.3 | 4.3 | 13.7 | 7.9 | 6.4 | 7.9 | 6.8 | |
| Catarrhini R | log F, MS, Arb | 0.020 | | 15.5 | | 11.7 | | | | 0.5 | 15.3 | 8.5 | | 8.1 | | |
| Catarrhini R | log F, MS, Ter | 0.004 | | 12.2 | | 8.2 | | | | 0.0 | 13.8 | 6.8 | | | 5.5 | |
| Catarrhini R | log F, MS | 0.000 | 0.000 | | | | | | | | 12.6 | 1.2 | | | | |
| Catarrhini R | log F, Arb, Ter | 0.001 | | | | 11.7 | 8.5 | | | | 15.7 | | 2.2 | 6.2 | 4.4 | |
| Catarrhini R | log F, Arb | 0.000 | 0.000 | | 0.001 | | | | | | 17.2 | | | 0.7 | | |
| Catarrhini R | log F, Ter | 0.000 | 0.001 | | 0.005 | | | | | | 20.7 | | | | 0.2 | |
| Catarrhini R | MS, Arb, Ter | 0.251 | | | | | | | | 4.9 | 7.3 | 11.2 | 8.9 | 10.1 | 8.6 | |
| Catarrhini R | MS, Arb | 0.051 | 0.473 | | | | | | 0.031 | | | 16.6 | | 12.0 | | |
| Catarrhini R | MS, Ter | 0.017 | 0.920 | | | | | | 0.009 | | | 13.8 | | | 8.4 | |
| Catarrhini R | log F | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | | | | | | | | |
| Catarrhini R | MS | 0.000 | 0.001 | 0.002 | 0.270 | | | | 0.000 | 0.000 | | | | | | |
| Catarrhini R | Arb, Ter | 0.001 | | | 0.141 | | | | 0.000 | | | | | 10.1 | 6.4 | |
| Catarrhini R | Arb | 0.000 | 0.000 | | 0.003 | 0.413 | | | 0.000 | 0.000 | | | 0.002 | | | |
| Catarrhini R | Ter | 0.000 | 0.002 | | 0.016 | 0.648 | | | 0.000 | 0.001 | | | 0.013 | | | |

Table G.9. F- and p-values for comparisons of linear models: Catarrhini, traditional linear models.

| Group | Reduced Model Variables | log F, MS, Arb, Ter | | | log F, MS, Arb, Ter | | | log F, MS, Arb, Ter | | | log F, MS, Arb, Ter | | | log F, MS, Arb, Ter | | |
|--------------|-------------------------|---------------------|---------------------|--------------|---------------------|---------------------|--------------|---------------------|--------------|---------------------|---------------------|---------------------|--------------|---------------------|--------------|--|
| | | MS, Arb, Ter | log F, MS, Arb, Ter | MS, Arb, Ter | MS, Arb, Ter | log F, MS, Arb, Ter | MS, Arb, Ter | log F, MS, Arb, Ter | MS, Arb, Ter | log F, MS, Arb, Ter | MS, Arb, Ter | log F, MS, Arb, Ter | MS, Arb, Ter | log F, MS, Arb, Ter | MS, Arb, Ter | |
| Catarrhini F | log F, MS, Arb, Ter | 3.5 | 1.2 | 2.9 | 3.7 | 3.3 | 3.2 | 0.6 | 1.8 | 0.7 | 3.3 | 2.0 | 2.5 | 2.5 | 2.4 | |
| Catarrhini F | log F, MS, Arb | 0.064 | | 2.3 | | 3.2 | | | 0.2 | | 3.2 | 1.1 | | 2.1 | | |
| Catarrhini F | log F, MS, Ter | 0.268 | | 4.6 | | | 4.1 | | | 0.2 | 4.0 | 2.3 | | | 2.8 | |
| Catarrhini F | log F, MS | 0.059 | 0.134 | 0.035 | | | | | | | 3.6 | 0.0 | | | | |
| Catarrhini F | log F, Arb, Ter | 0.029 | | | | 2.6 | 2.1 | | | | 2.9 | | 0.2 | 1.3 | 1.1 | |
| Catarrhini F | log F, Arb | 0.022 | 0.046 | | 0.113 | | | | | | 3.1 | | | 0.0 | | |
| Catarrhini F | log F, Ter | 0.027 | 0.019 | | 0.150 | | | | | | 3.6 | | | | 0.0 | |
| Catarrhini F | MS, Arb, Ter | 0.456 | | | | | | | 3.1 | 0.9 | | 2.7 | 3.5 | 3.2 | 3.0 | |
| Catarrhini F | MS, Arb | 0.163 | 0.668 | | | | | 0.079 | | | | 2.1 | | 3.1 | | |
| Catarrhini F | MS, Ter | 0.495 | 0.677 | | | | | 0.356 | | | | 4.5 | | | 4.1 | |
| Catarrhini F | log F | 0.013 | 0.027 | 0.010 | 0.031 | 0.062 | 0.062 | | | | | | | | | |
| Catarrhini F | MS | 0.126 | 0.322 | 0.105 | 0.898 | | | 0.075 | 0.148 | 0.037 | | | | | | |
| Catarrhini F | Arb, Ter | 0.064 | | | 0.675 | | | 0.034 | | | | | | 2.4 | 1.9 | |
| Catarrhini F | Arb | 0.047 | 0.102 | | 0.280 | 0.884 | | 0.028 | 0.049 | | | | 0.123 | | | |
| Catarrhini F | Ter | 0.056 | 0.046 | | 0.352 | 0.948 | | 0.034 | | 0.020 | | | 0.166 | | | |
| Catarrhini R | log F, MS, Arb, Ter | 1.8 | 2.8 | 2.5 | 1.7 | 1.8 | 2.3 | 0.0 | 0.9 | 1.7 | 2.4 | 2.1 | 1.2 | 1.5 | 2.1 | |
| Catarrhini R | log F, MS, Arb | 0.185 | | 3.3 | | 1.8 | | | 0.1 | | 2.6 | 2.2 | | 1.3 | | |
| Catarrhini R | log F, MS, Ter | 0.101 | | 2.3 | | | 2.0 | | | 0.5 | 2.2 | 1.7 | | | 1.8 | |
| Catarrhini R | log F, MS | 0.086 | 0.076 | 0.137 | | | | | | | 2.1 | 1.2 | | | | |
| Catarrhini R | log F, Arb, Ter | 0.187 | | | | 2.0 | 3.4 | | | | 3.0 | | 0.1 | 1.2 | 2.4 | |
| Catarrhini R | log F, Arb | 0.149 | 0.167 | | 0.158 | | | | | | 3.9 | | | 0.3 | | |
| Catarrhini R | log F, Ter | 0.084 | 0.139 | | 0.068 | | | | | | 2.5 | | | | 1.3 | |
| Catarrhini R | MS, Arb, Ter | 0.964 | | | | | | | 1.9 | 3.4 | | 3.2 | 1.8 | 2.0 | 2.8 | |
| Catarrhini R | MS, Arb | 0.398 | 0.787 | | | | | 0.173 | | | | 4.5 | | 2.0 | | |
| Catarrhini R | MS, Ter | 0.198 | 0.469 | | | | | 0.071 | | | | 2.9 | | | 2.5 | |
| Catarrhini R | log F | 0.059 | 0.062 | 0.095 | 0.125 | 0.056 | 0.120 | | | | | | | | | |
| Catarrhini R | MS | 0.108 | 0.114 | 0.185 | 0.281 | | | 0.047 | 0.038 | 0.090 | | | | | | |
| Catarrhini R | Arb, Ter | 0.325 | | | 0.758 | | | 0.174 | | | | | | 2.3 | 4.8 | |
| Catarrhini R | Arb | 0.224 | 0.270 | | 0.313 | 0.572 | | 0.126 | 0.144 | | | | 0.134 | | | |
| Catarrhini R | Ter | 0.092 | 0.153 | | 0.097 | | 0.252 | 0.045 | | 0.092 | | | 0.032 | | | |

Table G.10. F- and p-values for comparisons of linear models: Catarrhini, phylogenetic linear models (Best Branches).

Appendix H: Distributions of CTM and PBM

As defined in the text, point body mass (PBM) can be modeled as varying about an idealized central tendency for adult body mass in a given individual; that is, central tendency mass (CTM). This relationship can be expressed for a single individual as follows:

$$\text{PBM}_i = \text{CTM}_i + \varepsilon_i, \quad [\text{H.1}]$$

where CTM_i is a constant and the error term ε_i has a mean of zero and variance $\sigma_{\varepsilon_i}^2$. No assumptions are made regarding the distribution of ε_i other than its mean and variance.

If a population of CTM measurements are sampled, its mean may be calculated as

$$\mu_c = \frac{1}{n} \sum_{i=1}^n \text{CTM}_i, \quad [\text{H.2}]$$

regardless of the distribution of CTM measurements. That group of measurements will have some variance σ_c^2 , and the mean will have a variance of

$$\text{Var}(\mu_c) = \frac{\sigma_c^2}{n} \quad [\text{H.3}]$$

(the square of the standard error of the mean).

The mean for a population of PBM measurements for those same individuals can be calculated as

$$\mu_p = \frac{1}{n} \sum_{i=1}^n (\text{CTM}_i + \varepsilon_i) = \frac{1}{n} \sum_{i=1}^n \text{CTM}_i + \frac{1}{n} \sum_{i=1}^n \varepsilon_i. \quad [\text{H.4}]$$

Because all of the error terms have a mean of zero they cancel out of the equation, and thus

$$\mu_p = \mu_c. \quad [\text{H.5}]$$

Because the error terms for each individual are distributed independently of each other, the variance of the mean for PBM can be expressed as

$$\text{Var}(\mu_p) = \sum_{i=1}^n \left(\frac{1}{n}\right)^2 \text{Var}(\text{CTM}_i) + \sum_{i=1}^n \left(\frac{1}{n}\right)^2 \text{Var}(\varepsilon_i). \quad [\text{H.6}]$$

Since each individual CTM measurement is a constant, the first term sums to zero. Equation H.6 can be rewritten as

$$\text{Var}(\mu_p) = \left(\frac{1}{n}\right)^2 \sum_{i=1}^n \sigma_{\varepsilon_i}^2. \quad [\text{H.7}]$$

Although the same population of individuals will have identical population means for CTM and PBM (as shown in equation H.5), there is no relationship between the variance of those means (compare equations H.3 and H.7). Even in the special case that all ε_i have identical variances, *i.e.*,

$$\text{Var}(\mu_p) = \frac{\sigma_{\varepsilon}^2}{n}, \quad [\text{H.8}]$$

the variance of the mean for PBM is not equal to that of CTM (equations H.3 and H.8 are not equivalent). Comparison of equations H.3 and H.7 shows that the variance of PBM is entirely dependent on the variance of the error terms ε_i , and it is completely independent of the variance of the collection of CTM measurements.

