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Comparative tests of reproductive skew in male primates: the roles of demographic factors and incomplete control

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Abstract Reproductive skew models have been proposed as a unifying framework for understanding animal social systems, but few studies have investigated reproductive skew in a broad evolutionary context. We compiled data on the distribution of mating among males for 31 species of primates and calculated skew indices for each study. We analyzed the determinants of mating skew with phylogenetic comparative methods to investigate two models from reproductive skew theory, the concession model and the tug-of-war model. Mating skew decreased as the number of males increased in multimale groups, suggesting that monopolization of females becomes more difficult when there are more rivals, and therefore supporting the tug-of-war model. We predicted that single males are unable to monopolize receptive females as overlap in female receptivity increases (estrous synchrony) and, as a result, that mating skew decreases. However, we did not find any

evidence for a link between female estrous synchrony and male mating skew. Finally, the concession model predicts high skew in male philopatric species relative to species in which males disperse, yet our measures of mating skew showed no significant associations with qualitative scores of male dispersal. More definitive tests of the concession model will require more quantitative measures of relatedness, which are presently unavailable for most primate species in our study. Overall, our results provide support for the tug-of-war model in primates, and the approach developed here can be applied to study comparative patterns of skew in other biological systems.

Keywords Reproductive skew · Primates · Tug-of-war model · Estrous synchrony · Phylogenetic comparative test

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Introduction

In group-living animals, species differ greatly in the distribution of reproduction among same-sexed individuals. In some species, one individual of a group monopolizes the vast majority of reproductive output (i.e., reproductive skew is high), whereas reproduction is more equally distributed in groups of other species (reproductive skew is low). Reproductive skew theory proposes that the degree of skew is affected by multiple social, ecological, and genetic factors, including relatedness among group members, ecological constraints on reproduction outside the group, and opportunities to control the reproductive activities of other individuals in groups (Vehrencamp 1983a,b; Keller and Reeve 1994; Emlen 1997; Clutton-Brock 1998; reviewed in Johnstone 2000).

Previous models of reproductive skew theory can be classified into two broad categories: transactional models (Vehrencamp 1983a,b; Keller and Reeve 1994; Clutton-Brock 1998; Johnstone 2000) and compromise models (Reeve et al. 1998; Cant 1998; Clutton-Brock 1998). In one transactional model—the concession model—a dominant

individual is assumed to control the reproduction of subordinates, and the presence of subordinates increases the dominant's fitness benefits. The concession model predicts that the dominant offers subordinates "staying incentives" in the form of opportunities to reproduce in the group (albeit at a lower level than by the dominant). It is further predicted that staying incentives are more commonly offered to unrelated than to related subordinates, and that the incentive is offered when a possibility of reproduction outside of the group is high, thereby providing an incentive for subordinates to remain in the group. The dominant may concede reproductive opportunities to subordinates as "peaceful" incentives when the risk of dyadic aggression is high for the dominant such as when the power differential between dominant and subordinate is small.

In contrast, a compromise model called the tug-of-war model assumes that the dominant individual is unable to control the reproduction of subordinates completely (Reeve et al. 1998; Cant 1998; Clutton-Brock 1998). As a result, the degree of reproductive skew is an outcome of struggles between the dominant and subordinate, and this struggle decreases group productivity (Reeve et al. 1998; Johnstone 2000). The concession and the tug-of-war models have been tested empirically in social insects (reviewed in Reeve and Keller 2001; Nonacs 2001) and birds (Magrath and Heinsohn 2000; Magrath et al. 2004). Some studies provided support for the concession model [e.g., moorhen (*Gallinula chloropus*), McRae 1996; pukeko (*Porphyrio porphyrio*), Jamieson 1997; social paper wasp (*Polistes fuscatus*), Reeve et al. 2000; see Keller and Reeve 1994; Bourke 1997; Emlen 1997]. Other studies supported the tug-of-war model [e.g., social wasp (*Polistes carolina*), Seppä et al. 2002; Australian allodapine bees (*Exoneura nigrescens*), Langer et al. 2004; see Clutton-Brock 1998; Field et al. 1998]. The tug-of-war model has similarities to the priority of access model used to study links between male rank and reproductive success (Altmann 1962). In strict application of the priority of access model, however, the dominant male loses complete control over mating access only when multiple females are in estrus (Altmann 1962); such effects of female synchrony can exist in the tug-of-war model (see below), but this model also considers the effects of male competition due to more rivals.

