

Does body mass dimorphism increase male–female dietary niche separation? A comparative study of primates

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Summary

Body mass plays an important role in shaping an individual's behavior, especially with respect to dietary behavior. Larger animals tend to consume higher quantities of low quality foods. In contrast, smaller individuals, with relatively higher metabolic rates require a high quality diet. Therefore, species that exhibit high amounts of sexual dimorphism in body mass should also display high levels of male–female dietary differentiation. This study investigated the relationship between body mass dimorphism and dietary sex differences for 38 primate species. We conducted multiple regressions using female body mass and body mass dimorphism as independent variables. We found that body mass dimorphism was significantly negatively correlated with male–female differences in fauna consumption using species values as well as phylogenetically independent contrasts. In addition, body mass dimorphism was positively related to male–female differences in percent time feeding using phylogenetically independent contrasts. Body mass dimorphism was not significantly related to male–female differences in the percent of fruit and leaves in the diet. The results suggest that, as body mass dimorphism increases, there is some degree of dietary niche separation between the sexes of primates. These results will be discussed in the context of existing studies of intersexual niche separation.

Keywords: sex differences, feeding ecology, sexual selection, phylogenetically independent contrasts.

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Introduction

Sex differences in feeding ecology have been observed in a variety of taxa and may range from subtle variations in diet and feeding technique to more extreme degrees of sexual segregation in terms of sociality and habitat use (Clutton-Brock et al., 1987; duToit, 1995; Main et al., 1996; Thirgood, 1996; Stokke, 1999). Such differences are most commonly attributed to three major factors including (1) variation in costs of reproduction, (2) avoidance of competition between the sexes and (3) differences in body size/mass (sexual dimorphism) (Clutton-Brock, 1977). Among primates, sex differences are often observed in both diet and feeding behavior (Gautier-Hion, 1980; Harrison, 1983; Cords, 1986; Boinski, 1988; Mitani, 1989; Rose, 1994; Doran, 1997), yet there does not appear to be consistency in terms of factors driving these distinctions. In particular, despite the varying degrees of sexual dimorphism throughout the primate order, the effect of body size in relation to intraspecific differences is still uncertain. Moreover, studies that do cite sexual dimorphism as an influence on primate feeding behavior are often referring specifically to effects of body size on positional behavior rather than energetic and nutritional demands (Cant, 1987; Rose, 1994; Doran, 1997).

Sexual dimorphism is most often considered in reference to sexual selection, with large male body size being selected for due to competition among males for access to females (Trivers, 1972; Plavcan & van Schaik, 1997). Yet in addition to social implications, the resulting size difference is expected to influence dietary characteristics. The influence of sexual dimorphism on male–female ecological differences may result from the interplay between morphology and access to dietary resources. Larger bodied individuals are expected to be more constrained in terms of arboreal habitat use and are often more terrestrial than smaller individuals who are more adept at exploiting terminal branches (Fleagle & Mittermeier, 1980; McGraw, 1998). Masticatory morphology differences may also exist between small and large individuals, particularly in terms of canine size, musculature, and gape, leading to differences in bite size and food choice (Wheatley, 1982; Ginnett & Demment, 1997).

The importance of digestive morphology and body mass may also be observed in the general energetic and nutritional requirements of an animal. While gut capacity/retention times increase with body size (Jarman, 1974), relative energetic requirements per unit mass decrease with body size

(Bell, 1971; Geist, 1974). Therefore, larger bodied animals typically require a higher absolute intake of resources, yet are able to subsist on a wider variety of lower quality items (Demment & van Soest, 1985). Smaller animals, on the other hand, require more energy per unit mass and are, therefore, expected to be more selective and feed on higher quality items. This relationship has been particularly well studied in large herbivores. These studies suggest that a level of sexual dimorphism of at least 20% will result in ecological segregation of the sexes (Illius & Gordon, 1987; Ruckstuhl & Neuhaus, 2002).

Primates, however, are quite variable in terms of sexual dimorphism ranging from monomorphic species such as *Callicebus torquatus* to highly dimorphic species such as *Pongo pygmaeus*, in which males may be more than twice as large as females (Smith & Jungers, 1997). In species with particularly high levels of sexual dimorphism (male body mass > 160% female body mass), energetic costs of large males may in fact exceed those of females even when the high energetic demands of female reproduction are accounted for (Key & Ross, 1999). Unlike ungulates, primates encompass a variety of dietary guilds including insectivory, frugivory and folivory (Flea-gle, 1999).

Despite specific dietary needs, primate species typically select for foods high in energy (Conklin-Brittain et al., 1998) and protein (Barton & Whiten, 1994). Ripe fruit often serves as a high energy resource that is easily digestible whereas leaves are typically lower in sugars but are an important source of protein and are abundant in the environment. Insects are high in protein and may contain high levels of energy per unit weight. According to Kay (1984), large primates will tend to supplement a fruit based diet with more folivorous items as they will be more efficient at extracting available energy and protein, whereas small primates will be more likely to incorporate insects into their diet as they will be better able to utilize the nutrients available in these small prey (Kay, 1984; Leigh, 1994). If larger animals are able to feed more efficiently on lower quality items but have higher absolute requirements, it follows that they will also have to devote relatively more time to feeding in order to obtain sufficient energy, as compared to smaller animals.

If body mass does indeed play a significant role in the overall ecological niche of an organism, increasing degrees of body mass dimorphism should result in increasing levels of niche separation between males and females.

Therefore, the aim of this study is to investigate the relationship between body mass dimorphism and aspects of a species' dietary behavior, specifically sex differences in (1) feeding time, (2) leaf intake, (3) invertebrate fauna intake and (4) fruit intake. We predict that as the degree of body mass dimorphism increases across species, differentiation in male–female feeding behavior should also increase. This relationship is expected because males should consume more leaves and less fruit and fauna in their diet as they get bigger. If size dimorphism and sex differences in feeding are measured as a ratio of male to female values, we expect to find a positive correlation between size dimorphism and sex differences in folivory (because bigger males eat more leaves than females) and a negative correlation between size dimorphism and faunivory and frugivory (because bigger males eat proportionally less fruits and insects than females).

