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## SEXUAL DIMORPHISM, THE OPERATIONAL SEX RATIO, AND THE INTENSITY OF MALE COMPETITION IN POLYGYNOUS PRIMATES

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**Abstract.**—Male mating competition is generally regarded to account for sexual dimorphism in body size, but levels of sexual dimorphism do not appear to be associated with the intensity of intrasexual selection in polygynous mammals. In contrast, observations of accentuated dimorphism in certain taxa and in large species are consistent with nonadaptive explanations for the evolution of sexual size dimorphism based on phylogenetic inertia and allometry. Here we employ a weight-corrected measure of sexual dimorphism and a biologically realistic assay of mating competition, the operational sex ratio, to reexamine the factors favoring the evolution of sexual size dimorphism in primates. Independent contrasts that control for the effects of allometry and phylogeny produce results consistent with the sexual selection hypothesis; a strong relationship exists between sexual dimorphism in size and the intensity of male mating competition among polygynously mating primates. Increased sexual dimorphism in large primates may not be an inevitable consequence of allometry but instead may result from a reduction in the temporal availability of fertile females due to long birth intervals.

One enduring problem in evolutionary biology concerns the factors responsible for the evolution of sexual dimorphism in size. Males are larger than females in the majority of mammals and birds. Comparisons within and between species suggest that sex differences in size are attributable to sexual selection acting through male-male competition (Darwin 1871). Within species, large males are competitively superior to small males (Price 1984; Robinson 1985; Clutton-Brock et al. 1988; LeBoeuf and Reiter 1988), while the degree of dimorphism correlates positively with levels of mate competition across species (Clutton-Brock et al. 1977; Alexander et al. 1979; Jehl and Murray 1986).

Despite theoretical and empirical support for the role intrasexual selection plays in the evolution of sexual size dimorphism, several studies continue to cast doubt on the posited functional relationship. For example, while there is no reason to expect that intrasexual selection will be weak among polygynous species, the correlation between sexual dimorphism and mating competition frequently disappears when monogamous species are excluded from interspecific comparisons (Clutton-Brock et al. 1977; Ralls 1977; Alexander et al. 1979). Nonadaptive explanations for sexual size dimorphism provide alternatives to functional hypotheses based on sexual selection. Beginning with Rensch (1959), several researchers have suggested that sexual dimorphism in body size tends to increase

in large species (Wiley 1974; Clutton-Brock et al. 1977; Ralls 1977; Berry and Shine 1980; Leutenegger and Cheverud 1982, 1985; Gaulin and Sailer 1984; Payne 1984; Gautier-Hion and Gautier 1985; Bjorklund 1990), leading some to propose that dimorphism is an incidental by-product of allometry (Wiley 1974; Leutenegger and Cheverud 1982, 1985; Bjorklund 1990). Alternatively, others hypothesize that the widespread occurrence of sexual dimorphism in size represents a phylogenetic artifact; some studies suggest that there is no relationship between sexual dimorphism and male competition when the effects of phylogeny are controlled (Cheverud et al. 1985; Hoglund 1989; Bjorklund 1990; Hoglund and Sillen-Tullberg 1994).

Several problems hinder resolving the conflicting findings of previous research. First, measuring the intensity of male-male competition has proved difficult. Theoretically relevant measures such as the potential reproductive rates of the sexes (Clutton-Brock and Parker 1992) or relative and lifetime variance in reproduction (Payne 1979; Wade and Arnold 1983) are difficult to estimate for long-lived species with internal fertilization (reviews in Clutton-Brock 1988; Newton 1989). As a consequence, previously employed measures of male competition include the adult sex ratio of groups (Clutton-Brock et al. 1977), mean or maximum female group size (Alexander et al. 1979; Webster 1992), and dichotomous mating system variables, such as monogamy and polygyny (Leutenegger and Cheverud 1982; Gaulin and Sailer 1984; Kappeler 1990). Virtually all investigators recognize that these measures may not provide an accurate estimate of the intensity of male-male competition. For example, male dominance hierarchies (Clutton-Brock et al. 1977; Gautier-Hion and Gautier 1985) and seasonal influxes of males into groups during mating seasons (Rowell and Chism 1986) make the use of the group sex ratio problematic for mammals. More importantly, measures such as female group size assess the degree of male competition primarily in terms of female availability in space. For animals whose birth intervals are relatively long, it is equally important to consider the availability of fertile females in time. A group sex ratio of two females to one male cannot be considered to have the same intensity of male-male competition in baboons (*Papio anubis*) and gorillas (*Gorilla gorilla*) (Clutton-Brock et al. 1977) since in the former females breed once every 2 yr, while in the latter females reproduce only once every 3–4 yr (fig. 1; table 1).