Appendix I: Properties of Isometric Variables

Suppose that a global skeletal size variable (GSV) scales isometrically with central tendency mass (CTM), indicating that the two variables are directly proportional to each other. The relationship can be expressed as

$$\mathbf{M} = c\mathbf{G}, \quad [\text{I.1}]$$

where \mathbf{M} is CTM, \mathbf{G} is the GSV, and c is the proportionality constant. Longitudinal body mass and GSV are variables in raw data space; *i.e.*, they have not been logarithmically transformed.

Distribution parameters for the two variables can be shown to also be directly proportional. For example, the arithmetic means are related as follows:

$$\bar{\mathbf{M}} = \frac{\sum_{i=1}^n \mathbf{M}_i}{n} = \frac{\sum_{i=1}^n c\mathbf{G}_i}{n} = \frac{c \sum_{i=1}^n \mathbf{G}_i}{n} = c\bar{\mathbf{G}}. \quad [\text{I.2}]$$

Standard deviations are also directly proportional (s is standard deviation, s^2 is variance):

$$s_M^2 = \frac{\sum_{i=1}^n (\mathbf{M}_i - \bar{\mathbf{M}})^2}{n-1} = \frac{\sum_{i=1}^n (c\mathbf{G}_i - c\bar{\mathbf{G}})^2}{n-1} = \frac{\sum_{i=1}^n c^2 (\mathbf{G}_i - \bar{\mathbf{G}})^2}{n-1} = c^2 \frac{\sum_{i=1}^n (\mathbf{G}_i - \bar{\mathbf{G}})^2}{n-1} = c^2 s_G^2, \quad [\text{I.3}]$$

thus,

$$s_M = cs_G. \quad [\text{I.4}]$$

It can be demonstrated using equation I.2 that ratios of arithmetic means calculated in one variable are identical with means ratios calculated in the other. Consider a common index of sexual dimorphism, the male mean divided by the female mean. It can be shown that the ratios based on CTM and GSV are identical as follows:

$$\frac{\bar{\mathbf{M}}_m}{\bar{\mathbf{M}}_f} = \frac{c\bar{\mathbf{G}}_m}{c\bar{\mathbf{G}}_f} = \frac{\bar{\mathbf{G}}_m}{\bar{\mathbf{G}}_f}, \quad [\text{I.5}]$$

where the subscripts **m** and **f** refer to males and females, respectively. Likewise, it can be shown with equations I.2 and I.4 that coefficients of variation (**V**) of body size will be identical using either variable:

$$V_M = \frac{S_M}{M} = \frac{cS_G}{cG} = \frac{S_G}{G} = V_G. \quad [I.6]$$

Similarly, application of equation 2.3 shows that F-statistics, which are ratios of sample variances, will also be identical for both variables. In general, any statistic where the proportionality constant *c* cancels out will be identical for CTM and GSV.

Additionally, allometric scaling relationships between body size and other variables are related for CTM and GSV. Regression analyses used to determine the scaling relationship between variables log-transform data in order to identify the power relationship between the untransformed variables. In such analyses, the slope of the regression corresponds to the exponent of the power relationship. Consider the relationship between logarithms of CTM and GSV:

$$\log(M) = \log(cG). \quad [I.7]$$

This relationship can also be expressed as

$$\log(M) = \log(c) + \log(G). \quad [I.8]$$

(Note that equation I.8 is also the equation for a regression of $\log(\mathbf{M})$ against $\log(\mathbf{G})$ in which the slope is equal to 1, indicating that the GSV scales isometrically with CTM.) An ordinary least squares regression (OLS) of the log-transformed variable **Y** (where **Y** is another variable such as femoral length, eye orbit area, endocranial volume, *etc.*) against body mass will yield the following result:

$$\log(Y) = \beta_1 \log(M) + \beta_0 \quad [I.9]$$

Combining equations I.8 and I.9 yields

$$\log(Y) = \beta_1 * (\log(c) + \log(G)) + \beta_0 = \beta_1 \log(G) + [\beta_1 \log(c) + \beta_0] \quad [I.10]$$

where the constants have been grouped together in square brackets. It follows from equation 2.10 that using GSV rather than CTM in an OLS analysis of log-transformed data will change only the intercept of the regression line and not its slope. Thus indications of isometry or allometry will be identical using either CTM or a directly proportional GSV. Additionally, the intercept will be changed by a known value (*i.e.*, the addition of the logarithm of the proportionality constant multiplied by the slope of the regression). It can also be demonstrated that the slopes are identical and the intercepts are translated as shown above for major axis and reduced major axis regressions.

If the GSV has been shown to be directly proportional to body mass, then the proportionality constant (c) is known. Equation 10 can then be used to transform log-log plots of Y against GSV to units equivalent to log-log plots of Y against CTM, and vice versa. However, care should be used in interpreting individual data points in transformed plots – simply because GSV plots can be transformed to “body mass plots” does not mean that the individual data points are now measures of body mass (for a detailed discussion see Smith, 1984). Transformation of plots also involves consideration of the confidence interval about c , which introduces a new source of error. Plots need not be transformed to be compared, however – slopes of non-transformed regression lines based on GSV can be compared directly to the slopes of non-transformed regression lines based on body mass data.

References

- (1999). SAS, version 8.02. Cary, NC: SAS Institute, Inc.
- Abouheif, E. & Fairbairn, D.J. (1997). A comparative analysis of allometry for sexual size dimorphism: Assessing Rensch's rule. *Am. Nat.* 149, 540-562.
- Aiello, L.C. (1981). Locomotion in the Miocene Hominoidea. In (C. Stringer, Ed) *Aspects of Human Evolution*, pp. 63-97. London: Taylor and Francis, Ltd.
- Aiello, L.C., Collard, M., Thackeray, J.F. & Wood, B.A. (2000). Assessing exact randomization-based methods for determining the taxonomic significance of variability in the human fossil record. *South African Journal of Science* 96, 179-183.
- Alport, L. & Overdorff, D.J. (2002). The role of the accessory olfactory bulb in nocturnal mating systems. *Am. J. Phys. Anthropol. Suppl.* 34, 37.
- Anapol, F., Turner, T.R., Mott, C.S. & Jolly, C.J. (1995). Postcranial proportions of *Cercopithecus aethiops* and *C. mitis*. *Am. J. Phys. Anthropol.* 20 (Suppl.), 57.
- Andersen, N.M. (1994). The evolution of sexual size dimorphism and mating systems in the water striders (Hemiptera: Gerridae): a phylogenetic approach. *Ecoscience* 1, 208-214.
- Andersson, M. (1994). *Sexual Selection*. Princeton: Princeton University Press.
- Andrews, P.J., Begun, D.R. & Zylstra, M. (1997). Paleocology of Miocene hominoids. In (D.R. Begun, C.V. Ward & M.D. Rose, Eds) *Function, Phylogeny, and Fossils*, pp. 29-58. New York: Plenum.
- Arnqvist, G. (1992). Spatial variation in selective regimes: sexual selection in the water strider, *Gerris odontogaster*. *Evolution* 46, 914-929.
- Arsuaga, J.L., Carretero, J.M., Lorenzo, C., Gracia, A., Martinez, I., Bermudez de Castro, J.M. & Carbonell, E. (1997). Size variation in middle Pleistocene humans. *Science* 277, 1086-1088.
- Atsalis, S. (1999). Seasonal fluctuations in body fat and activity levels in a rain-forest species of mouse lemur, *Microcebus rufus*. *Int. J. Primatol.* 20, 883-910.
- Barton, R.A. (2000). Socioecology of baboons: the interaction of male and female strategies. In (P.M. Kappeler, Ed) *Primate Males: Causes and Consequences of Variation in Group Composition*, pp. 97-107. Cambridge: Cambridge University Press.

- Bearder, S.K. & Martin, R.M. (1980). The social organisation of a nocturnal primate revealed by radio-tracking. In (C.J. Amlaner & D. Macdonald, Eds) *A Handbook on Biotelemetry and Radio Tracking: International Conference: Biotelemetry and Radio Tracking in Biology and Medicine, Oxford, 20-22 March 1979*, pp. 633-648. Oxford: Pergamon Press.
- Begun, D.R. & Kordos, L. (1997). Phyletic affinities and functional convergence in *Dryopithecus* and other Miocene living hominids. In (D.R. Begun, C.V. Ward & M.D. Rose, Eds) *Function, Phylogeny, and Fossils*, pp. 291-316. New York: Plenum.
- Berger, M.E. (1972). Live-weights and body measurements of olive baboons (*Papio anubis*) in the Laikipia District of Kenya. *J. Mammal.* 53, 404-406.
- Bernstein, I.S., Weed, J.L., Judge, P.G. & Ruehlmann, T.E. (1989). Seasonal weight changes in male rhesus monkeys (*Macaca mulatta*). *Am. J. Primatol.* 18, 251-257.
- Berry, J.F. & Shine, R. (1980). Sexual size dimorphism and sexual selection in turtles (order Testudines). *Oecologia* 44, 185-191.
- Bicca-Marques, J.C. (1999). Hand specialization, sympatry, and mixed-species associations in callitrichines. *J. Hum. Evol.* 36, 349-378.
- Boinski, S. & Cropp, S.J. (1999). Disparate data sets resolve squirrel monkey (*Saimiri*) taxonomy: implications for behavioral ecology and biomedical usage. *Int. J. Primatol.* 20, 237-256.
- Boinski, S., Sughrue, K., Selvaggi, L., Quatrone, R., Henry, M. & Cropp, S. (2002). An expanded test of the ecological model of primate social evolution: Competitive regimes and female bonding in three species of squirrel monkeys (*Saimiri oerstedii*, *S. boliviensis*, and *S. sciureus*). *Behaviour* 139, 227-261.
- Bolter, D.R. & Zihlman, A.L. (2003). Morphometric analysis of growth and development in wild-collected vervet monkeys (*Cercopithecus aethiops*), with implications for growth patterns in Old World monkeys, apes and humans. *J. Zool. (Lond.)* 260, 99-110.
- Bonvicino, C.R., Lemos, B. & Seuanez, H.N. (2001). Molecular phylogenetics of howler monkeys (*Alouatta*, Platyrrhini): a comparison with karyotypic data. *Chromosoma* 110, 241-246.
- Bradley, B., Stumpf, R.M. & Wright, P.C. (1997). Morphometrics of *Eulemur fulvus albocollaris* in Vevembe Forest, Madagascar. *Am. J. Phys. Anthropol.* 24 (Supplement), 79-80.