Methods

Data collection

Data were compiled from the published literature and personal communication with field researchers (Appendix A). Data were obtained for both males and females from a total of 38 primate species, yet not all of the desired data were present for all species. Therefore, different species are included in different analyses depending on the completeness of the available data. Body mass data for both sexes were obtained from Smith & Jungers (1997) for all species, except for chimpanzees living in Gombe, Tanzania. The data concerning the Gombe chimpanzees were reported by Wrangham & Smuts (1980) and are used in this analysis. For the dietary data, the goal was to include variables that best captured any existing differences between the sexes, while also being commonly reported in the literature. Therefore, four dependent variables were gathered for males and females: (1) the percent of time spent feeding, (2) the proportion of leaves in the diet, (3) the proportion of fauna in the diet and (4) the proportion of fruit in the diet.

For *Gorilla gorilla*, *Pongo pygmaeus*, *Pan troglodytes*, *Chlorocebus aethiops*, *Procolobus badius* and *Varecia variegata* data were available for more than one site and/or time period. The mean value for the species was used in the analyses.

Data analyses

Although we are interested in the relationship between body mass dimorphism and male–female differences in feeding in this paper, we need to account for the possible effect of body mass itself. Previous studies have suggested that there is higher body mass dimorphism in large primate species compared to small ones (Clutton-Brock et al., 1977; Leutenegger & Cheverud, 1985; Mitani et al., 1996). Therefore, to examine the independent effects of body mass and body mass dimorphism, we included female body mass and body mass dimorphism as predictor variables in all multiple regression models, using both species values and independent contrasts.

To calculate the degree of sex dimorphism, each variable was converted to a ratio, and then \log_{10} transformed (Smith, 1999). Since all species do not have a complete data set, different sets of species were included in the regressions. For all regressions, studentized residuals were calculated to detect potential outliers that may produce spurious results. We defined outliers as samples that exhibited studentized residuals of ± 2.70 . If outliers were detected, they were removed from the dataset and the regression was subsequently re-analyzed. Because feeding ecology variables are related to each other, the alpha level for each regression was adjusted after implementing sequential Bonferroni corrections (Rice, 1989). Therefore, with this method, the alpha level of the regression yielding the lowest p value was set at 0.0125, the regression that exhibited the next lowest p value had an α value of 0.0167, with the third and fourth regressions using alpha α of 0.0250 and 0.0500, respectively.

All regressions and correlations were conducted with Statistica 6.0.

Analyses using species values

The first set of analyses used species values. Least square multiple regressions were performed (Sokal & Rohlf, 1995) to examine the possible relationship between the two independent variables, female body mass and body mass dimorphism, and the dependent variables, male–female differences in (1) percent time spent feeding, (2) percent fauna, (3) percent leaves and (4) percent fruit.

Analyses using phylogenetically independent contrasts

In addition to employing regression analyses on the species data, another set of regressions were performed using phylogenetically independent contrasts. Since this paper is investigating patterns across numerous taxa, phylogenetically independent contrasts were used to attempt to minimize the non-independence of data due to species evolutionary relationships (Felsenstein, 1985; Harvey & Pagel, 1991). The independent contrasts were calculated using the PDAP module for Mesquite (Midford et al., 2003; Maddison & Maddison, 2007). This software is based on Felsenstein's (1985) method for computing phylogenetically independent data. The phylogeny and branch lengths (based on estimated divergence times between taxa) were obtained from a recent mammal phylogeny presented by Bininda-Emonds and colleagues (2007) (see Appendix A).

Generating phylogenetically independent contrasts relies on bifurcating branches, yet a fully resolved phylogenetic tree is rare when numerous taxa are involved. Most commonly, researchers choose the method of producing only one contrast at a multifurcating node. Alternatively, Garland & Diaz-Uriate (1999) suggest that more statistical power is obtained when polytomies are arbitrarily resolved using zero branch lengths. To account for Type I error rate inflation from this method, subsequent regression analyses should include a reduction in the degrees of freedom based on the number of zero branch lengths in the phylogeny. They propose that a range of p values should be presented, a minimum p value based on the no degrees of freedom modification, and a maximum p value resulting from reducing the degrees of freedom. We follow this latter approach in our paper.

An important assumption of the phylogenetically independent contrasts method is the lack of relationship between the branch lengths and the absolute values of the standardized contrasts (Nunn & Barton, 2001). The PDAP software has a test for this assumption and has several branch length transformation schemes to potentially better meet the assumption. If any variable failed the assumption test, we implemented the two most common branch length transformations, equal branch lengths, and Nee transformed branch lengths. We will present the results using all branch length schemes as this essentially provides a sensitivity test of our results.

All regressions using the contrast data were conducted with the regression line through the origin. This is necessary when using PICS data since the

expected value of a contrast is zero (Garland Jr., 1992; Nunn & Barton, 2001).