In addition to problems surrounding the measurement of male competition, operational definitions of sexual dimorphism have differed considerably. While the majority of investigators employ a simple or logarithmically transformed ratio of male to female weight, Leutenegger and Cheverud (1982) adopt an absolute measure of the difference between male and female weight. This index increases as a function of size and therefore biases toward finding that sexual dimorphism increases in large species (see discussions in Gaulin and Sailer 1984; Webster 1992). Less appreciated but equally problematic is that conventional measures of sexual dimorphism based on ratios also vary with size if the relationship between male and female size is not isometric (Huxley 1932; Ranta et al. 1994). Finally, with few exceptions (Cheverud et al. 1985; Hoglund 1989; Bjorklund 1990; Oakes 1992; Hoglund and Sillen-Tullberg 1994), investigations into the factors responsible for sexual size dimorphism in animals have been hampered by a general failure

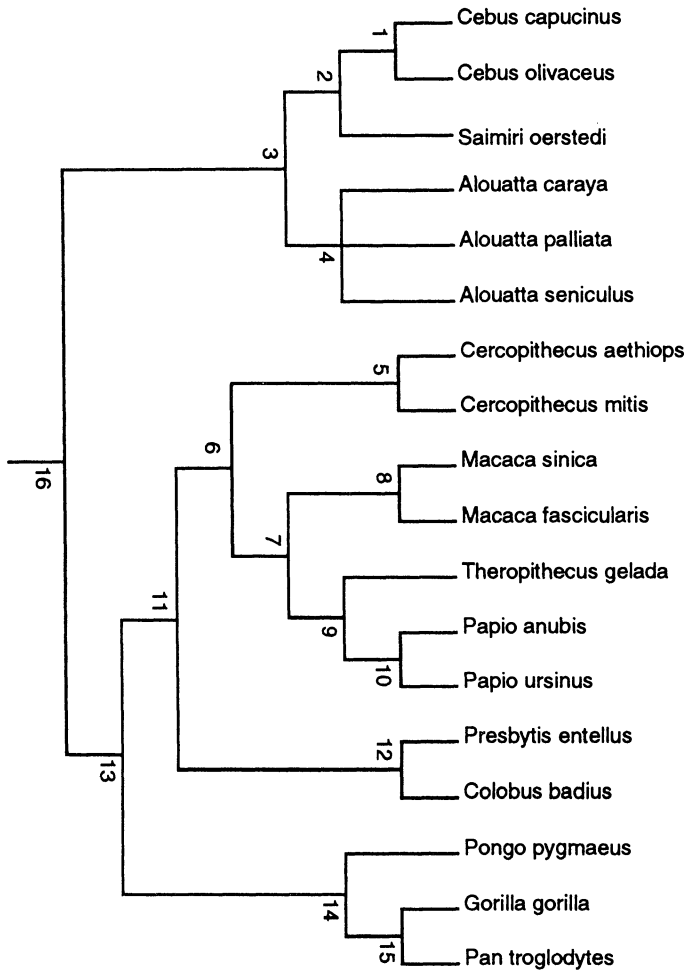


FIG. 1.—A primate phylogeny. The phylogeny represents a consensus tree based on molecular, karyotypic, paleontological, morphological, and behavioral data (Purvis 1995). Numbered nodes indicate independent contrasts plotted in fig. 2.

to control for the possible influence of phylogeny. A convincing demonstration that male contest competition plays a role in the evolution of dimorphism must account for potentially confounding third variables, for example, body size and effects associated with phylogeny (Harvey and Pagel 1991).