In social mammals, a dominant male usually gains an advantage in mating or reproductive success, but subordinates regularly reproduce (Altmann 1962; Cowlshaw and Dunbar 1991; Pemberton et al. 1992; Bulger 1993; Keane et al. 1994; Creel et al. 1997; Girman et al. 1997; Launhardt et al. 2001; Engh et al. 2002; Griffin et al. 2003; Alberts et al. 2003). Previous studies in social mammals supported both the concession [e.g., dwarf mongooses (*Helogale parvula*), Creel and Waser 1991; wild dogs (*Lycaon pictus*), Creel and Creel 2002; but see Clutton-Brock 1998] and tug-of-war models [e.g., meerkats (*Suricata suricatta*), Clutton-Brock et al. 2001; rhesus macaques (*Macaca mulatta*), Widdig et al. 2004; mountain gorillas (*Gorilla beringei beringei*), Bradley et al. 2005;

mandrills (*Mandrillus sphinx*), Charpentier et al. 2005; Setchell et al. 2005].

Although previous studies have investigated reproductive skew models in different species, including in primates (Hager 2003; Widdig et al. 2004; Bradley et al. 2005), to our knowledge, no studies have used cross-species variation to test skew models, which is necessary for understanding broad evolutionary patterns of reproductive skew and the factors that generate these patterns. The comparative approach is possible only in well-studied clades that exhibit a large amount of interspecific variation in reproductive skew and other traits. Primates are therefore an excellent clade for testing these models because male and female sexual behavior has been studied intensively in many species (Dixon 1998), and these species exhibit variation in social systems, mating systems, and reproductive traits.

The goal of this study is to investigate determinants of male mating skew across primate species using phylogenetic comparative analyses. Although molecular methods provide information on actual patterns of reproduction, data based on paternity tests are not yet available for a sufficient number of primate species. Instead, we focused on mating frequency because data on this variable can be obtained from species in all major primate radiations. We also investigated the association between female reproductive traits and male skew because only a few previous studies have considered how behavior of the opposite sex influences patterns of skew [Cant and Reeve 2002; Haydock and Koenig 2002 for acorn woodpecker (*Melanerpes formicivorus*); Williams 2004 for brown jays (*Cyanocorax morio*)]. We focused in particular on two major types of reproductive skew models by investigating the following set of variables that were known to play important roles in the previous studies of reproductive behavior and social systems in primates (Altmann 1962; Cowlshaw and Dunbar 1991; Dixon 1998).

Demographic factors The tug-of-war model predicts that mating skew decreases as the number of males in a group increases based on the reasoning that it will be difficult for one male to control or monitor reproductive attempts by other males when more rivals are present (Cowlshaw and Dunbar 1991; Pawlowski et al. 1998; van Noordwijk and van Schaik 2004). Similarly, increases in the number of females in a group can decrease skew if this provides more mating opportunities for subordinate males (Altmann 1962; Cowlshaw and Dunbar 1991; van Noordwijk and van Schaik 2004). The concession model makes no predictions for how these demographic factors correlate with mating skew.

Female reproductive traits Primate species exhibit remarkable variation in female reproductive physiology and behavior (Dixon 1998), and these traits are likely to impact the ability of males to defend access to females. Difficulty of monopolizing a receptive female may permit subordinate males to mate with receptive females, thus decreasing mating skew among males. We investigated

three sets of female reproductive traits. First, it may be difficult for one male to monopolize all estrous females in a species with a short breeding season because multiple females are more likely to enter estrus simultaneously during a shorter season (Ridley 1986; Cowlshaw and Dunbar 1991; Paul 1997). Second, one male may be unable to guard a female throughout her entire estrus when the duration of estrus is long because mate guarding is costly to males in terms of time, energy, and opportunity costs (Packer 1979; Bercovitch 1983; Alberts et al. 1996; Matsubara 2003). Third, if estrous overlap among females is high (i.e., many females are simultaneously receptive), a subordinate male may have more opportunities to mate with females who are left unguarded by more dominant males (Emlen and Oring 1977; Ims 1988; Paul 1997; Say et al. 2001; Shuster and Wade 2003; Takahashi 2004), which would therefore tend to reduce skew. As noted above, these predictions would also support the “priority of access” model that has been widely used in primate studies (Altmann 1962; Alberts et al. 2003). Although the tug-of-war model predicts that mating skew should be lower in species with longer estrous periods and a higher level of estrous synchrony, the concession model makes no specific predictions in this regard.