Results

Regressions using species values

Using species values, the regression examining the male–female ratio of fauna in the diet was not statistically significant ($p = 0.139$), yet an outlier existed in this analysis (*Cercopithecus petaurista*). When this outlier was removed the model was statistically significant at the 0.003 level, with body mass dimorphism being negatively correlated with sex differences in the amount of fauna in the diet (Figure 1). The negative relationship between these two variables indicates that as body mass dimorphism increases, the ratio of fauna in the diet decreases because females are consuming more fauna than males. The models examining male–female feeding time, and the percent of leaves

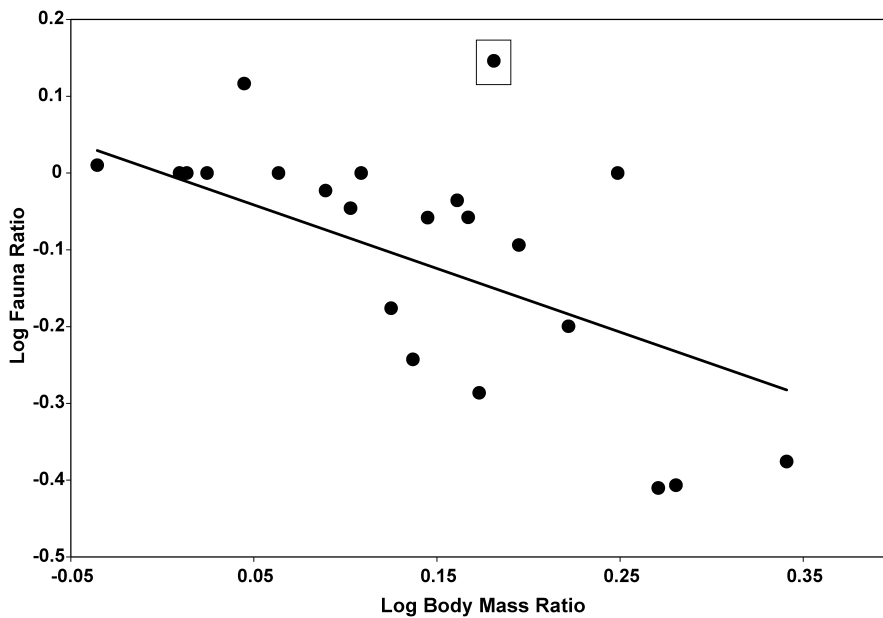


Figure 1. Plots of the relationship between body mass dimorphism and male–female differences in the percent of fauna in the diet. This plot does not account for female body mass itself. The highlighted data point is the species *Cercopithecus petaurista*.

Table 1. Results of multiple regression models examining the effects of female body mass and body mass dimorphism on male–female differences in feeding ecology using species values.

Dependent variable	Multiple r^2	df	F	p
Fauna	0.188	19	2.194	0.139
Fauna ^a	0.482	18	8.376	0.003
Leaves	0.131	21	1.584	0.229
Fruit	0.174	21	2.215	0.134
Feeding time	0.074	25	0.995	0.384

^a Model without the outlier, *Cercopithecus petaurista*, studentized residual >3.4.

Table 2. Independent effects of predictor variables examining male–female difference in feeding ecology using species values.

Dependent variable	Intercept	Female body mass		Body mass dimorphism	
	p	β	p	β	p
Fauna	0.450	0.084	0.753	−0.480	0.084
Fauna ^a	0.040	0.224	0.315	−0.811	0.001
Leaves	0.002	0.377	0.144	−0.407	0.117
Fruit	0.032	−0.018	0.940	0.426	0.080
Feeding time	<0.001	−0.058	0.803	0.299	0.206

^a Model without the outlier, *Cercopithecus petaurista*, studentized residual >3.4.

and fruit in the diet did not yield statistically significant results (Table 1). In all of the analyses, female body mass was not a significant predictor. The independent effect of body mass dimorphism was the only significant variable in the model predicting the male–female ratio of fauna in the diet (Table 2).

Regressions using phylogenetically independent contrasts

Most variables failed to meet the branch length vs. standardized contrast assumption using the estimated branch lengths. Using the Nee transformed branch lengths, three variables failed to meet the assumption test, log female mass ($p = 0.003$), log feeding time ratio ($p = 0.001$), and the ratio of percent leaves in the diet (0.020). Using equal branch lengths produced the best results, with only two variables failing the assumption test, log female

mass ($p = 0.013$) and log feeding time ratio ($p = 0.002$) (see Appendix). We attempted additional branch length transformation methods, yet these two variables did not meet the assumption in any case.

Using phylogenetically independent contrasts, the multiple regression model explaining male–female difference in the amount of fauna in the diet was statistically significant using estimated and Nee transformed branch lengths ($p = 0.003$ – 0.008). Using equal branch lengths the total model was significant at the $p = 0.0158$ – 0.018 level. In each analysis an extreme outlier existed (*Cercopithecus petaurista* vs. *Cercopithecus cephus* vs. *Cercopithecus ascanius*). Reanalyzing these data without the outlier produced a significant model at the <0.001 level under all branch length methods (Figure 2a and Table 3). The strength of the relationship between body mass dimorphism and male–female differences in the percent fauna in the diet is further emphasized by two important findings. The first finding is related

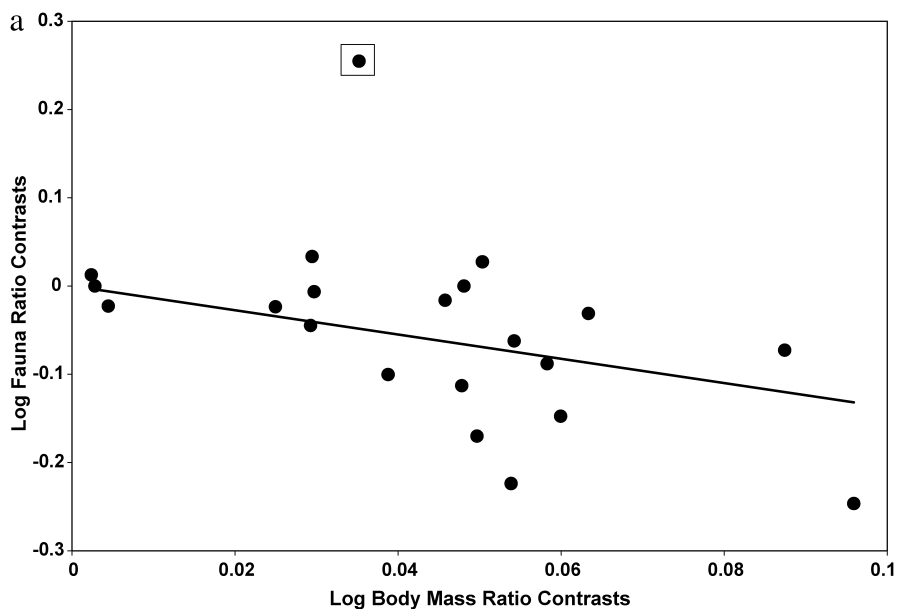


Figure 2. Plots of the relationship between body mass dimorphism and (a) male–female differences in the percent of fauna in the diet, and (b) male–female differences in time spent feeding, using phylogenetically independent contrasts and equal branch lengths. When using phylogenetically independent contrasts, all best fit lines pass through the origin. These plots do not account for female body mass itself. The highlighted data point is the contrast (a) *Cercopithecus petaurista* vs. *Cercopithecus cephus* vs. *Cercopithecus ascanius* and (b) *Erythrocebus patas* vs. *Chlorocebus aethiops*.