- Brandon-Jones, D. (1993). The taxonomic affinities of the Mentawai Islands sureli, *Presbytis potenziani* (Bonaparte, 1856) (Mammalia: Primata: Cercopithecidae). *Raffles Bulletin of Zoology* 41, 331-357.
- Braza, F., Alvarez, F. & Azcarate, T. (1983). Feeding habits of the red howler monkeys (*Alouatta seniculus*) in the Llanos of Venezuela. *Mammalia* 47, 205-214.
- Brown, J.H. (1995). *Macroecology*. Chicago: University of Chicago Press.
- Brown, J.L. (1975). *The Evolution of Behavior*. New York: Norton.
- Buchanan, D.B., Mittermeier, R.A. & van Roosmalen, M.G.M. (1981). The saki monkeys, genus *Pithecia*. In (A.F. Coimbra-Filho & R.A. Mittermeier, Eds) *The Ecology and Behavior of Neotropical Primates, Vol. 1*, pp. 371-417. Rio de Janeiro: Academia Brasileira Ciencias.
- Bulmer, M.G. (1971). The effect of selection on genetic variability. *Am. Nat.* 105, 201-211.
- Bulmer, M.G. (1976). The effects of selection on genetic variability: a simulation study. *Genet. Res.* 28, 101-117.
- Cabana, G., Frewin, A., Peters, R.H. & Randall, L. (1982). The effect of sexual size dimorphism on variations in reproductive effort of birds and mammals. *Am. Nat.* 120, 17-25.
- Cerling, T.E., Ehleringer, J.R. & Harris, J.M. (1998). Carbon dioxide starvation, the development of C-4 ecosystems, and mammalian evolution. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.* 353, 159-170.
- Cerling, T.E., Harris, J.M., MacFadden, B.J., Leakey, M.G., Quade, J., Eisenmann, V. & Ehleringer, J.R. (1997). Global change through the Miocene/Pliocene boundary. *Nature* 389, 153-158.
- Cerling, T.E., Wang, Y. & Quade, J. (1993). Expansion of C₄ ecosystems as an indicator of global ecological change in the late Miocene. *Nature* 361, 344-345.
- Charles-Dominique, P. (1972). Ecologie et vie sociale de *Galago demidovii* (Fischer 1808; Prosimii). *Fortschritte der Verhaltensforschung (Zeitschrift für Tierpsychologie Supplement)* 9, 7-41.
- Chernick, M.R. (1999). *Bootstrap Methods: A Practitioner's Guide*. New York: John Wiley & Sons.
- Cheverud, J.M., Dow, M.M. & Leutenegger, W. (1985). The quantitative assessment of phylogenetic constraints in comparative analyses: sexual dimorphism in body weight among primates. *Evolution* 39, 1335-1351.

- Cheverud, J.M., Wilson, P. & Dittus, W.P.J. (1992). Primate population studies at Polonnaruwa. III. Somatometric growth in a natural population of toque macaques (*Macaca sinica*). *J. Hum. Evol.* 23, 51-77.
- Clutton-Brock, T.H. (1977). Some aspects of intraspecific variation in feeding and ranging behaviour in primates. In (T.H. Clutton-Brock, Ed) *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes*. New York: Academic Press.
- Clutton-Brock, T.H. (1985). Size, sexual dimorphism, and polygyny in primates. In (W.L. Jungers, Ed) *Size and Scaling in Primate Biology*, pp. 51-60. New York: Plenum Press.
- Clutton-Brock, T.H., Albon, S.D. & Guinness, F.E. (1988). Reproductive success in male red deer. In (T.H. Clutton-Brock, Ed) *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems*, pp. 325-343. Chicago: University of Chicago Press.
- Clutton-Brock, T.H. & Harvey, P.H. (1977). Primate ecology and social organization. *J. Zool. (Lond.)* 183, 1-39.
- Clutton-Brock, T.H., Harvey, P.H. & Rudder, B. (1977). Sexual dimorphism, sociometric sex ratio and body weight in primates. *Nature* 269, 797-800.
- Coe, C.L. & Rosenblum, L.A. (1978). Annual reproductive strategy of the squirrel monkey (*Saimiri sciureus*). *Folia Primatol.* 29, 19-42.
- Colyn, M. (1994). Données pondérales sur les primates Cercopithecidae d'Afrique Centrale (Bassin du Zaïre/Congo). *Mammalia* 58, 483-487.
- Cooper, V.J. & Hosey, G.R. (2003). Sexual dichromatism and female preference in *Eulemur fulvus* subspecies. *Int. J. Primatol.* 24, 1177-1188.
- Cortés-Ortiz, L., Bermingham, E., Rico, C., Rodriguez-Luna, E., Sampaio, I. & Ruiz-Garcia, M. (2003). Molecular systematics and biogeography of the Neotropical monkey genus, *Alouatta*. *Molecular Phylogenetics and Evolution* 26, 64-81.
- Covert, H.H. (2002). The earliest fossil primates and the evolution of prosimians: Introduction. In (W.C. Hartwig, Ed) *The Primate Fossil Record*, pp. 13-20. Cambridge: Cambridge University Press.
- Crile, G. & Quiring, D.P. (1940). A record of the body weight and certain organ and gland weights of 3690 animals. *Ohio Journal of Science* 40, 219-259.
- Cunningham, E.J.A. & Birkhead, T.R. (1998). Sex roles and sexual selection. *Anim. Behav.* 56, 1311-1321.

- Dagosto, M. & Terranova, C.J. (1992). Estimating the body size of Eocene primates: a comparison of results from dental and postcranial variables. *Int. J. Primatol.* 13, 307-344.
- Darwin, C. (1871). *The Descent of Man, and Selection in Relation to Sex*. London: J. Murray.
- Dawson, G.A. & Dukelow, W.R. (1976). Reproductive characteristics of free-ranging Panamanian tamarins (*Saguinus oedipus geoffroyi*). *Journal of Medical Primatology* 5, 266-275.
- Delson, E., Terranova, C.J., Jungers, W.L., Sargis, E.J., Jablonski, N.G. & Dechow, P.C. (2000). Body mass in Cercopithecidae (Primates, Mammalia): estimation and scaling in extinct and extant taxa. American Museum of Natural History, Anthropological Papers, no 83. New York: American Museum of Natural History.
- Demes, B. & Jungers, W.L. (1993). Long bone cross-sectional dimensions, locomotor adaptations and body size in prosimian primates. *J. Hum. Evol.* 25, 57-74.
- Demment, M.W. (1983). Feeding ecology and the evolution of body size of baboons. *Afr. J. Ecol.* 21, 219-233.
- Diamond, J.M. (1984). 'Normal' extinctions of isolated populations. In (M.H. Nitecki, Ed) *Extinctions*, pp. 191-246. Chicago: University of Chicago Press.
- Diaz-Uriarte, R. & Garland, T., Jr. (1996). Testing hypotheses of correlated evolution using phylogenetically independent contrasts: Sensitivity to deviations from Brownian motion. *Syst. Biol.* 45, 27-47.
- Diaz-Uriarte, R. & Garland, T., Jr. (1998). Effects of branch length errors on the performance of phylogenetically independent contrasts. *Syst. Biol.* 47, 654-672.
- Dietz, J.M., Baker, A.J. & Miglioretti, D. (1994). Seasonal variation in reproduction, juvenile growth, and adult body mass in gold lion tamarins (*Leontopithecus rosalia*). *Am. J. Primatol.* 34, 115-132.
- Dixson, A.F. (1998). *Primate Sexuality: Comparative Studies of the Prosimians, Monkeys, Apes, and Human Beings*. Oxford: Oxford University Press.
- Dobson, F.S. & Yu, J. (1993). Rarity in neotropical forest mammals revisited. *Conserv. Biol.* 7, 586-591.
- Downhower, J.F. (1976). Darwin's finches and evolution of sexual dimorphism in body size. *Nature* 263, 558-563.
- Du Mond, F.V. & Hutchison, T.C. (1967). Squirrel monkey reproduction: the fatted male phenomenon and seasonal spermatogenesis. *Science* 158, 1067-1070.

- Dunbar, R.I.M. (2000). Male mating strategies: a modeling approach. In (P.M. Kappeler, Ed) *Primate Males: Causes and Consequences of Variation in Group Composition*, pp. 259-268. Cambridge: Cambridge University Press.
- Duncan, A.S., Kappelman, J. & Shapiro, L.J. (1994). Metatarsophalangeal joint function and positional behavior in *Australopithecus afarensis*. *Am. J. Phys. Anthropol.* 93, 67-81.
- Earhart, C.M. & Johnson, N.K. (1970). Size dimorphism and food habits of North American owls. *Condor* 72, 251-264.
- Eley, R.M., Strum, S.C., Muchemi, G. & Reid, G.D.F. (1989). Nutrition, body condition, activity patterns, and parasitism of free-ranging troops of olive baboons (*Papio anubis*) in Kenya. *Am J Primatol* 18, 209-219.
- Emerson, S.B. (1994). Testing predictions of sexual selection. *Am. Nat.* 143, 848-869.
- Emlen, S.T. & Oring, L.W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science* 197, 215-223.
- Endler, J.A. (1993). Some general comments on the evolution and design of animal communication systems. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.* 340, 215-225.
- Fairbairn, D.J. (1990). Factors influencing sexual size dimorphism in temperate water striders. *Am. Nat.* 136, 61-86.
- Fairbairn, D.J. (1997). Allometry for sexual size dimorphism: Pattern and process in the coevolution of body size in males and females. *Annu. Rev. Ecol. Syst.* 28, 659-687.
- Fairbairn, D.J. & Preziosi, R. (1994). Sexual selection and the evolution of allometry for sexual size dimorphism in the water strider *Aquaris remigis*. *Am. Nat.* 144, 101-118.
- Fairbairn, D.J. & Shine, R. (1993). Patterns of sexual size dimorphism in seabirds of the Southern Hemisphere. *Oikos* 68, 139-145.
- Falconer, D.S. & Mackay, T.F.C. (1996). *Introduction to Quantitative Genetics*. Essex, England: Longman.
- Falsetti, A.B., Jungers, W.L. & Cole, T.M. (1993). Morphometrics of the callitrichid forelimb: a case-study in size and shape. *Int. J. Primatol.* 14, 551-572.
- Felsenstein, J. (1985). Phylogenies and the comparative method. *Am. Nat.* 125, 1-15.
- Fleagle, J.G. (1999). *Primate Adaptation and Evolution*. San Diego, CA: Academic Press.