Male dispersal pattern If the concession model applies to male primates, mating skew is expected to be higher among species in which males remain resident in their native groups (no male dispersal) as compared with species in which males disperse to new groups. Two assumptions underlie this prediction. First, among male philopatric species, the probability of a subordinate male dispersing from and reproducing outside of his natal group is extremely low. Thus, the dominant male’s necessity to offer “staying incentives” to subordinates should be low when males are philopatric, resulting in higher mating skew. Second, relatedness among philopatric males is likely to be higher than in situations in which males disperse (Morin et al. 1994), although several recent molecular studies have shown that this is not always the case (Lukas et al. 2005). The concession model predicts increasing skew with increasing relatedness (Vehrencamp 1983a,b); thus, we expected to find higher skew in male philopatric species than in species in which males disperse. The tug-of-war model makes no predictions or even predicts a negative relation between male relatedness and skew if males exert weaker control over close relatives (Reeve et al. 1998).

Methods

Mating distribution among males in multimale groups

We collected data on the distribution of mating among males in multimale primate groups from previously published articles and reviews (see “[Electronic Appendix](#)”). In total, we obtained data from 84 studies representing 31 species in 17 genera, with 3 species of

strepsirrhines, 6 species of New World monkeys, 19 Old World monkeys, and 3 species of great apes (“[Electronic Appendix](#)”). Studies were mainly from wild groups (nonprovisioned: 43 records, 53.8%; provisioned: 20 records, 25.0%), semi-free-ranging provisioned groups (6 records, 7.5%) or captive groups (11 records, 13.8%). Our data set includes 10 of 12 species included in a previous comparative study (Cowlshaw and Dunbar 1991), which investigated 12 species in total. Our data set increases the sample size by including 21 species from 34 studies that were not included in the study of Cowlshaw and Dunbar (1991) (in most cases because the articles appeared after their article was published). Our data set does not include two species (*Alouatta caraya* and *Papio cynocephalus*) that were analyzed by Cowlshaw and Dunbar (1991) because it was impossible to calculate indices of the mating skew from the data reported in the original articles. Similarly, we could not calculate indices of mating skew from 21 studies that were sampled by Cowlshaw and Dunbar (1991), although other estimates were available for these species, and so they were included in our sample.

To calculate mating skew, we required information on at least one of the following measures: (1) the number of copulations performed by all adult males in a group; (2) the relative frequency of mating by all adult males in a group; and (3) the proportion of mating by the most successful male. Although some sneak copulations occur in primates (e.g., Berard et al. 1994), copulation behavior is generally easy to observe in primates when systematic data collection methods are used. Thus, we included studies only if they used all occurrence or focal sampling methods (Altmann 1974). Whenever possible, we used data that are most tightly linked to male reproductive success. Thus, we preferred data on ejaculation frequency more than copulation frequencies when both were reported in an article. We also preferred copulation data at times when conception was most likely to take place (Cords 1984; Bercovitch 1986; Struhsaker and Pope 1991; Perry 1997; Robbins 1999; Possamai et al. 2005; see [Electronic Appendix](#)). Subadult males generally fail to mate or mate well outside the period of peak fertility, and inclusion of these males can inflate variance in male mating success (Bercovitch 1986; McMillan 1989; Cowlshaw and Dunbar 1991). We therefore excluded mating by subadult males in our calculations. We also collected data on the number of the adult males and adult females in each study.

Female reproductive traits

We used five female reproductive traits: duration of the breeding season, duration of estrus, and three measures of estrous overlap. Data on breeding season duration were collected from Mitani et al. (1996), whereas data on the duration of estrus were taken from Nunn (1999a). We obtained data on the percentage of time that two or more females were observed to be in estrus from Nunn (1999a), which provided published or unpublished data from field researchers, with additional data from Dr. Mandy Korstjens

(personal communication, 2005) for olive colobus monkeys (*Procolobus verus*). As a second proxy for female overlap, we calculated the probability that two or more females are simultaneously receptive during the mating season (Dunbar 1988, 1999; Nunn 1999a; see [Electronic Appendix](#) for details).