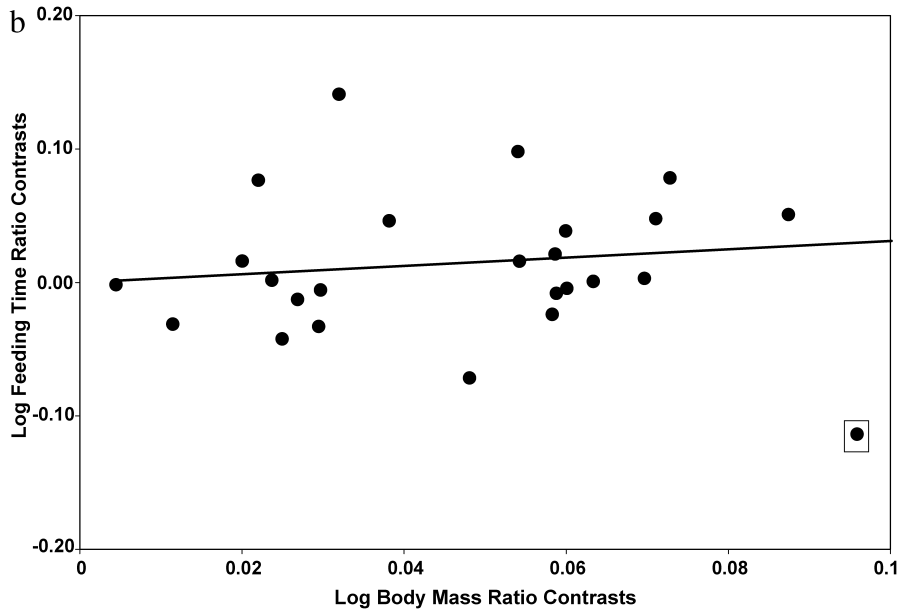


Figure 2. (Continued.)

to the relative importance of each predictor variable (Table 4). Female body mass is not a significant predictor of sex differences in fauna consumption. In contrast, body mass dimorphism is significantly related to male–female differences in the percent of fauna in the diet, with or without outliers included in the dataset. Second, the importance of body mass on fauna consumption is confirmed by a significant negative relationship between female body mass and female fauna consumption (estimated branch lengths, $p = 0.033$; equal branch lengths, $p < 0.001$; Nee transformed branch lengths, $p < 0.006$). Therefore, as body size increases across species, fauna consumption decreases.

The multiple regressions predicting male–female differences in the percent of leaves and fruit in the diet yielded statistically non-significant results using all branch length methods, and even when outliers were removed. Finally, the initial multiple regressions examining male–female differences in time spent feeding did not yield statistically significant results, yet one outlier was present (*Erythrocebus patas* vs. *Cercopithecus* spp. using equal and Nee transformed branch lengths, and *Cebus olivaceus* vs. *Cebus capucinus* using estimated branch lengths). When the outlier was removed, a positive

Table 3. Results of multiple regression models examining the effects of female body mass and body mass dimorphism on male–female differences in feeding ecology using phylogenetically independent contrasts.

Dependent variable	df	Estimated branch lengths				Equal branch lengths				Nee transformed branch lengths			
		Multiple r^2	F	p_{\min}	p_{\max}	Multiple r^2	F	p_{\min}	p_{\max}	Multiple r^2	F	p_{\min}	p_{\max}
Fauna	2, 19	0.418	6.82	0.005	0.008	0.357	5.28	0.015	0.018	0.457	8.01	0.003	0.004
Fauna ^a	2, 18	0.691	20.17	<0.001	<0.001	0.610	14.09	<0.001	<0.001	0.690	20.06	<0.001	<0.001
Leaves	2, 19	0.018	0.18	0.838	0.838	0.027	0.26	0.771	0.774	0.053	0.53	0.597	0.599
Leaves ^b	2, 18	–	–	–	–	0.000	0.00	0.999	0.999	0.002	0.02	0.984	0.984
Fruit	2, 20	0.088	0.98	0.394	0.397	0.192	0.38	0.687	0.690	0.084	0.92	0.415	0.420
Fruit ^c	2, 19	0.117	1.26	0.306	0.312	0.165	0.27	0.767	0.768	0.097	1.02	0.379	0.386
Feeding time	2, 25	0.113	1.58	0.225	0.228	0.128	1.84	0.179	0.181	0.114	1.61	0.219	0.222
Feeding time ^c	2, 24	0.086	1.14	0.336	0.338	0.279	4.64	0.019	0.021	0.283	4.74	0.018	0.019

p_{\max} is the p value of the regression after adjusting the degrees of freedom due to polytomies in the phylogeny. The degrees of freedom were reduced by four for the fauna, leaves and fruit regressions, and two for the feeding time regression.

^a Model without the outlier contrast *Cercopithecus petaurista* vs. *Cercopithecus cephus* vs. *Cercopithecus ascanius*, studentized residual >3.1 for all branch lengths.

^b Model without the outlier contrast *Cercopithecus mitis* vs. *Cercopithecus nictitans*, studentized residual >2.7. Note, there was no outlier using estimated branch lengths.