- Fleagle, J.G. & Mittermeier, R.A. (1980). Locomotor behavior, body size, and comparative ecology of seven Surinam monkeys. *Am. J. Phys. Anthropol.* 52, 301–314.
- Foley, R.A. (1994). Speciation, extinction and climatic change in hominid evolution. *J. Hum. Evol.* 26, 275-289.
- Foley, R.A. & Lee, P.C. (1989). Finite social space, evolutionary pathways, and reconstructing hominid behavior. *Science* 243, 901–906.
- Fooden, J. (1971). Report on primates collected in western Thailand January–April, 1967. *Fieldiana Zoologica* 59, 1-62.
- Fooden, J. (1975). Taxonomy and evolution of liontail and pigtail macaques (Primates: Cercopithecidae). *Fieldiana Zoologica* 67, 1–169.
- Fooden, J. (1988). Taxonomy and evolution of the Sinica group of macaques: 6. Interspecific comparisons and synthesis. *Fieldiana Zoologica* N. S. 45, 1–44.
- Ford, S.M. (1986). Subfossil platyrrhine tibia (Primates: Callitrichidae) from Hispaniola: a possible further example of island gigantism. *Am. J. Phys. Anthropol.* 70, 47-62.
- Ford, S.M. (1990). Platyrrhine evolution in the West Indies. *J. Hum. Evol.* 19, 237-254.
- Ford, S.M. (1994). Evolution of sexual dimorphism in body weight in platyrrhines. *Am. J. Primatol.* 34, 221-244.
- Galdikas, B.M.F. (1985). Subadult male orangutan sociality and reproductive behavior at Tanjung Puting. *Int. J. Primatol.* 8, 87–99.
- Garber, P.A., Encarnación, F., Moya, L. & Pruett, J.D. (1993). Demographic and reproductive patterns in moustached tamarin monkeys (*Saguinus mystax*): Implications for reconstructing platyrrhine mating systems. *Am. J. Primatol.* 29, 235-254.
- Garber, P.A., Rosenberger, A.L. & Norconk, M.A. (1996). Marmoset misconceptions. In (M.A. Norconk, A.L. Rosenberger & P.A. Garber, Eds) *Adaptive Radiations of Neotropical Primates*, pp. 87-95. New York: Plenum Press.
- Garland, T., Jr., Harvey, P.H. & Ives, A.R. (1992). Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst. Biol.* 41, 18-32.
- Garland, T., Jr. & Ives, A.R. (2000). Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. *Am. Nat.* 155, 346-364.

- Gaulin, S.J.C. & Sailer, L.D. (1984). Sexual dimorphism in weight among the primates: The relative impact of allometry and sexual selection. *Int. J. Primatol.* 5, 515-535.
- Gautier-Hion, A. & Gautier, J.-P. (1976). Croissance, maturité sexuelle et sociale, reproduction chez les cercopithecinés forestiers africains. *Folia Primatol.* 26, 165-184.
- Geissmann, T. (1993). Evolution of communication in gibbons (Hylobatidae). Ph.D. Dissertation, University of Zürich.
- Gerald, M.S. (2003). How color may guide the primate world: possible relationship between sexual selection and sexual dichromatism. In (C.B. Jones, Ed) *Sexual Selection and Reproductive Competition in Primates: New Perspectives and Directions*, pp. 141-171. Norman, Oklahoma: American Society of Primatologists.
- Gest, T.R. & Siegel, M.I. (1983). The relationship between organ weights and body weights, facial dimensions, and dental dimensions in a population of olive baboons (*Papio cynocephalus anubis*). *Am. J. Phys. Anthropol.* 61, 189-196.
- Glander, K.E. (1994). Aye-aye weight and gestation. *Am. J. Phys. Anthropol.* 18 (Supplement), 94.
- Glander, K.E., Wright, P.C., Daniels, P.S. & Merenlender, A.M. (1992). Morphometrics and testicle size of rain-forest lemur species from southeastern Madagascar. *J. Hum. Evol.* 22, 1-17.
- Gleason, T.M. & Norconk, M.A. (1995). Intragroup spacing and agonistic interactions in white-faced sakis. *Am. J. Primatol.* 36, 125.
- Godfrey, L.R. (1988). Adaptive diversification of Malagasy strepsirhines. *J. Hum. Evol.* 17, 93-134.
- Godfrey, L.R., Jungers, W.L., Wunderlich, R.E. & Richmond, B.G. (1997). Reappraisal of the postcranium of *Hadropithecus* (Primates, Indroidea). *Am. J. Phys. Anthropol.* 103, 529-556.
- Godfrey, L.R., Lyon, S.K. & Sutherland, M.R. (1993). Sexual dimorphism in large-bodied primates: the case of the sub-fossil lemurs. *Am. J. Phys. Anthropol.* 90, 315-334.
- Godfrey, L.R., Sutherland, M.R., Paine, R.R., Williams, F.L., Boy, D.S. & Vuillaume-Randriamanantena, M. (1995). Limb joint surface areas and their ratios in Malagasy lemurs and other mammals. *Am. J. Phys. Anthropol.* 97, 11-36.

- Goldizen, A.W., Terborgh, J., Cornejo, F., Porras, D.T. & Evans, R. (1988). Seasonal food shortage, weight loss, and the timing of births in saddle-back tamarins (*Saguinus fuscicollis*). *Journal of Animal Ecology* 57, 893-901.
- Gordon, A.D. (2001). Sexual size dimorphism in primates: Consideration of relative variation between sexes. *Am. J. Phys. Anthropol.* Supplement 32, 72.
- Gould, L. & Overdorff, D.J. (2002). Adult male scent-marking in *Lemur catta* and *Eulemur fulvus rufus*. *Int. J. Primatol.* 23, 575-586.
- Grafen, A. (1989). The phylogenetic regression. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.* 326, 119-157.
- Griffin, D.L. (2002). Aridity and humidity: two aspects of the late Miocene climate of North Africa and the Mediterranean. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 182, 65-91.
- Grine, F.E., Demes, B., Jungers, W.L. & Cole, T.M. (1993). Taxonomic affinity of the early *Homo* cranium from Swartkrans, South Africa. *Am. J. Phys. Anthropol.* 92, 411-426.
- Grine, F.E., Jungers, W.L. & Schultz, J. (1996). Phenetic affinities among early *Homo* crania from East and South Africa. *J. Hum. Evol.* 30, 189-225.
- Gursky, S. (1998). Effects of radio transmitter weight on a small nocturnal primate. *Am. J. Primatol.* 46, 145-155.
- Gwynne, D.T. (1991). Sexual competition among females: What causes courtship-role reversal? *Trends Ecol. Evol.* 6, 118-121.
- Gwynne, D.T. & Simmons, L.W. (1990). Experimental reversal of courtship roles in an insect. *Nature* 346, 171-174.
- Hamilton, M. (1975). Variations in the sexual dimorphism of skeletal size in five populations of Amer-indians. Ph.D. Dissertation, University of Michigan.
- Harcourt, C.S. & Bearder, S.K. (1989). A comparison of *Galago moholi* in South Africa with *Galago zanzibaricus* in Kenya. *Int. J. Primatol.* 10, 35-45.
- Harcourt, C.S. & Nash, L.T. (1986). Social organization of galagos in Kenyan coastal forests. I. *Galago zanzibaricus*. *Am. J. Primatol.* 10, 339-355.
- Harmon, E.H., Behrensmeier, A.K., Kimbel, W.H. & Johanson, D.C. (2003). Preliminary taphonomic analysis of hominin remains from A.L. 333, Hadar Formation, Ethiopia: Abstracts of the 2003 meetings of the Paleoanthropology Society (<http://www.paleoanthro.org/abst2003.htm>).

- Hartwig, W.C., Ed (2002). *The Primate Fossil Record*. Cambridge: Cambridge University Press.
- Hartwig-Scherer, S. (1993). Body weight prediction in early fossil hominids: towards a taxon-“independent” approach. *Am. J. Phys. Anthropol.* 92, 17–36.
- Hartwig-Scherer, S. & Martin, R.D. (1992). Allometry and prediction in hominoids: A solution to the problem of intervening variables. *Am. J. Phys. Anthropol.* 88, 37-57.
- Harvey, P.H., Kavanagh, M. & Clutton-Brock, T.H. (1978). Sexual dimorphism in primate teeth. *J. Zool. (Lond.)* 186, 474-485.
- Hasegawa, T. & Hiraiwai-Hasegawa, M. (1990). Sperm competition and mating behavior. In (T. Nishida, Ed) *The Chimpanzees of the Mahale Mountains: Sexual and Life History Strategies*, pp. 115-132. Tokyo: University of Tokyo Press.
- Head, G. (1995). Selection on fecundity and variation in the degree of sexual size dimorphism among spider species (class Areneae). *Evolution* 49, 776-781.
- Hernandez-Camacho, J. & Defler, T.R. (1985). Some aspects of the conservation of non-human primates in Columbia. *Primate Conservation* 6, 42–50.
- Heymann, E.W. (2000). The number of adult males in callitrichine groups and its implications for callitrichine social evolution. In (P.M. Kappeler, Ed) *Primate Males: Causes and Consequences of Variation in Group Composition*, pp. 64-71. Cambridge: Cambridge University Press.
- Heymann, E.W. (2003). Scent marking, paternal care, and sexual selection in callitrichines. In (C.B. Jones, Ed) *Sexual Selection and Reproductive Competition in Primates: New Perspectives and Directions*, pp. 305-325. Norman, Oklahoma: American Society of Primatologists.
- Horovitz, I. & MacPhee, R.D.E. (1999). The Quaternary Cuban platyrrhine *Paralouatta varonai* and the origin of the ANtillean monkeys. *J. Hum. Evol.* 36, 33-68.
- Horrocks, J.A. (1986). Life-history characteristics of a wild population of vervets (*Cercopithecus aethiops sabaues*) in Barbados, West Indies. *Int. J. Primatol.* 7, 31–47.
- Housworth, E.A. & Martins, E.P. (2001). Random sampling of constrained phylogenies: conducting phylogenetic analyses when the phylogeny is partially known. *Syst. Biol.* 50, 628-639.
- Huelsenback, J.P. & Rannala, B. (2003). Detecting correlations between characters in a comparative analysis with uncertain phylogeny. *Evolution* 57, 1237-1247.