In this article, we reexamine the relationship between sexual selection and sexual dimorphism in size among polygynous primates. Primates are an appropriate choice for this investigation since prior studies differ markedly in their conclusions regarding the effects of phylogeny, body size, and sexual selection on sexual dimorphism (cf. Clutton-Brock et al. 1977; Leutenegger and Cheverud 1982; Cheverud et al. 1985). We begin by constructing a measure of male-male

TABLE 1

BEHAVIORAL AND ANATOMICAL MEASURES: SEX RATIOS, THE PATTERNING OF SEXUAL ACTIVITY, AND BODY WEIGHTS

Species	Adult Sex Ratio (m:f)	Breeding Season Length (d)	Interbirth Interval (yr)	Estrus Period (d)	No. of Cycles to Conception	Male Body Weight (kg)	Female Body Weight (kg)	Operational Sex Ratio	References*
<i>Alouatta caraya</i>	.64	365	1.32	2.9†	15.6†	6.42	4.33	6.83	1
<i>Alouatta palliata</i>	.31	365	1.76	3.0	15.6	6.53	4.02	4.19	2, 3, 4, 5
<i>Alouatta seniculus</i>	.84	365	1.27	2.8	15.6†	6.70	4.50	9.02	6, 7, 8
<i>Cebus capucinus</i>	.50	365	1.61	5.5†	7.0	3.30	2.28	7.67	5, 9, 10, 11, 12
<i>Cebus olivaceus</i>	.27	334	2.17	5.5†	7.0†	4.50	3.20	4.99	12, 13, 14, 15
<i>Cercopithecus aethiops</i>	.53	122	1.43	32.5	1.0	5.08	3.56	2.87	16, 17, 18, 19
<i>Cercopithecus mitis</i>	.38	273	2.75	11.3	1.5†	6.90	4.15	17.05	20, 21, 22, 23
<i>Colobus badius</i>	.39	305	2.03	5.4	3.0	10.50	5.75	14.79	24, 25, 26, 27
<i>Gorilla gorilla</i>	.83	365	3.25	2.5	4.7	159.20	97.70	83.75	28, 29, 30, 31, 32
<i>Macaca badius</i>	.44	205	1.90	31.3‡	2.4	5.50	3.50	2.29	33, 34, 35, 36, 37
<i>Macaca sinica</i>	.43	151	1.21	14.0	2.2†	5.71	3.16	2.55	38, 39, 40, 41
<i>Pan troglodytes</i>	.29	365	3.11	12.5	5.9	42.00	35.20	4.54	42, 43, 44, 45
<i>Papio anubis</i>	.40	365	1.92	8.5	4.7	24.30	12.71	7.01	46, 47, 48, 49
<i>Papio ursinus</i>	.74	365	1.83	5.3	4.0†	28.80	14.63	23.54	50, 51, 52, 53
<i>Pongo pygmaeus</i>	.92	365	7.72	31.3‡	1.5	83.60	37.80	55.02	54, 55, 56, 57, 58
<i>Presbytis entellus</i>	.20	365	1.39	4.0	4.6	18.50	11.70	5.60	59, 60
<i>Saimiri oerstedii</i>	.19	61	1.00	7.0	1.0	.89	.74	1.69	61, 62, 63
<i>Theropithecus gelada</i>	.38	365	1.89	8.5	2.5	26.10	13.95	12.46	64, 65, 66, 67

\* 1, Rumiz 1990; 2, Clarke and Zucker 1994; 3, Glander 1980; 4, K. Glander, personal communication; 5, Glander et al. 1991; 6, Rudran 1979; 7, Crockett and Rudran 1987; 8, Crockett and Sekulic 1984; 9, Chapman et al. 1989; 10, S. Perry, personal communication; 11, L. Rose, personal communication; 12, Janson 1984; 13, Robinson 1988; 14, Robinson and Janson 1987; 15, Mittermeier 1977; 16, Cheney and Seyfarth 1987; 17, D. Cheney and R. Seyfarth, personal communication; 18, Else et al. 1986; 19, Leutenegger and Cheverud 1982; 20, Cords et al. 1986; 21, Cords and Rowell 1987; 22, Cords 1987; 23, M. Cords, personal communication; 24, Struhsaker and Leakey 1990; 25, Struhsaker 1975; 26, Struhsaker and Leland 1987; 27, Starin 1988; 28, Harcourt et al. 1981; 29, Fossey 1982; 30, Harcourt et al. 1980; 31, Watts 1990; 32, Jungers and Susman 1984; 33, van Schaik and van Noordwijk 1988; 34, van Noordwijk and van Schaik 1987; 35, van Noordwijk 1985; 36, C. van Schaik and M. van Noordwijk, personal communication; 37, MacDonald 1971; 38, Dittus 1979; 39, W. Dittus, personal communication; 40, Dittus 1986; 41, Cheverud et al. 1992; 42, Nishida et al. 1985; 43, Nishida et al. 1990; 44, Takahata et al. in press; 45, Uehara and Nishida 1987; 46, Smuts 1985; 47, Strum 1982; 48, Nicholson 1982; 49, Smuts and Nicholson 1989; 50, Hamilton 1985; 51, DeVore and Hall 1965; 52, Bulger and Hamilton 1987; 53, Bulger 1993; 54, Galdikas 1979; 55, Galdikas 1981; 56, Galdikas and Wood 1990; 57, Rodman 1984; 58, Nadler 1988; 59, Sommer and Rajpuhrit 1989; 60, Sommer et al. 1992; 61, S. Boinski, personal communication; 62, Boinski 1987; 63, Schultz 1941; 64, Ohsawa and Dunbar 1984; 65, Dunbar 1980; 66, Dunbar 1984; 67, Kawai 1979.