^c Model without the outlier contrast *Erythrocebus patas* vs. *Chlorocebus aethiops*, studentized residual >2.7 using equal and Nee transformed branch lengths. For the regression using estimated branch lengths, the outlier contrast *Cebus olivaceus* vs. *Cebus capucinus* displayed a studentized residuals of >3.0.

Table 4. Independent effects of predictor variables examining male–female difference in feeding ecology using phylogenetically independent contrasts.

Dependent variable	Estimated branch lengths			Equal branch lengths			Nee transformed branch lengths					
	Female body mass		Body mass dimorphism	Female body mass		Body mass dimorphism	Female body mass		Body mass dimorphism			
	β	p	β	p	β	p	β	p				
Fauna	-0.016	0.932	-0.638	0.004	-0.028	0.892	-0.583	0.013	0.089	0.661	-0.719	0.002
Fauna ^a	0.044	0.767	-0.851	<0.001	0.036	0.830	-0.799	<0.001	0.163	0.309	-0.907	<0.001
Leaves	-0.007	0.976	0.138	0.580	-0.085	0.737	0.182	0.476	-0.142	0.578	0.256	0.320
Leaves ^b	-	-	-	-	-0.008	0.975	0.002	0.994	-0.047	0.861	0.031	0.909
Fruit	0.014	0.952	0.292	0.228	0.093	0.708	0.130	0.602	0.254	0.310	0.064	0.793
Fruit ^c	-0.069	0.774	0.365	0.139	0.121	0.638	0.071	0.782	0.304	0.233	0.015	0.953
Feeding time	-0.151	0.455	0.353	0.088	-0.086	0.673	0.382	0.069	-0.106	0.605	0.362	0.085
Feeding time ^c	-0.152	0.470	0.308	0.149	-0.077	0.680	0.551	0.007	-0.083	0.653	0.555	0.006

Similar to the full models results, unadjusted p values are similar to those with reduced degrees of freedom. Only unadjusted p values are presented here.

^a Model without the outlier contrast *Cercopithecus petaurista* vs. *Cercopithecus cephus* vs. *Cercopithecus ascanius*, studentized residual > 3.1 for all branch lengths.

^b Model without the outlier contrast *Cercopithecus mitis* vs. *Cercopithecus nictitans*, studentized residual > 2.7. Note, there was no outlier using estimated branch lengths.

^c Model without the outlier contrast *Erythrocebus patas* vs. *Chlorocebus aethiops*., studentized residual > 2.7 using equal and Nee transformed branch lengths. For the regression using estimated branch lengths, the outlier contrast *Cebus olivaceus* vs. *Cebus capucinus* displayed a studentized residuals of > 3.0.

relationship was found at the $p = 0.018$ to 0.021 level using both equal and Nee transformed branch lengths (Figure 2b and Table 3). These values approached statistical significance once the sequential Bonferroni correction is taken into account, with our accepted significance level for this test being 0.0167 . Examining the relative effect of each independent variable for predicting sex differences in feeding time illustrates the importance of body mass dimorphism. Using both equal and Nee transformed branch lengths, there was a significant positive relationship between body mass dimorphism and sex differences in feeding time ($p < 0.008$) (Table 4). This relationship was weaker using estimated branch lengths, yet this may be due to the violation of the statistical assumption relating branch lengths to standardized contrast values. It is also important to note that in all cases there was little relationship between female body mass itself and sex differences in feeding ecology (Table 4).

The outliers are due to differences between closely related species that exhibit patterns contrary to those of the overall pattern. This may be the result of real biological differences among closely related taxa or measurement error in the data (Nunn & Barton, 2001) with the latter explanation being more common for outlier contrasts at the tips of the phylogeny. In this case, *C. petaurista* displays similar levels of body mass dimorphism to *C. cephus* and *C. ascanius*, yet males consume more fauna compared to females. It is interesting to note that there were no outlier contrasts involving deeper nodes (e.g., anthropoids vs. prosimians). This suggests that the patterns of body mass dimorphism and male–female dietary niche separation are similar across various primate lineages (i.e., grade shifts do not exist) despite the relatively high degree of ecological diversity within primates (Fleagle, 1999).

Discussion

Once outliers were removed from the dataset, this study reveals that body mass dimorphism is related to intraspecific primate dietary diversity in terms of male–female differences in the degree of faunivory and in the percentage of time feeding. The regressions examining male–female difference in the amount of fauna in the diet are consistent using species values or phylogenetically independent contrasts, where the results of sex differences in feeding time are only significant once evolutionary history is taken into account. The results of the phylogenetic analyses should be most emphasized

since our dataset is not evenly distributed among clades. For instance, in the analysis examining sex differences in feeding time, data for 28 species were included. Of these 28 species, three were from the entire suborder Prosimii, whereas four species were from a single genus, *Alouatta*. Therefore, treating these sampling units as independent data points would place equal weight on each species, which would be statistically invalid.

The relatively high level of faunivory among the smaller females is likely the result of a combination of factors influenced by body size, including increased physical dexterity of smaller individuals as well as the need of smaller animals to rely on high quality foods. Likewise, patterns in overall time spent feeding fit with the predictions of body size dimorphism, with larger animals spending relatively more time feeding. This relationship is particularly driven by species characterized by high levels of sexual dimorphism (*Gorilla* sp., *Pongo* sp.). These results lend support to the findings of Key & Ross (1999), which suggest that effects of body size may supersede those of female reproduction in species with extreme mass dimorphism. The importance of body mass for influencing the amount of fauna in the diet of species is emphasized by the phylogenetic analyses examining sex specific mass and fauna consumption (as opposed to sex differences in these traits). The significant negative relationship between female mass and female consumption of fauna supports the adaptive nature of the across-species variation in faunivory.