- Ihaka, R. & Gentleman, R. (1996). R: a language for data analysis and graphics. *J. Comput. Graph. Stat.* 5, 299-314.
- Ique, C. (1990). Estudio de la bioecología de *Saimiri sciureus* en la Isla de Iquitos, Loreto, Peru) *La Primatología en el Peru. Investigaciones Primatológicas (1973-1985)*, pp. 489-505. Lima, Peru: Ministerio de Agricultura.
- Isbell, L.A. (1991). Contest and scramble competition: Patterns of female aggression and ranging behavior among primates. *Behav. Ecol.* 2, 143-155.
- Isbell, L.A. & Pruett, J.D. (1998). Differences between vervets (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*) in agonistic interactions between adult females. *Int. J. Primatol.* 19, 837-855.
- Ishida, H. & Pickford, M. (1997). A new Late Miocene hominoid from Kenya: *Samburupithecus kiptalami* gen. et sp. nov. *C. R. Acad. Sci. Paris, Ser. II* 325, 823-829.
- Jacobs, B.F. (2002). Estimation of low-latitude paleoclimates using fossil angiosperm leaves: examples from the Miocene Tugen Hills, Kenya. *Paleobiology* 28, 399-421.
- Janis, C.M. (1993). Tertiary mammal evolution in the context of changing climates, vegetation, and tectonic events. *Annu. Rev. Ecol. Syst.* 24, 467-500.
- Janson, C.H. & Chapman, C.A. (1999). Resources and primate community structure. In (J.G. Fleagle, C.H. Janson & K.E. Reed, Eds) *Primate Communities*, pp. 237-267. Cambridge: Cambridge University Press.
- Jantz, L.M. & Jantz, R.L. (1999). Secular change in long bone length and proportion in the United States, 1800-1970. *Am. J. Phys. Anthropol.* 110, 57-67.
- Jarman, P. (1983). Mating system and sexual dimorphism in large, terrestrial, mammalian herbivores. *Biological Reviews* 58, 485-520.
- Johnson, S.E., Gordon, A.D., Stumpf, R.M., Overdorff, D.J. & Wright, P. (in review). Sexual dimorphism and testes size in brown lemurs (*Eulemur albocollaris* and *E. fulvus rufus*). *Int. J. Primatol.*
- Jolly, A. (1966). *Lemur Behavior: A Madagascar Field Study*. Chicago: University of Chicago Press.
- Jungers, W.L. (1985). Body size and scaling of limb proportions in primates. In (W.L. Jungers, Ed) *Size and Scaling in Primate Biology*, pp. 345-381. New York and London: Plenum Press.

- Jungers, W.L. (1987). Body size and morphometric affinities of the appendicular skeleton in *Oreopithecus bambolii* (IGF 11778). *J. Hum. Evol.* 16, 445-456.
- Jungers, W.L. (1990a). Problems and methods in reconstructing body size in fossil primates. In (J. Damuth & B. MacFadden, Eds) *Body Size in Mammalian Paleobiology: Estimation and Biological Implications*, pp. 103-118. Cambridge: Cambridge University Press.
- Jungers, W.L. (1990b). Scaling of postcranial joint size in hominoid primates. In (F.K. Jouffroy, S.M. H & C. Niemitz, Eds) *Gravity, Posture and Locomotion in Primates*, pp. 87-95. Florence, Italy: Il Sedicesimo.
- Jungers, W.L. & Burr, D.B. (1994). Body size, long bone geometry and locomotion in quadrupedal monkeys. *Z. Morphol. Anthropol.* 80, 89-97.
- Jungers, W.L., Burr, D.B. & Cole, M.S. (1998). Body size and scaling of long bone geometry, bone strength, and positional behavior in cercopithecoid primates. In (E. Strasser, J.G. Fleagle, A. Rosenberger & H. McHenry, Eds) *Primate Locomotion. Recent Advances*, pp. 309-330. New York: Plenum Press.
- Jungers, W.L., Falsetti, A.B. & Wall, C.E. (1995). Shape, relative size, and size-adjustments in morphometrics. *Yearb. phys. Anthropol.* 38, 137-161.
- Jungers, W.L., Godfrey, L.R., Simons, E.L., Wunderlich, R.E., Richmond, B.G. & Chatrath, P.S. (2002). Ecomorphology and behavior of giant extinct lemurs from Madagascar. In (J.M. Plavcan, R.F. Kay, W.L. Jungers & C.P. van Schaik, Eds) *Reconstructing behavior in the primate fossil record*, pp. 297-338. New York: Kluwer Academic/Plenum Publishers.
- Jungers, W.L. & Stern, J.T., Jr. (1983). Body proportions, skeletal allometry and locomotion in the Hadar hominids: a reply to Wolpoff. *J. Hum. Evol.* 12, 673-684.
- Jungers, W.L. & Susman, R.L. (1984). Body size and skeleton allometry in African apes. In (R.L. Susman, Ed) *The Pygmy Chimpanzee*, pp. 131-177. New York: Plenum Press.
- Kamilar, J. (2003). The relationship between sexual dimorphism and male-female dietary niche separation in haplorhine primates. *Am. J. Phys. Anthropol.* Supplement 36, 126.
- Kano, T. (1992). *The Last Ape: Pygmy Chimpanzee Behaviour and Ecology*. Stanford, CA: Stanford University Press.
- Kappeler, P.M. (1990). The evolution of sexual size dimorphism in prosimian primates. *Am. J. Primatol.* 21, 201-214.

- Kappeler, P.M. (1991). Patterns of sexual dimorphism in body weight among prosimian primates. *Folia Primatol.* 57, 132-146.
- Kappeler, P.M. (1997a). Determinants of primate social organization: Comparative evidence and new insights from Malagasy lemurs. *Biological Reviews* 72, 111-151.
- Kappeler, P.M. (1997b). Intrasexual selection and testis size in strepsirrhine primates. *Behav. Ecol.* 8, 10-19.
- Kappeler, P.M. (1997c). Intrasexual selection in *Mirza coquereli*: Evidence for scramble competition polygyny in a solitary primate. *Behav. Ecol. Sociobiol.* 41, 115-127.
- Kappeler, P.M. (2000a). Causes and consequences of unusual sex ratios among lemurs. In (P.M. Kappeler, Ed) *Primate Males: Causes and Consequences of Variation in Group Composition*, pp. 55-63. Cambridge: Cambridge University Press.
- Kappeler, P.M., Ed (2000b). *Primate Males: Causes and Consequences of Variation in Group Composition*. Cambridge: Cambridge University Press.
- Kappelman, J. (1996). The evolution of body mass and relative brain size in fossil hominids. *J. Hum. Evol.* 30, 243-276.
- Kappelman, J., Plummer, T., Bishop, L., Duncan, A. & Appleton, S. (1997). Bovids as indicators of Plio-Pleistocene paleoenvironments in East Africa. *J. Hum. Evol.* 32, 229-256.
- Kingston, J.D., Jacobs, B.F., Hill, A. & Deino, A. (2002). Stratigraphy, age and environments of the late Miocene Mpesida Beds, Tugen Hills, Kenya. *J. Hum. Evol.* 42, 95-116.
- Kingston, J.D., Marino, B.D. & Hill, A. (1994). Isotopic Evidence for Neogene Hominid Paleoenvironments in the Kenya Rift-Valley. *Science* 264, 955-959.
- Kinzey, W.G., Norconk, M.A. & Alvarez-Cordero, E. (1988). Primate survey of eastern Bolivar, Venezuela. *Primate Conservation* 9, 66-70.
- Koyama, N. (1988). Mating behavior of ring-tailed lemurs (*Lemur catta*) at Berenty, Madagascar. *Primates* 29, 163-175.
- Kramer, A., Donnelly, S.M., Kidder, J.H., Ousley, S.D. & Olah, S.M. (1995). Craniometric variation in large-bodied hominoids: testing the single-species hypothesis for *Homo habilis*. *J. Hum. Evol.* 29, 443-462.
- Kraus, C., Heistermann, M. & Kappeler, P.M. (1999). Physiological suppression of sexual function of subordinate males: A subtle form of intrasexual competition

- among male sifakas (*Propithecus verreauxi*)? *Physiology & Behavior* 66, 855-861.
- Krupa, J.J. & Sih, A. (1993). Experimental studies on water strider mating dynamics: spatial variation in density and sex ratio. *Behav. Ecol. Sociobiol.* 33, 107-120.
- Lague, M.R. & Jungers, W.L. (1996). Morphometric variation in Plio-Pleistocene hominid distal humeri. *Am. J. Phys. Anthropol.* 101, 401-427.
- Lande, R. (1980). Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution* 34, 292-305.
- Latimer, B. & Lovejoy, C.O. (1989). The calcaneus of *Australopithecus afarensis* and its implications for the evolution of bipedality. *Am. J. Phys. Anthropol.* 78, 369-386.
- Leigh, S.R. (1992). Patterns of variation in the ontogeny of primate body size dimorphism. *J. Hum. Evol.* 23, 27-50.
- Leigh, S.R. (1995). Socioecology and the ontogeny of sexual size dimorphism in anthropoid primates. *Am. J. Phys. Anthropol.* 97, 339-356.
- Leigh, S.R. & Shea, B.T. (1995). Ontogeny and the evolution of adult body size dimorphism in apes. *Am. J. Primatol.* 36, 37-60.
- Leigh, S.R. & Shea, B.T. (1996). Ontogeny of body size variation in African apes. *Am. J. Phys. Anthropol.* 99, 43-65.
- Leigh, S.R. & Terranova, C.J. (1998). Comparative perspectives on bimaturism, ontogeny, and dimorphism in lemurid primates. *Int. J. Primatol.* 19, 723-749.
- Lemos de Sá, R.M. & Glander, K.E. (1993). Capture techniques and morphometrics for the wholly spider monkey, or muriqui (*Brachyteles arachnoides*, E. Geoffroy 1806). *Am. J. Primatol.* 29, 145-153.
- Leutenegger, W. (1978). Scaling of sexual dimorphism in body size and breeding system in primates. *Nature* 272, 610-611.
- Leutenegger, W. & Cheverud, J. (1982). Correlates of sexual dimorphism in Primates: ecological and size variables. *Int. J. Primatol.* 3, 387-402.
- Leutenegger, W. & Cheverud, J.M. (1985). Sexual dimorphism in primates: the effects of size. In (W.L. Jungers, Ed) *Size and Scaling in Primate Biology*, pp. 33-50. NY: Plenum Press.
- Leutenegger, W. & Kelly, J.T. (1977). Relationship of sexual dimorphism in canine size and body size to social, behavioral, and ecological correlates in anthropoid primates. *Primates* 18, 117-136.