† Generic mean.

‡ Data derived from studies of animals in captivity.

competition, the operational sex ratio (Emlen and Oring 1977), that considers the temporal distribution of fertile females. Using this estimate, we proceed to examine the relationship between male mating competition and sexual dimorphism in body weight. Here we use data on body weights from a sample of wild primates and employ the method of independent contrasts to control for the effects of phylogeny (Felsenstein 1985; Pagel 1992; Purvis and Rambaut 1994). Our results provide support for the hypothesis that the intensity of male competition affects sexual dimorphism in size among polygynous primates and provide a simple rationale that can be used to explain previously documented relationships between body weight and sexual dimorphism.

#### METHODS

##### *The Operational Sex Ratio*

Sexual selection theory suggests that intrasexual competition among males leads to size dimorphism (Darwin 1871), with the degree of dimorphism a direct result of the intensity of competition. Theory predicts intense competition when the operational sex ratio, the number of reproductively active males to females, is skewed heavily toward males (Emlen and Oring 1977). We follow Sutherland (1985) and Clutton-Brock and Parker (1992) by dividing the total time active by males ( $T_m$ ) and females ( $T_f$ ) into two parts, a period during which individuals are ready to mate ( $S$ ) and an interval during which mating does not occur. If  $f$  equals the number of females and  $m$  is the number of males, it follows that the probability a given female is available to mate is

$$\frac{S_f}{T_f}, \quad (1)$$

and the expected number of available females is

$$f \cdot \frac{S_f}{T_f}. \quad (2)$$

Similarly, the number of reproductively active males will be

$$m \cdot \frac{S_m}{T_m}, \quad (3)$$

and the operational sex ratio is

$$\frac{m \cdot \frac{S_m}{T_m}}{f \cdot \frac{S_f}{T_f}}. \quad (4)$$

If we measure all periods in days per year with  $T_m = T_f = 365$  d/yr, the operational sex ratio simplifies to

$$\frac{m \cdot S_m}{f \cdot S_f} \quad (5)$$

The mating period for females ( $S_f$ ), also measured in days per year, will be a function of the number and length of estrous cycles females typically experience before conception:

$$S_f = \frac{\sum_{i=1}^n c}{B}, \quad (6)$$

where  $c$  is the duration of estrus in days,  $n$  is the number of estrous cycles females experience before conception, and  $B$  is the birth interval in years.

For seasonally breeding primates who breed every year and whose males are limited in their mating opportunities by female receptivity, we assume the male mating period ( $S_m$ ) to be equal to the duration of the mating season,  $d$  days per year. Substitution into equation (5) yields

$$\text{operational sex ratio} = \frac{m \cdot B \cdot d}{f \cdot \sum_{i=1}^n c} \quad (7)$$

For primates who do not breed seasonally, we assume males to be sexually active throughout the year, resulting in

$$\text{operational sex ratio} = \frac{m \cdot B \cdot 365}{f \cdot \sum_{i=1}^n c} \quad (8)$$

Since  $d$  will always be less than 365, our measures of the operational sex ratio will tend to produce lower estimates for seasonal breeders, a result that conforms to qualitative arguments made regarding the effect of the temporal distribution of females on the degree of male competition (Emlen and Oring 1977). We also note that our formulation of the operational sex ratio leads to the expectation that male competition will vary positively with birth intervals ( $B$ ).