Interestingly, no significant relationship exists between body mass dimorphism and male–female differences in folivory or frugivory. This may be a true biological phenomenon, yet it may also be due to our particular dataset. A biological reason may be related to female reproduction. Although this study does not account for variation in female reproductive status, lactation, gestation and rearing offspring are particularly energetically demanding and may affect foraging behavior and selectivity (Dufour & Sauther, 2002). Such factors may mask sex differences in feeding time in species with low to moderate levels of sexual dimorphism.

Alternatively, although our dataset is the most comprehensive compilation to date, it is still relatively small, and may only be able to detect large effects. More likely, the available dietary data were relatively gross in nature. Therefore, the general fruit and leaf categories utilized may obscure the importance of the phenological phase of these food items. On average ripe fruit contains considerably more energy compared to unripe fruit. Similarly,

young leaves often contain relatively high levels of protein and are more easily digestible compared to mature leaves (Glander, 1982; Ganzhorn, 1992; Aide, 1993). The variation within these dietary classes may be critical for detecting differences between the sexes.

The relationship between diet and body size in primates may also be influenced by variation in dietary specialization. In a comparative study of large herbivores, Mysterud (2000) found that sexual dimorphism was only positively correlated with ecological segregation in browsers as opposed to intermediate feeders and grazers. For primates, species vary in their gut morphology and, thus, their efficiency in extracting nutrients from fibrous resources, regardless of body size. For instance, while the mantled howler monkey (*Alouatta palliata*) is able to subsist on a highly folivorous diet due to a gut specialized for caeco-colic fermentation, the similarly sized spider monkey (*Ateles geoffroyi*) is characterized by a relatively simple gut and, thus, must rely on fruit for its primary source of energy (Milton, 1981). Although we did not quantify the dietary niche of primate species in our analyses, dietary specialization has a strong phylogenetic component. Our results did not yield any of the expected grade shifts among different primate clades (e.g., colobines vs. cercopithecines or *Alouatta* vs. *Ateles*), suggesting that with our dataset, dietary specialization does not have a strong effect on the relationship between body mass dimorphism and feeding ecology.

Most evidence points to sexual selection as being the major force causing body size dimorphism in animals (Selander, 1972; Trivers, 1972; Clutton-Brock et al., 1987). Alternative hypotheses to explain body size dimorphism include niche separation (reviewed in Shine, 1989) and natural selection acting in a sex specific manner (Gordon, 2006). Several non-primate studies have examined intersexual differences in morphology and its ramifications for dietary niche separation. An elegant study of carpet pythons (*Morelia spilota*) by Pearson and colleagues (2002) showed that the degree of sexual dimorphism varied among five geographically separated populations. Females grew to a larger size and exhibited relatively larger heads compared to males in areas where large prey was available. The authors suggest that the variability in body size dimorphism was the results of prey size variation in different habitats. In another study, an examination of mink carcasses by Thom et al. (2004) showed that the degree of sexual dimorphism in anatomical structures related to feeding was greater compared to traits unassociated

with prey size. These results imply that the benefits of intersexual niche separation may maintain or increase dimorphism in the feeding apparatuses of minks. In primates, a community level study simultaneously focused on several closely related sympatric forest guenons (*Cercopithecus* spp.) supports the idea that body size is intimately tied to an animal's ecological niche and that this may affect the degree of niche separation between species' sexes. This research showed that females of different species were more ecologically similar to one another than any were to males of the same species (Gautier-Hion, 1980). These species tend to exhibit moderate levels of body size dimorphism, where males of different species exhibit more similar body sizes compared to conspecific females, with body size variation impacting diet and microhabitat preferences.

Although the results of this current study may appear to support the niche separation hypothesis, niche separation influenced by body size dimorphism could also arise as a byproduct of sexual selection. In primates, sexual selection is an important force in shaping various morphological and behavioral traits (Mitani, 1985; Plavcan & van Schaik, 1997; Nunn et al., 2001; Palombit et al., 2001). For instance, canine size dimorphism is well known in many primates and is largely due to male–male competition for females (Plavcan et al., 1995). Therefore, sexual selection may be the initial cause of body mass dimorphism, with male–female differences in ecology being a secondary effect.

A more complex picture emerges when dietary patterns are considered in the context of social relationships. For instance, the effect of body size on feeding behavior and access to resources may also be confounded by the effects of social dominance as body size may influence rank and vice versa (Pelletier & Festa-Bianchet, 2004). If sexual dimorphism arose as a result of a competitive 'arms race' among males, a by-product of such increased intrasexual competitive ability may also translate into increased intersexual competitive ability in regards to access to resources. For instance, larger individuals may have a competitive advantage over smaller ones, where it is, therefore, difficult to tease the social and physical effects of dimorphism apart. In addition, aggressive behavior that is independent of the individual's body size may lead to a high ranking status and, therefore, influence the ability to exploit food resources (Janson, 1985).

In conclusion, while many factors may affect sex differences in feeding ecology in primates, this study shows that body mass dimorphism may be

particularly important when considering differences in fauna feeding as well as overall feeding time in species characterized by high levels of dimorphism. Establishing such relationships provides a useful tool in interpreting the intraspecific ecological diversity of extant animals. The connection between body mass dimorphism and male–female niche separation may have important implications for several aspects of a species' biology. The exploitation of different food resources between males and females of sexually dimorphic species may reduce intragroup competition for food, which may in turn have ramifications for inter-individual social relationships and group size. In addition, the broader niche space occupied by dimorphic taxa may be detrimental in fragmented or degraded habitats, where resources are more limited. Under this scenario, these species may be at more risk of population decline.

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Appendix A

Table A1. Species data.