- Lewis, R.J. & Kappeler, P.M. (in review). Seasonality, body condition, and the timing of reproduction in *Propithecus verreauxi verreauxi*. *Am. J. Primatol.*
- Lindenfors, P. (2002). Sexually antagonistic selection on primate size. *J. Evol. Biol.* 15, 595-607.
- Lindenfors, P. & Tullberg, B.S. (1998). Phylogenetic analyses of primate size evolution: the consequences of sexual selection. *Biol. J. Linn. Soc. Lond.* 64, 413-447.
- Lockwood, C.A. (1999). Sexual dimorphism in the face of *Australopithecus afarensis*. *Am. J. Phys. Anthropol.* 108, 97-127.
- Lockwood, C.A., Kimbel, W.H. & Johanson, D.C. (2000). Temporal trends and metric variation in the mandibles and dentition of *Australopithecus afarensis*. *J. Hum. Evol.* 39, 23-55.
- Lockwood, C.A., Richmond, B.G., Jungers, W.L. & Kimbel, W.H. (1996). Randomization procedures and sexual dimorphism in *Australopithecus afarensis*. *J. Hum. Evol.* 31, 537-548.
- Lovejoy, C.O. (1981). The origin of man. *Science* 211, 341-350.
- MacKinnon, J.R. (1974). The behaviour and ecology of wild orang-utans (*Pongo pygmaeus*). *Anim. Behav.* 22, 3-74.
- MacPhee, R.D.E. & Horowitz, I. (2002). Extinct Quaternary platyrrhines of the Greater Antilles and Brazil. In (W.C. Hartwig, Ed) *The Primate Fossil Record*, pp. 189-200. Cambridge: Cambridge University Press.
- Maddison, W.P. & Maddison, D.R. (2003). Mesquite: a modular system for evolutionary analysis. Version 1.0.
- Martin, R.D., Willner, L.A. & Dettling, A. (1994). The evolution of sexual size dimorphism in primates. In (R.V. Short & E. Balaban, Eds) *The Differences Between the Sexes*, pp. 159-200. Cambridge: Cambridge University Press.
- Martins, E.P. (1996a). Conducting phylogenetic comparative studies when the phylogeny is not known. *Evolution* 50, 12-22.
- Martins, E.P. (1996b). Phylogenies, spatial autocorrelation, and the comparative method: A computer simulation test. *Evolution* 50, 1750-1765.
- Martins, E.P. (2003). COMPARE, version 4.5. Computer programs for the statistical analysis of comparative data. Bloomington, IN: Department of Biology, Indiana University.

- Martins, E.P. & Garland, T., Jr. (1991). Phylogenetic analyses of the correlated evolution of continuous characters: A simulation study. *Evolution* 45, 534-557.
- Martins, E.P. & Hansen, T.F. (1997). Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *Am. Nat.* 149, 646-667. Erratum 153:448.
- Martins, E.P. & Housworth, E.A. (2002). Phylogeny shape and the phylogenetic comparative method. *Syst. Biol.* 51, 873-880.
- Martins, E.P. & Lamont, J. (1998). Estimating ancestral states of a communicative display: a comparative study of *Cyclura* rock iguanas. *Anim. Behav.* 55, 1685-1706.
- Mathers, K. & Henneberg, M. (1996). Were we ever that big? Gradual increase in hominid body size over time. *Homo* 46, 141-173.
- Maynard Smith, J. (1977). Parental investment: a prospective analysis. *Anim. Behav.* 25, 1-9.
- McHenry, H.M. (1986). Size variation in the postcranium of *Australopithecus afarensis* and extant species of Hominoidea. *J. Hum. Evol.* 1, 149-156.
- McHenry, H.M. (1992). Body size and proportions in early hominids. *Am. J. Phys. Anthropol.* 87, 407-431.
- McHenry, H.M. (1994a). Behavioral ecological implications of early hominid body size. *J. Hum. Evol.* 27, 77-87.
- McHenry, H.M. (1994b). Sexual dimorphism in fossil hominids and its sociological implications. In (S. Shennan & J. Steele, Eds) *Power, Sex and Tradition: The Archeology of Human Ancestry*, pp. 91-109. London: Routledge and Keegan Paul.
- Midford, P.E., Garland, T., Jr. & Maddison, W.P. (2002). PDAP:PDTREE: A translation of the PDTREE application of Garland *et al.*'s Phenotypic Diversity Analysis Programs.
- Milton, K.M. (1985a). Mating patterns of woolly spider monkeys, *Brachyteles arachnoides*: implications for female choice. *Behav. Ecol. Sociobiol.* 17, 53-59.
- Milton, K.M. (1985b). Multimale mating and absence of canine tooth dimorphism in woolly spider monkeys, *Brachyteles arachnoides*. *Am. J. Phys. Anthropol.* 68, 519-523.
- Mitani, J.C. (1985). Mating behaviour of male orangutans in the Kutai Game Reserve, Indonesia. *Anim. Behav.* 33, 392-402.

- Mitani, J.C., Gros-Louis, J. & Richards, A.F. (1996). Sexual dimorphism, the operational sex ratio, and the intensity of male competition in polygynous primates. *Am. Nat.* 147, 966-980.
- Mitchell, C.L., Boinski, S. & van Schaik, C.P. (1991). Competitive regimes and female bonding in two species of squirrel monkey (*Saimiri oerstedii* and *S. sciureus*). *Behav. Ecol. Sociobiol.* 28, 55-60.
- Morell, V. (1994). Decoding chimp genes and lives. *Science* 265, 1172-1173.
- Morgan, M.E., Kingston, J.D. & Marino, B.D. (1994). Carbon isotope evidence for the emergence of C4 plants in the Neogene from Pakistan and Kenya. *Nature* 367, 162-165.
- Morin, P.A., Moore, J.J., Chakraborty, R., Jin, L., Goodall, J. & Woodruff, D.S. (1994). Kin selection, social structure, gene flow, and the evolution of chimpanzees. *Science* 265, 1193-1201.
- Mosimann, J.E. (1970). Size allometry: size and shape variables with characterizations of the lognormal and generalized gamma distributions. *J. Am. Stat. Assoc.* 65, 930-945.
- Moya, L., Verdi, L., Bocanegra, G. & Rimachi, J. (1990). Analisis poblacional de *Saguinus mystax* (Spix 1823) (Callitrichidae) en la cuenca del Rio Yarapa, Loreto, Peru) *La Primatologia en el Peru. Investigaciones Primatologicas (1973-1985)*, pp. 80-95. Lima, Peru: Ministerio de Agricultura.
- Müller, A.E. & Thalmann, U. (2000). Origin and evolution of primate social organisation: a reconstruction. *Biological Reviews* 75, 405-435.
- Napier, P.H. (1981). *Catalogue of Primates in the British Museum (Natural History) and Elsewhere in the British Isles. Part II. Family Cercopithecidae, subfamily Cercopithecinae*. London: British Museum (Natural History).
- Napier, P.H. (1985). *Catalogue of Primates in the British Museum (Natural History) and Elsewhere in the British Isles. Part III. Family Cercopithecidae, subfamily Colobinae*. London: British Museum (Natural History).
- Nishimura, A. (1988). Mating behavior of woolly monkeys, *Lagothrix lagothrica*, at La Macarena, Colombia. *Field Studies of New World Monkeys* 1, 19-27.
- Nowak, R.M. (1999). *Walker's Primates of the World*. Baltimore, MD: The Johns Hopkins University Press.
- Nunn, C.L. & van Schaik, C.P. (2002). A comparative approach to reconstructing the socioecology of extinct primates. In (J.M. Plavcan, R.F. Kay, W.L. Jungers &

- C.P. van Schaik, Eds) *Reconstructing behavior in the primate fossil record*, pp. 159-215. New York: Kluwer Academic/Plenum Publishers.
- Oates, J.F., Davies, A.G. & Delson, E. (1994). The diversity of living colobines. In (A.G. Davies & J.F. Oates, Eds) *Colobine monkeys: their ecology, behaviour and evolution*, pp. 47-73. New York, NY: Cambridge University Press.
- Oates, J.F., Whitesides, G.H., Davies, A.G., Waterman, P.G., Green, S.M., Dasilva, G.L. & Mole, S. (1990). Determinants of variation in tropical forest primate biomass: New evidence from West Africa. *Ecology* 71, 328–343.
- Parga, J.A. (2003). Copulatory plug displacement evidences sperm competition in *Lemur catta*. *Int. J. Primatol.* 24, 889-899.
- Parker, G.A. & Simmons, L.W. (1996). Parental investment and the control of sexual selection: Predicting the direction of sexual competition. *Proc. R. Soc. Lond. B* 263, 315-321.
- Pereira, M.E. (1991). Asynchrony within estrous synchrony among ringtailed lemurs (Primates: Lemuridae). *Physiology & Behavior* 49, 47-52.
- Pereira, M.E. & Weiss, M.L. (1991). Female mate choice, male migration, and the threat of infanticide in ringtailed lemurs. *Behav. Ecol. Sociobiol.* 28, 141-152.
- Perret, M. & Aujard, F. (2001). Regulation by photoperiod of seasonal changes in body mass and reproductive function in gray mouse lemurs (*Microcebus murinus*): differential responses by sex. *Int. J. Primatol.* 22, 5-24.
- Petrie, M. (1983). Mate-choice in role-reversed species. In (P. Bateson, Ed) *Mate Choice*, pp. 167-179. Cambridge: Cambridge University Press.
- Phillips-Conroy, J.E. & Jolly, C.J. (1981). Sexual dimorphism in two subspecies of Ethiopian baboons (*Papio hamadryas*) and their hybrids. *Am. J. Phys. Anthropol.* 56, 115-129.
- Pianka, E.R. (1976). Natural-Selection of Optimal Reproductive Tactics. *Am. Zool.* 16, 775-784.
- Pianka, E.R. & Parker, W.S. (1975). Age-Specific Reproductive Tactics. *Am. Nat.* 109, 453-464.
- Pickford, M. (1991). Growth of the Ruwenzoris and their impact on paleoanthropology. In (A. Ehara, T. Kimura, O. Takenaka & M. Iwamoto, Eds) *Primate Today*, pp. 513-516. New York: Elsevier.

- Pickford, M., Sola, S.M. & Kohler, M. (1997). Phylogenetic implications of the first African Middle Miocene hominoid frontal bone from Otavi, Namibia. *C. R. Acad. Sci. Paris, Ser. II* 325, 459-466.
- Plavcan, J.M. (1990). Sexual dimorphism in the dentition of extant anthropoid primates. Ph.D. Dissertation, Duke University.
- Plavcan, J.M. (1999). Mating systems, intrasexual competition and sexual dimorphism in primates. In (P.C. Lee, Ed) *Comparative Primate Socioecology*, pp. 241-269. Cambridge, England: Cambridge University Press.
- Plavcan, J.M. (2000a). Inferring social behavior from sexual dimorphism in the fossil record. *J. Hum. Evol.* 39, 327-344.
- Plavcan, J.M. (2000b). Variance dimorphism in primates. *Am. J. Phys. Anthropol.* Supplement 30, 251.
- Plavcan, J.M. (2001). Sexual dimorphism in primate evolution. *Yearb. phys. Anthropol.* 44, 25-53.
- Plavcan, J.M. (2002). Reconstructing social behavior from dimorphism in the fossil record. In (J.M. Plavcan, R.F. Kay, W.L. Jungers & C.P. van Schaik, Eds) *Reconstructing behavior in the primate fossil record*, pp. 297-338. New York: Kluwer Academic/Plenum Publishers.
- Plavcan, J.M. (2003). Scaling relationships between craniofacial sexual dimorphism and body mass dimorphism in primates: Implications for the fossil record. *Am. J. Phys. Anthropol.* 120, 38-60.
- Plavcan, J.M. (in press). Sexual selection, measures of sexual selection, and sexual dimorphism in primates. In (P.M. Kappeler & C.P. van Schaik, Eds) *Sexual Selection in Primates*. Cambridge: Cambridge University Press.
- Plavcan, J.M. & Kay, R.F. (1988). Sexual dimorphism and dental variability in platyrrhine primates. *Int. J. Primatol.* 9, 169-178.
- Plavcan, J.M. & van Schaik, C.P. (1992). Intrasexual competition and canine dimorphism in anthropoid primates. *Am. J. Phys. Anthropol.* 87, 461-477.
- Plavcan, J.M. & van Schaik, C.P. (1997a). Interpreting hominid behavior on the basis of sexual dimorphism. *J. Hum. Evol.* 32, 346-374.
- Plavcan, J.M. & van Schaik, C.P. (1997b). Intrasexual competition and body weight dimorphism in anthropoid primates. *Am. J. Phys. Anthropol.* 103, 37-68.
- Plavcan, J.M., van Schaik, C.P. & Kappeler, P.M. (1995). Competition, coalitions and canine size in primates. *J. Hum. Evol.* 28, 245-276.