### Variables

*Body weights and sexual dimorphism.*—Prior studies rely on compilations of body weights derived from secondary sources, captive animals, or specimens of unknown or unspecified provenance (e.g., Clutton-Brock et al. 1977). For the following analyses, we include only those species for which body weights of wild individuals are available. Although the ratio of male to female size is commonly employed in studies of sexual dimorphism, this measure is unaffected by size only in situations when the relationship between male and female size is isometric (review in Ranta et al. 1994). For the following analyses, we removed the potential confounding effects of allometry from our measure of sexual size dimorphism by

using the residuals from a phylogenetic contrast (see below) between male and female weights (cf. Garland et al. 1992; DeVoogd et al. 1993; Ranta et al. 1994).

*The operational sex ratio.*—The operational sex ratio as defined above requires information regarding adult sex ratios ( $m$  and  $f$ ), mating season durations ( $d$ ), the duration of female estrous cycles ( $c$ ), the number of estrous cycles females experience before conceiving ( $n$ ), and interbirth intervals ( $B$ ). We used population estimates of adult sex ratios for each species based on population-wide censuses or counts of groups and floating individuals. Since birth intervals and mating season durations are likely to be affected by captivity (e.g., Rowell 1970), we included only those species for which data from the wild exist. Patterns of infant survival are known to influence birth intervals. For example, chimpanzee females take much longer to reproduce if their previous infants have survived than if their infants have died (Nishida et al. 1990). In cases where relevant data existed, we used birth intervals that account for the effects of infant survivorship by computing weighted averages. For these calculations, birth intervals for individuals whose infants died and survived were weighted by the numbers of females in each sample.

Female primates are sexually active for restricted periods during their estrous cycles (Hrdy and Whitten 1987) and experience a variable number of cycles before conceiving. In computing the operational sex ratio for each species, we employed the average periods of female sexual activity and numbers of cycles to conception. Few data exist regarding estrous durations and cycles to conception. We expect captivity to affect these reproductive parameters less than birth intervals and mating seasons, and in some cases we estimated these variables by computing generic means from animals living in captivity or the wild (table 1).

We limited our analyses to those studies that have published figures for body weights, sex ratios, and the reproductive parameters listed above. To deal with the problem posed by intraspecific variation in these variables (Gittleman 1989), we used observations derived from long-term research of known individuals, giving preference to field studies that covered the longest periods and numbers of groups or had reported all of the parameters of interest. These criteria necessarily limited our sample, but we believe that any trade-off in terms of sample size is more than compensated by the quality of the data utilized.

### *Analyses*

We employed Felsenstein's (1985) method of independent contrasts, modified by Pagel (1992) and implemented in the Comparative Analysis by Independent Contrasts (CAIC) program for the Macintosh (Purvis and Rambaut 1994), to examine the relationship between the operational sex ratio and sexual dimorphism in size. This technique employs a known or inferred phylogeny to derive a set of independent comparisons between pairs of extant or ancestral species. For the following analyses we employed a consensus tree based on neontological and paleontological evidence (fig. 1) (Purvis 1995). Sexually selected traits, critical for successful reproduction, are likely to be subject to strong and rapid selection (West Eberhard 1983). For this reason, we explicitly adopted a punctuated view of evolution in our tests and assigned equal lengths to the branches of the phyloge-



nies (Pagel 1992; Purvis and Rambaut 1994). A second analysis using branch lengths derived from the fossil record and molecular clocks (Purvis 1995) produced results consistent with those using equal branch lengths.

Our application of Felsenstein's (1985) method of independent contrasts assumes that the evolution of size dimorphism, body weight, and the operational sex ratio can be modeled through a random walk process, where the size of contrasts is independent of the estimated values of characters at which contrasts are computed. We performed all tests on logarithmically transformed variables in order to conform with this evolutionary model (Harvey and Pagel 1991; Garland et al. 1992; Purvis and Rambaut 1994). Here our working assumption is that different lineages are equally likely to show similar proportional changes in size and sex ratio. We tested the validity of this assumption by conducting regressions between the absolute values of contrasts and their estimated nodal values. All tests produced lines whose slopes were not significantly different from zero, thereby confirming the efficacy of the logarithmic transformations (Purvis and Rambaut 1994).