Species	Male mass	Female mass	log male mass	log female mass	Female leaf mass ratio	Body mass ratio	log body mass ratio	Male feeding time ratio	Female feeding time ratio	Feeding time ratio	log feeding time ratio	Male fruit ratio	Female fruit ratio	Fruit ratio	log fruit ratio	Male leaf ratio	Female leaf ratio	Leaf ratio	log leaf ratio	Male fauna ratio	Female fauna ratio	Animal fauna ratio	log fauna ratio	Reference
<i>Alouatta caraya</i>	6.42	4.33	0.808	0.636	0.620	1.483	0.171	0.110	0.140	0.786	-0.105	0.220	0.290	0.759	-0.120	0.680	0.620	1.097	0.040	-	-	-	-	Bicca-Marques & Calegario-Marques (1994)
<i>Alouatta palliata</i>	7.80	6.60	0.892	0.820	-	1.182	0.073	0.140	0.180	0.778	-0.109	-	-	-	-	-	-	-	-	-	-	-	-	Smith (1977)
<i>Alouatta pigra</i>	11.40	6.43	1.057	0.808	0.217	1.773	0.249	0.233	0.234	0.996	-0.002	0.689	0.734	0.939	-0.027	0.244	0.217	1.124	0.051	0.000	0.000	1.000	0.000	Rizzo (2004)
<i>Alouatta seniculus</i>	6.69	5.21	0.825	0.717	0.536	1.284	0.109	0.123	0.120	1.025	0.011	0.372	0.456	0.816	-0.088	0.534	0.536	0.996	-0.002	0.000	0.000	1.000	0.000	Gaulin (1978)
<i>Brachyteles arachnoides</i>	9.61	8.07	0.983	0.907	0.439	1.191	0.076	0.180	0.190	0.947	-0.023	0.318	0.293	1.084	0.035	0.476	0.439	1.085	0.035	-	-	-	-	Strier (1991)
<i>Callitrichus torquatus</i>	1.28	1.21	0.107	0.083	-	1.058	0.024	0.240	0.240	1.000	0.000	-	-	-	-	-	-	-	-	0.140	0.140	1.000	0.000	Kinzey (1977)
<i>Cebus capucinus</i>	3.68	2.54	0.566	0.405	-	1.449	0.161	0.475	0.525	0.905	-0.043	-	-	-	-	-	-	-	-	0.152	0.165	0.921	-0.036	Rose (1994)
<i>Cebus olivaceus</i>	3.29	2.52	0.517	0.401	-	1.306	0.116	0.240	0.420	0.571	-0.243	-	-	-	-	-	-	-	-	-	-	-	-	Fragazy (1990)
<i>Cercopithecus ascanius</i>	3.70	2.92	0.568	0.465	0.090	1.267	0.103	-	-	-	-	0.590	0.540	1.093	0.038	0.080	0.090	0.889	-0.051	0.270	0.300	0.900	-0.046	Lawes and Piper (1992)
<i>Cercopithecus campbelli</i>	4.50	2.70	0.653	0.431	0.110	1.667	0.222	-	-	-	-	0.670	0.500	1.340	0.127	0.070	0.110	0.636	-0.196	0.240	0.380	0.632	-0.200	Cords (1986)
<i>Cercopithecus cephus</i>	4.29	2.88	0.632	0.459	0.080	1.490	0.173	-	-	-	-	0.813	0.712	1.141	0.057	0.080	0.080	0.997	-0.001	0.108	0.208	0.517	-0.286	Buzzard (2004)
<i>Cercopithecus diana</i>	5.20	3.90	0.716	0.591	0.150	1.333	0.125	-	-	-	-	0.710	0.630	1.127	0.052	0.120	0.150	0.800	-0.097	0.120	0.180	0.667	-0.176	Gautier-Hion (1980)
<i>Cercopithecus mitis</i>	7.93	4.25	0.899	0.628	0.230	1.866	0.271	-	-	-	-	0.600	0.490	1.224	0.088	0.240	0.230	1.043	0.018	0.070	0.180	0.389	-0.410	Buzzard (2004)
<i>Cercopithecus nictitans</i>	6.67	4.26	0.824	0.629	0.282	1.566	0.195	-	-	-	-	0.789	0.605	1.303	0.115	0.121	0.282	0.428	-0.368	0.091	0.113	0.806	-0.094	Gautier-Hion (1980)
<i>Cercopithecus patagonicus</i>	4.40	2.90	0.643	0.462	0.450	1.517	0.181	-	-	-	-	0.400	0.350	1.143	0.058	0.430	0.450	0.956	-0.020	0.070	0.050	1.400	0.146	Buzzard (2004)
<i>Cercopithecus pogonius</i>	4.26	2.90	0.629	0.462	0.023	1.469	0.167	-	-	-	-	0.844	0.807	1.045	0.019	0.008	0.023	0.342	-0.466	0.148	0.170	0.876	-0.058	Gautier-Hion (1980)

Table A1. (Continued).