- Popp, J.L. (1983). Ecological determinism in the life histories of baboons. *Primates* 24, 198-210.
- Powzyk, J.A. (1996). A comparison of feeding strategies between the sympatric *Indri indri* and *Propithecus diadema diadema* in primary rain forest. *Am. J. Phys. Anthropol.* 22 (Supplement), 190.
- Purvis, A. (1995). A composite estimate of primate phylogeny. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.* 348, 405-421.
- Purvis, A. & Webster, A.J. (1999). Phylogenetically independent comparisons and primate phylogeny. In (P.C. Lee, Ed) *Comparative Primate Socioecology*, pp. 44-68. Cambridge, England: Cambridge University Press.
- Rafferty, K.L., Walker, A., Ruff, C.B., Rose, M.D. & Andrews, P.J. (1995). Postcranial estimates of body weight in *Proconsul*, with a note on a distal tibia of *P. major* from Napak, Uganda. *Am. J. Phys. Anthropol.* 97, 391-402.
- Ralls, K. (1976). Mammals in which females are larger than males. *Q. Rev. Biol.* 51, 245-276.
- Ralls, K. (1977). Sexual dimorphism in mammals: Avian models and unanswered questions. *Am. Nat.* 111, 917-938.
- Rasoloharijaona, S., Rakotosamimanana, B., Randrianambinina, B. & Zimmermann, E. (2003). Pair-specific usage of sleeping sites and their implications for social organization in a nocturnal Malagasy primate, the Milne Edwards' sportive lemur (*Lepilemur edwardsi*). *Am. J. Phys. Anthropol.* 122, 251-258.
- Ravosa, M.J. (1998). Cranial allometry and geographic variation in slow lorises (*Nycticebus*). *Am. J. Primatol.* 45, 225-243.
- Reeder, D.M. (2003). The potential for cryptic female choice in primates: Behavioral, anatomical, and physiological considerations. In (C.B. Jones, Ed) *Sexual Selection and Reproductive Competition in Primates: New Perspectives and Directions*, pp. 255-303. Norman, Oklahoma: American Society of Primatologists.
- Reeve, J.P. & Fairbairn, D.J. (1996). Sexual size dimorphism as a correlated response to selection on body size: an empirical test of the quantitative genetic model. *Evolution* 50, 1927-1938.
- Reiss, M.J. (1986). Sexual dimorphism in body size: Are larger species more dimorphic? *Journal of Theoretical Biology* 121, 163-172.
- Reno, P.L., Meindl, R.S., McCollum, M.A. & Lovejoy, C.O. (2003). Sexual dimorphism in *Australopithecus afarensis* was similar to that of modern humans. *Proc. Natl. Acad. Sci. U.S.A.* 100, 9404-9409.

- Rensch, B. (1950). Die Abhängigkeit der relativen Sexualdifferenz von der Körpergröße. *Bonner Zoologische Beiträge* 1, 58-69.
- Rensch, B. (1959). *Evolution Above the Species Level*. New York: Columbia University Press.
- Richard, A.F., Dewar, R.E., Schwartz, M. & Ratsirarson, J. (2000). Mass change, environmental variability and female fertility in wild *Propithecus verreauxi*. *J. Hum. Evol.* 39, 381-391.
- Richmond, B.G., Aiello, L.C. & Wood, B.A. (2002). Early hominin limb proportions. *J. Hum. Evol.* 43, 529-548.
- Richmond, B.G. & Jungers, W.L. (1995). Size variation and sexual dimorphism in *Australopithecus afarensis* and living hominoids. *J. Hum. Evol.* 29, 229-245.
- Robbins, M.M. (1999). Male mating patterns in wild multimale mountain gorilla groups. *Anim. Behav.* 57, 1013-1020.
- Robertson, A. (1977). Artificial selection with a large number of linked loci. In (E. Pollak, O. Kempthorne & T.B. Bailey, Jr., Eds) *Proceedings of the International Conference on Quantitative Genetics*, pp. 307-322. Ames, Iowa: Iowa State University Press.
- Robinson, J.G., Wright, P.C. & Kinzey, W.G. (1987). Monogamous cebids and their relatives: Intergroup calls and spacing. In (B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham & T.T. Struhsaker, Eds) *Primate Societies*, pp. 44-53. Chicago: University of Chicago Press.
- Rodman, P.S. & Mitani, J.C. (1987). Orangutans: sexual dimorphism in a solitary species. In (B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham & T.T. Struhsaker, Eds) *Primate Societies*, pp. 146-154. Chicago: University of Chicago Press.
- Rodríguez, G.A.C. & Boher, S. (1988). Notes on the biology of *Cebus nigrivittatus* and *Alouatta seniculus* in Northern Venezuela. *Primate Conservation* 9, 61-66.
- Rohlf, F.J. (2001). Comparative methods for the analysis of continuous variables: geometric interpretations. *Evolution* 55, 2143-2160.
- Rose, M.D. (1984). Food acquisition and the evolution of positional behaviour: the case of bipedalism. In (D.J. Chivers, B.A. Wood & A. Bilsborough, Eds) *Food Acquisition and Processing in Primates*, pp. 509-524. New York: Plenum Press.
- Rosenberger, A.L. (1992). Evolution of feeding niches in New World monkeys. *Am. J. Phys. Anthropol.* 88, 525-562.

- Rosenberger, A.L. (2002). Platyrrhine paleontology and systematics: The paradigm shifts. In (W.C. Hartwig, Ed) *The Primate Fossil Record*, pp. 151-159. Cambridge: Cambridge University Press.
- Rosenberger, A.L. & Coimbra-Filho, A.F. (1984). Morphology, taxonomic status and affinities of the lion tamarins, *Leontopithecus* (Callitrichinae, Cebidae). *Folia Primatol.* 42, 149–179.
- Rosenberger, A.L., Norconk, M.A. & Garber, P.A. (1996). New perspectives on the pitheciines. In (M.A. Norconk, A.L. Rosenberger & P.A. Garber, Eds) *Adaptive Radiations of Neotropical Primates*, pp. 329-333. New York: Plenum Press.
- Rowe, L., Arnqvist, G., Sih, A. & Krupa, J.J. (1994). Sexual conflict and the evolutionary ecology of mating patterns: water striders as model system. *Trends Ecol. Evol.* 9, 289-293.
- Rudran, R. (1979). The demography and social mobility of red howler (*Alouatta seniculus*) population in Venezuela. In (J.G. Eisenberg, Ed) *Vertebrate Ecology in the Northern Neotropics*, pp. 107-126. Washington, DC: Smithsonian Institution Press.
- Ruff, C.B. (1987). Structural allometry of the femur and tibia in Hominoidea and *Macaca*. *Folia Primatol.* 48, 9-49.
- Ruff, C.B. (1988). Hindlimb articular surface allometry in Hominoidea and *Macaca*, with comparisons to diaphyseal scaling. *J. Hum. Evol.* 17, 687-714.
- Ruff, C.B. (1990). Body mass and hindlimb bone cross-sectional and articular dimensions in anthropoid primates. In (J. Damuth & B. MacFadden, Eds) *Body Size in Mammalian Paleobiology: Estimation and Biological Implications*, pp. 119-149. Cambridge: Cambridge University Press.
- Ruff, C.B. (2002). Long bone articular and diaphyseal structure in old world monkeys and apes. II: estimation of body mass. *Am. J. Phys. Anthropol.* 120, 16-37.
- Ruff, C.B., Walker, A.C. & Teaford, M.F. (1989). Body mass, sexual dimorphism and femoral proportions of *Proconsul* from Rusinga and Mfangano Islands, Kenya. *J. Hum. Evol.* 18, 515-536.
- Rumpler, Y. (2002). Chromosomal and molecular primatology. *Evolutionary Anthropology, Supplement 1*, 145-149.
- Sanders, W.J. & Bodenbender, B.E. (1994). Morphometric analysis of lumbar vertebra UMP 67-28: Implications for spinal function and phylogeny of the Miocene Moroto hominoid. *J. Hum. Evol.* 26, 203–237.

- Sauther, M.L. (1991). Reproductive behavior of free-ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar. *Am. J. Phys. Anthropol.* 84, 463-477.
- Schmid, J. & Ganzhorn, J.U. (1996). Resting metabolic rates of *Lepilemur ruficaudatus*. *Am. J. Primatol.* 38, 169-174.
- Schoener, T.W. (1970). Size patterns in West Indian *Anolis* lizards. II. Correlations with the size of particular sympatric species-displacement and convergence. *Am. Nat.* 104, 155-174.
- Schroder, I. (1993). Human sexual behavior, social organization, and fossil evidence: a reconsideration of human evolution. *Homo* 43, 263-277.
- Schultz, A.H. (1941). The relative size of the cranial capacity in primates. *Am. J. Phys. Anthropol.* 28, 273-287.
- Schürmann, C.L. & van Hooff, J.A.R.A.M. (1986). Reproductive strategies of the orang-utan: new data and a reconsideration of existing sociosexual models. *Int. J. Primatol.* 7, 265-287.
- Schwab, D. (2000). A preliminary study of spatial distribution and mating system of pygmy mouse lemurs (*Microcebus cf myoxinus*). *Am. J. Primatol.* 51, 41-60.
- Schwartz, J.H. (2003). Another perspective on hominid diversity. *Science* 301, 763.
- Scott, N.J., Jr, Scott, A.F. & Malmgren, L.A. (1976). Capturing and marking howler monkeys for field behavioral studies. *Primates* 17, 527-533.
- Selander, R.K. (1966). Sexual dimorphism and differential niche utilization in birds. *Condor* 68, 113-151.
- Selander, R.K. (1972). Sexual selection and dimorphism in birds. In (B. Campbell, Ed) *Sexual Selection and the Descent of Man*, pp. 180-230. Chicago: Aldine.
- Setchell, J.M., Lee, P.C., Wickings, E.J. & Dixson, A.F. (2001). Growth and ontogeny of sexual size dimorphism in the mandrill (*Mandrillus sphinx*). *Am. J. Phys. Anthropol.* 115, 349-360.
- Shine, R. (1989). Ecological causes for the evolution of sexual dimorphism: A review of the evidence. *Q. Rev. Biol.* 64, 419-461.
- Sih, A. & Krupa, J.J. (1992). Predation risk, food deprivation and non-random mating by size in the stream water strider, *Aquarius remigis*. *Behav. Ecol. Sociobiol.* 31, 51-56.
- Sirgurjonsdottir, H. (1981). The evolution of sexual size dimorphism in gamebirds, waterfowl and raptors. *Ornis Scandinavica* 12, 249-260.