We removed the effects of weight on our independent and dependent variables by using the residuals from independent contrasts between the operational sex ratio and female weight, and male weight and female weight, respectively. We used Model I regression to compute residuals since values generated through this technique are uncorrelated with the dependent variable (Harvey and Pagel 1991). We examined the relationship between male mating competition and size dimorphism with the effects of size and phylogeny removed by conducting an additional correlation between contrasts in residual sexual dimorphism and residual operational sex ratio (Garland et al. 1992).

The method of independent comparisons produces contrasts or differences between  $x$  and  $y$  variables whose signs are arbitrary. For paired comparisons, as in these analyses, once the direction of subtraction for one contrast is chosen, the other difference must be computed in the same direction (i.e.,  $x - y$  or  $y - x$ ). Pairs of contrasts plotted in  $x - y$  space will therefore be equivalent to their reflections through the origin, and we accordingly forced regressions through the origin in all our tests using independent comparisons (Grafen 1989; Harvey and Pagel 1991; Garland et al. 1992).

## RESULTS

Table 1 shows values of behavioral and anatomical measures along with computed operational sex ratios for the 18 species in our sample. Independent contrasts using relationships specified by the consensus phylogeny (fig. 1) indicated a weak, positive correlation between contrasts in male weights and female weights ( $r^2 = 0.17$ ,  $n = 16$ ,  $P = .10$ ). A similar comparison between contrasts in the operational sex ratio and female body weight revealed a strong and significant association ( $r^2 = 0.37$ ,  $n = 16$ ,  $P < .01$ ). Table 2 presents the expected and residual values of sexual dimorphism and operational sex ratio derived from contrasts with female body weight. Correlation between contrasts in residual sexual dimorphism and residual operational sex ratio showed that the relationship be-

TABLE 2

EXPECTED AND RESIDUAL VALUES OF SEXUAL DIMORPHISM AND OPERATIONAL SEX RATIO BASED ON INDEPENDENT CONTRASTS WITH FEMALE BODY WEIGHT

Contrasts*	Expected Sexual Dimorphism	Expected Operational Sex Ratio	Residual Sexual Dimorphism	Residual Operational Sex Ratio
1	.0062	.0649	-.0144	-.1581
2	.0213	.2226	.0113	.0290
3	.0183	.1916	.0125	-.0600
4	.0018	.0192	-.0225	.1266
5	.0028	.0294	.0304	.3577
6	.0078	.0816	.0172	-.1263
7	.0210	.2193	-.0002	.0690
8	.0019	.0196	-.0322	-.0437
9	.0004	.0039	-.0074	-.0098
10	.0026	.0270	.0037	.2360
11	.0072	.0757	-.0021	-.0110
12	.0130	.1361	-.0443	-.3470
13	.0271	.2833	-.0117	-.0246
14	.0072	.0753	-.0968	-.2767
15	.0187	.1956	.0489	.4374
16	.0279	.2910	.0068	-.0606

\* Contrasts were made at numbered nodes indicated in fig. 1.

tween the two variables persists after holding female body weight constant ( $r^2 = 0.49$ ,  $t = 3.77$ ,  $n = 16$ ,  $P < .01$ ) (fig. 2).

Consideration of the operational sex ratio provides a possible explanation for the frequently documented association between increased levels of sexual dimorphism in large species (see earlier discussion). Note that the operational sex ratio will vary positively with the length of the birth interval (eqq. [7] and [8]). With increased spacing between births, fewer reproductively active females are available per unit time, which leads to a greater intensity of male competition. Birth intervals, in turn, are positively related to female body weight after controlling for the effects of phylogeny (independent contrasts test:  $r^2 = 0.24$ ,  $n = 16$ ,  $P < .05$ ). Thus, the commonly observed relationship between sexual dimorphism and body weight may be due to a hidden third variable, birth interval, which in turn plays a role in affecting dimorphism through the operational sex ratio. Consistent with this interpretation is the additional finding that sexual dimorphism shows no relationship with female body weight after birth interval is held constant (independent contrasts test:  $r^2 = 0.03$ ,  $n = 16$ ,  $P > .50$ ).