Species	Male mass	Female mass	log male mass	log female mass	Female leaf ratio	Body mass ratio	log body mass ratio	Male feeding time	Female feeding time	log feeding time ratio	Male fruit ratio	Female fruit ratio	Fruit ratio	log fruit ratio	Male leaf ratio	Female leaf ratio	Leaf ratio	log leaf ratio	Male fauna ratio	Female fauna ratio	Animal fauna ratio	log fauna ratio	Refer-ence	
<i>Chlorocebus aethiops</i>	4.68	3.35	0.670	0.525	-	1.396	0.145	0.323	0.307	1.053	0.022	-	-	-	-	-	-	-	0.070	0.080	0.875	-0.058	Harrison (1983)	
<i>Colobus guereza</i>	10.57	8.19	1.024	0.913	-	1.291	0.111	0.223	0.228	0.978	-0.010	-	-	-	-	-	-	-	-	-	-	-	Fishing (1999)	
<i>Erythrocebus patas</i>	12.40	6.50	1.093	0.813	0.032	1.908	0.281	0.080	0.110	0.727	-0.138	0.070	0.029	2.414	0.383	0.025	0.032	0.781	-0.107	0.020	0.051	0.392	-0.407	Isbell 1968
<i>Eulemur fulvus albifrons</i>	1.87	1.83	0.272	0.262	0.110	1.022	0.009	0.200	0.210	0.952	-0.021	0.710	0.730	0.973	-0.012	0.130	0.110	1.182	0.073	0.000	0.000	1.000	0.000	Vasey (1997)
<i>Gorilla gorilla lagotricha</i>	169.33	75.66	2.229	1.879	-	2.238	0.350	0.562	0.505	1.114	0.047	-	-	-	-	-	-	-	-	-	-	-	-	Bean (1997)
<i>Lophocebus albigena</i>	7.82	7.06	0.893	0.848	0.080	1.108	0.045	0.310	0.420	0.738	-0.132	0.640	0.700	0.914	-0.039	0.130	0.080	1.625	0.211	0.170	0.130	1.308	0.117	Di Fiore (1997)
<i>Macaca fascicularis</i>	8.25	6.02	0.916	0.780	0.052	1.370	0.137	0.410	0.489	0.838	-0.077	0.667	0.552	1.208	0.082	0.054	0.052	1.038	0.016	0.171	0.299	0.572	-0.243	Shah (2003)
	5.36	3.59	0.729	0.555	-	1.493	0.174	0.173	0.196	0.883	-0.054	-	-	-	-	-	-	-	-	-	-	-	-	Schaik & van Noordwijk (1986)
<i>Macaca nigra</i>	9.89	5.47	0.995	0.738	-	1.808	0.257	0.327	0.380	0.860	-0.066	-	-	-	-	-	-	-	-	-	-	-	-	Obrien and Kinnaird (1997)
<i>Pan troglodytes</i>	42.72	33.36	1.631	1.523	0.157	1.281	0.107	0.490	0.558	0.878	-0.056	0.719	0.616	1.167	0.067	0.130	0.157	0.831	-0.081	-	-	-	-	Bean (1999)
<i>Papio cynocephalus</i>	21.80	12.30	1.338	1.090	-	1.772	0.249	0.435	0.490	0.888	-0.052	0.159	0.126	1.262	0.101	-	-	-	-	-	-	-	-	Muruthi (1997)
<i>Phaner furcifer</i>	0.33	0.36	-0.484	-0.449	0.858	0.921	-0.036	0.750	0.770	0.974	-0.011	0.032	0.042	0.762	-0.118	0.858	0.858	0.999	0.000	0.085	0.083	1.024	0.010	Scheutle (2003)
<i>Pithecia pithecia</i>	1.94	1.58	0.288	0.199	0.052	1.228	0.089	-	-	0.897	0.896	1.001	0.000	0.053	0.052	1.019	0.008	0.037	0.039	0.949	-0.023	-	Norconk (pers. com- mun.)	

Table A1. (Continued).

Species	Male mass	Female mass	log male mass	log female mass	Female leaf	Body mass ratio	log body mass ratio	Male feeding time ratio	Female feeding time ratio	log feeding time ratio	Male fruit ratio	Female fruit ratio	Fruit ratio	log fruit ratio	Male leaf ratio	Female leaf ratio	Leaf ratio	log leaf ratio	Male fauna ratio	Female fauna ratio	Animal fauna ratio	log fauna ratio	Reference	
<i>Pongo</i>	78.50	35.80	1.895	1.554	0.232	2.193	0.341	0.489	0.415	1.177	0.071	0.586	0.671	0.873	-0.059	0.220	0.232	0.948	-0.023	0.008	0.019	0.421	-0.376	Bean (1999)
<i>Piganaeus</i>																								
<i>Procolobus baduus</i>	8.36	8.21	0.922	0.914	-	1.018	0.008	0.250	0.330	0.758	-0.121	-	-	-	-	-	-	-	-	-	-	-	-	Starrin 1991
<i>Saimiri oerstedii</i>	0.90	0.68	-0.047	-0.167	-	1.319	0.120	0.443	0.550	0.805	-0.094	-	-	-	-	-	-	-	-	-	-	-	-	Boinski (1988)
<i>Semnopithecus entellus</i>	13.00	9.89	1.114	0.995	-	1.314	0.119	0.284	0.289	0.983	-0.008	-	-	-	-	-	-	-	-	-	-	-	-	Newton (1984)
<i>Tarsius spectrum</i>	0.13	0.11	-0.903	-0.967	0.000	1.157	0.063	0.535	0.534	1.002	0.001	0.000	0.000	1.000	0.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	0.000	Gursky (1987)
<i>Theropithecus gelada</i>	19.00	11.70	1.279	1.068	-	1.624	0.211	0.420	0.454	0.925	-0.034	-	-	-	-	-	-	-	-	-	-	-	-	Dunbar (1977)
<i>Trachypithecus auratus</i>	7.70	7.35	0.886	0.866	-	1.048	0.020	0.230	0.325	0.708	-0.150	-	-	-	-	-	-	-	-	-	-	-	-	Kool (1989)
<i>Trachypithecus phayrei</i>	7.87	6.30	0.896	0.799	-	1.249	0.097	0.227	0.233	0.974	-0.011	-	-	-	-	-	-	-	-	-	-	-	-	Koenig et al. (pers. com.)
<i>Macaca variegata</i>	3.63	3.52	0.560	0.547	0.083	1.031	0.013	-	-	-	0.846	0.762	1.110	0.045	0.081	0.083	0.972	-0.012	0.000	0.000	1.000	0.000	0.000	Vasey (1997)

Table A2. Significance values of least square regressions between branch lengths and standard deviation of contrasts.

Variable	Real branch lengths	Equal branch lengths	Nee
log female mass	0.002	0.013	0.003
log body mass ratio	0.039	0.177	0.233
log feeding time ratio	0.006	0.002	0.001
log fruit ratio	0.488	0.313	0.997
log leaf ratio	0.035	0.302	0.020
log fauna ratio	0.049	0.151	0.076
log female feeding time	0.130	0.304	0.333
log female fruit	0.486	0.498	0.487
log female leaf	0.303	0.534	0.507
log female fauna	0.511	0.487	0.516