- Sivinski, J.M. & Dodson, G. (1992). Sexual dimorphism in *Anastrepha suspensa* (Loew) and other tephritid fruit flies (Diptera: Tephritidae): possible roles of developmental rate, fecundity, and dispersal. *Journal of Insect Behavior* 5, 491-506.
- Skinner, J.D. & Smithers, R.H.N. (1990). *The Mammals of the Southern African Subregion*. Pretoria, South Africa: University of Pretoria.
- Slatkin, M. (1984). Ecological causes of sexual dimorphism. *Evolution* 38, 622-630.
- Small, M.F. (1989). Female choice in nonhuman primates. *Yearb. phys. Anthropol.* 32, 103-127.
- Smith, R.J. (1984). Allometric scaling in comparative biology: problem of concept and method. *Am. J. Physiol.* 246, R152-R160.
- Smith, R.J. (1994). Degrees of freedom in interspecific allometry: an adjustment for the effects of phylogenetic constraint. *Am. J. Phys. Anthropol.* 93, 95-107.
- Smith, R.J. (1996). Biology and body size in human evolution. *Curr. Anthropol.* 37, 451-481.
- Smith, R.J. (1999). Statistics of sexual size dimorphism. *J. Hum. Evol.* 36, 423-459.
- Smith, R.J. & Cheverud, J.M. (2002). Scaling of sexual dimorphism in body mass: a phylogenetic analysis of Rensch's rule in Primates. *Int. J. Primatol.* 23, 1095-1135.
- Smith, R.J. & Jungers, W.L. (1997). Body mass in comparative primatology. *J. Hum. Evol.* 32, 523-559.
- Soini, P. (1986). A synecological study of a primate community in Pacaya-Saiiria National Reserve, Peru. *Primate Conservation* 7, 63-71.
- Soini, P. (1990). Ecología y dinámica poblacional de pichico común *Saguinus fuscicollis* (Callitrichidae, Primates)) *La Primatología en el Perú. Investigaciones Primatológicas (1973-1985)*, pp. 202-253. Lima, Perú: Ministerio de Agricultura.
- Soini, P. & de Soini, M. (1990). Distribución geográfica y ecología poblacional de *Saguinus mystax*) *La Primatología en el Perú. Investigaciones Primatológicas (1973-1985)*, pp. 272-313. Lima, Perú: Ministerio de Agricultura.
- Sorensen, D. & Kennedy, B.W. (1984). Estimation of genetic variables from selected and unselected populations. *J. Anim. Sci.* 59, 1213-1223.
- Stanger, K.F., Coffman, B.S. & Izard, M.K. (1995). Reproduction in Coquerel's dwarf lemur (*Mirza coquereli*). *Am. J. Primatol.* 36, 223-237.

- Stern, J.T., Jr. & Susman, R.L. (1983). The locomotor anatomy of *Australopithecus afarensis*. *Nature* 297, 676-678.
- Stern, J.T.J. & Larson, S.G. (1993). Electromyographic study of the obturator muscles in non-human primates: implications for interpreting the obturator externus groove of the femur. *J. Hum. Evol.* 24, 403-427.
- Struhsaker, T.T. (2000). Variation in adult sex ratios of red colobus monkey social groups: implications for interspecific comparisons. In (P.M. Kappeler, Ed) *Primate Males: Causes and Consequences of Variation in Group Composition*, pp. 108-119. Cambridge: Cambridge University Press.
- Susman, R.L., Stern, J.T., Jr. & Jungers, W.L. (1984). Arboreality and bipedality in the Hadar hominids. *Folia Primatol.* 43, 113-156.
- Symonds, M.R.E. (2002). The effects of topological inaccuracy in evolutionary trees on the phylogenetic comparative method of independent contrasts. *Syst. Biol.* 51, 542-553.
- Tague, R.C. & Lovejoy, C.O. (1998). AL 288-1-Lucy or Lucifer: gender confusion in the Pliocene. *J. Hum. Evol.* 35, 75-94.
- Thackeray, J.F. (1997). Probabilities of conspecificity. *Nature* 390, 30-31.
- Thorington, R.W., Jr., Rudran, R. & Mack, D. (1979). Sexual dimorphism of *Alouatta seniculus* and observations on capture techniques. In (J.G. Eisenberg, Ed) *Vertebrate Ecology in the Northern Neotropics*, pp. 97-106. Washington, DC: Smithsonian Institution Press.
- Tilson, R.L. & Tenaza, R.R. (1976). Monogamy and duetting in an Old World monkey. *Nature* 263, 320-321.
- Turner, T.R., Anapol, F. & Jolly, C.J. (1997). Growth, development, and sexual dimorphism in vervet monkeys (*Cercopithecus aethiops*) at four sites in Kenya. *Folia Primatol.* 103, 19-35.
- Tutin, C.E.G. (1979). Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behav. Ecol. Sociobiol.* 6, 29-38.
- Uehara, S. & Nishida, T. (1987). Body weights of wild chimpanzees (*Pan troglodytes schweinfurthii*) of the Mahale Mountains National Park, Tanzania. *Am. J. Phys. Anthropol.* 72, 315-321.
- Utami, S.S., Goossens, B., Bruford, M.W., de Ruiter, J.R. & van Hooff, J.A.R.A.M. (2002). Male bimaturism and reproductive success in Sumatran orang-utans. *Behav. Ecol.* 13, 643-652.

- van der Werf, J. & de Boer, I. (1990). Estimation of additive genetic variance when base populations are selected. *J. Anim. Sci.* 68, 3124-3132.
- van Hooff, J.A.R.A.M. (2000). Relationships among non human primate males: A deductive framework. In (P.M. Kappeler, Ed) *Primate Males: Causes and Consequences of Variation in Group Composition*, pp. 183-191. Cambridge: Cambridge University Press.
- van Hooff, J.A.R.A.M. & van Schaik, C.P. (1992). Cooperation in competition: The ecology of primate bonds. In (A.H. Harcourt & F.M.B. de Waal, Eds) *Coalitions and Alliances in Humans and Other Animals*, pp. 357-389: Oxford University Press.
- van Roosmalen, M.G.M. & Klein, L.L. (1988). The spider monkeys, genus *Ateles*. In (R.A. Mittermeier, A.B. Rylands, A.F. Coimbra-Filho & G.A.B. Fonseca, Eds) *Ecology and Behavior of Neotropical Primates, Vol. 2*, pp. 455-537. Washington, DC: World Wildlife Fund.
- van Schaik, C.P. (1989). The ecology of social relationships amongst female primates. In (V. Standen & F.A. Foley, Eds) *Comparative Socioecology: The Behavioral Ecology of Humans and Other Mammals*, pp. 195-218. Oxford: Blackwell Scientific Press.
- van Schaik, C.P. & Kappeler, P.M. (1996). The social systems of gregarious lemurs: lack of convergence with anthropoids due to evolutionary disequilibrium? *Ethology* 102, 915-941.
- Vogel, S. (1988). *Life's Devices: The Physical World of Animals and Plants*: Princeton University Press.
- Vollrath, F. & Parker, G.A. (1992). Sexual dimorphism and distorted sex ratios in spiders. *Nature* 360, 156-159.
- Vrba, E.S., Denton, G.H., Partridge, T.C. & Burckle, L.H., Eds. (1995). *Paleoclimate and Evolution, with Emphasis on Human Origins*. New Haven, CT: Yale University Press.
- Walter, R.C. (1994). Age of Lucy and the first family: single-crystal $^{40}\text{Ar}/^{39}\text{Ar}$ dating of the Denen Dora and lower Kada Hadar members of the Hadar Formation, Ethiopia. *Geology* 22, 6-10.
- Webster, M.S. (1992). Sexual dimorphism, mating system and body size in new world blackbirds (Icterinae). *Evolution* 46, 1621-1641.
- Weckerly, F.W. (1998). Sexual-size dimorphism: Influence of mass and mating systems in the most dimorphic mammals. *J. Mammal.* 79, 33-52.

- White, T.D. (2003). Another perspective on hominid diversity - response. *Science* 301, 763-764.
- Wickman, P.-O. (1992). Sexual selection and butterfly design - a comparative study. *Evolution* 46, 1525-1536.
- Wiley, R.H. (1974). Evolution of social organization and life-history patterns among grouse. *Q. Rev. Biol.* 49, 201-227.
- Williams, E.E. & Koopman, K.F. (1952). West Indian fossil monkeys. *American Museum Novitates* 1546, 1-16.
- WoldeGabriel, G., Haile-Selassie, Y., Renne, P.R., Hart, W.K., Ambrose, S.H., Asfaw, B., Heiken, G. & White, T. (2001). Geology and palaeontology of the Late Miocene Middle Awash valley, Afar rift, Ethiopia. *Nature* 412, 175-178.
- Wolpoff, M.H. (1976). Some aspects of the evolution of early hominid sexual dimorphism. *Curr. Anthropol.* 17, 579-606.
- Wolpoff, M.H. (1999). The systematics of *Homo*. *Science* 284, 1774-1775.
- Wood, B. & Collard, M. (1999). The systematics of *Homo* - response. *Science* 284, 1775.
- Wrangham, R.W. (1980). An ecological model of female-bonded primate groups. *Behaviour* 75, 262-300.
- Wright, P.C., Pochron, S.T., Haring, D.H. & Simons, E.L. (2003). Can we predict seasonal behavior and social organizations from sexual dimorphism and testes measurements? In (P.C. Wright, E.L. Simons & S. Gursky, Eds) *Tarsiers: Past, Present, Future*, pp. 260-273. New Brunswick, New Jersey: Rutgers University Press.
- Wright, S. (1968). *Evolution and the Genetics of Populations. Volume 1: Genetic and Biometric Foundations*. Chicago: The University of Chicago Press.
- Yu, J. & Dobson, F.S. (2000). Seven forms of rarity in mammals. *J. Biogeogr.* 27, 131-139.
- Zeng, Z.-B. (1988). Long term correlated response, interpopulation covariation, and interspecific allometry. *Evolution* 42, 363-374.

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