#### DISCUSSION

The results presented here are consistent with the hypothesis that sexual selection acting on males has played a role in the evolution of sexual size dimorphism among primates. The relationship between male mating competition and sexual dimorphism holds after removing the effects of body weight and controlling for phylogeny. These findings represent the first demonstration of a correlation be-

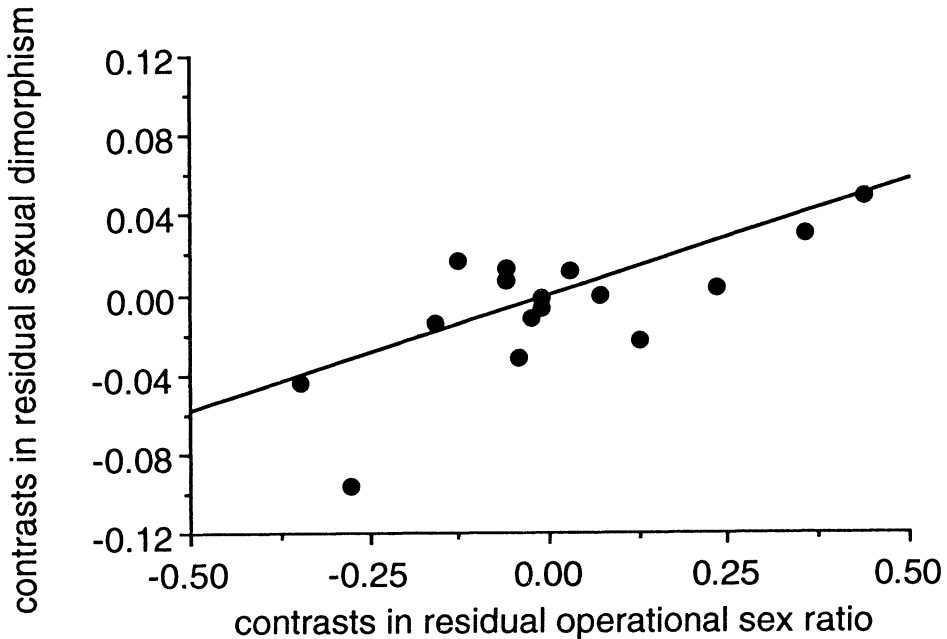


FIG. 2.—Correlation between residual sexual dimorphism and residual operational sex ratio. See text for further explanation.

tween intrasexual selection and sexual dimorphism among polygynous primates and appear to be critically dependent on the use of a biologically realistic assay of male competition.

Prior studies that suggest body weight is a good predictor of sexual size dimorphism among primates may have been influenced by the use of weight-biased measures of dimorphism (Clutton-Brock et al. 1977; Leutenegger and Cheverud 1982, 1985; Gaulin and Sailer 1984; Gautier-Hion and Gautier 1985). For example, indexes of dimorphism based on ratios are inevitably affected by size if the relationship between male and female size is not isometric (Ranta et al. 1994), and, as a result, the use of ratios to examine the effect of size on size dimorphism is questionable. While previously documented associations between size and dimorphism may represent, in part, a methodological artifact, our formulation of the operational sex ratio provides an alternate explanation for increased levels of sexual dimorphism in large species (review in Andersson 1994). Increased sexual dimorphism in large primates may not be an inevitable consequence of allometry but instead may result from a reduction in the temporal availability of fertile females due to long birth intervals.

While male mating competition appears to account for some of the variation in sexual size dimorphism, a nontrivial amount of variability remains unexplained. Complete understanding of the factors underlying the evolution of sexual size dimorphism will depend on determining the selective costs and benefits of large

size to both males and females. The operational sex ratio reflects the benefits gained by large males, unconstrained by any costs of becoming larger. Habitat utilization and feeding styles are two factors that may influence the costs of large body size. For example, large size inhibits efficient movement in arboreal environments; by this reasoning, we expect terrestrial species to show more sexual dimorphism than arboreal species (e.g., Clutton-Brock et al. 1977; Ford 1994). In addition, energetic considerations lead us to predict that the fitness costs of becoming ever larger will be lower for folivores relative to frugivores (Kleiber 1961) and that, other factors being equal, the former will show greater dimorphism than the latter (e.g., Ford 1994; but see Leutenegger and Cheverud 1982). Finally, consideration of the relative costs and benefits of large size to females promises to account for some of the residual variation in sex differences in body size left unexplained by selection acting on males. For example, the costs of lactation may be high for females with relatively large neonates or litter sizes. In these cases, selection for large size in females may reduce the costs of reproduction (Ralls 1976; Myers 1978; Kappeler 1990) and may counteract the effects of intrasexual selection operating on males. Assessing the simultaneous effects of selection acting on males and females to produce patterns of size dimorphism remains a central challenge for future studies (cf. Plavcan and van Schaik 1994).

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