In using the expected probability of female overlap, we assumed that the receptive cycle of one female was not affected by cycles of other females. However, this assumption may be incorrect if females synchronize (McClintock 1981, 1983) or asynchronize (Pereira 1991) their receptive periods with other females. Nunn (1999a) quantified the degree of synchrony by calculating least squares residuals of observed female overlap regressed on expected probability of overlap. Negative residuals indicate less overlap than expected by chance (possible asynchrony), whereas positive residuals indicate greater-than-expected overlap (i.e., possible socially mediated synchrony). Using these data, we predicted that this “synchrony index” correlates negatively with mating skew in the tug-of-war model (i.e., socially mediated synchrony tends to produce a more even distribution of mating among males).

Skew indices

With more than 20 skew indices available, it remains unclear which skew index should be preferred (Tsuji and Tsuji 1998; Kokko et al. 1999; Tsuji and Kasuya 2001; Nonacs 2003). Because each index has advantages and disadvantages (Kokko et al. 1999; Nonacs 2000, 2003), we used three different estimates. First, we used binomial skew index (hereafter B index; Nonacs 2000, 2003). Positive value of the B index indicates that skew is greater than expected, whereas negative values indicate reproduction is more equally distributed than expected. One advantage of using the B index is that the distribution of mating can be tested against a null hypothesis of random mating within groups, which is indicated by $B=0$. We can only calculate the B index for 22 species. However, the B index was not statistically associated with any of the independent variables investigated in this article, possibly due to lower sample sizes or because the data needed to calculate the B index biases this measure toward small group sizes (Nonacs 2000, 2003). We therefore used B index only to judge whether the distribution of copulations among males differs from random.

Second, we used the “lambda” index of mating skew (Kokko and Lindström 1997). Lambda ranges from 0 (mating evenly distributed) to 1 (mating completely skewed toward one male). In total, we were able to obtain the estimates of lambda for 28 species.

Third, we used the proportions of mating by the most successful male as a measure of mating skew (hereafter called “maximum mating proportion”). Although this index simplified the distribution of mating among males other than the most successful male, this proxy has an advantage in terms of sample size, with maximum mating

proportion commonly available in previous studies of primates (e.g., Curie-Cohen et al. 1983; Samuel et al. 1984; Inoue et al. 1991; de Ruiter et al. 1994; Brereton 1994). In total, we obtained estimates of maximum mating proportion for 31 species.

All three measures of skew were significantly correlated with one another (Spearman correlation test: lambda vs B: $r_s=0.89$, $n=57$; lambda vs maximum mating proportion: $r_s=0.94$, $n=72$; B vs maximum mating proportion: $r_s=0.75$, $n=57$, all P 's <0.0001), suggesting that the measures of mating skew were consistent with one another. For completeness, however, we ran analyses with both lambda and the maximum mating proportion. We also ran two tests of consistency in relation to intraspecific variation and living conditions (captive vs wild groups). In terms of intraspecific variation, the number of data points per species varies from 1 to 17 (see [“Electronic Appendix”](#)). We ran one-way analysis of variance (ANOVA) in which the identity of species was set as an independent variable, with the analysis including only species that provided three or more estimates (lambda, $n=8$ species; maximum mating proportion, $n=9$ species). We found significant differences among species [lambda: $F_{(7,36)}=3.01$, $P=0.01$; the maximum mating proportion: $F_{(8,45)}=3.68$, $P=0.002$], suggesting that there were consistent species differences in indices of mating skew. To test whether captive vs wild conditions impacted measures of skew, we ran an unpaired t test to compare the indices of mating skew using data from the genus *Macaca* because it was only for these species that sample sizes were large enough. We did not find a significant influence of living condition on lambda ($t_{11}=-1.79$, $P=0.10$) or the maximum mating proportion ($t_{21}=-1.68$, $P=0.11$).

Phylogenetic comparative methods

To test predictions of the concession model and the tug-of-war model, we calculated phylogenetically independent contrasts (Felsenstein 1985; Harvey and Pagel 1991; Nunn and Barton 2001) using the computer program Comparative Analysis by Independent Contrasts (CAIC) (Purvis and Rambaut 1995). We used two estimates of primate phylogeny to run these tests. The first phylogeny came from Purvis and Webster (1999), which updated the phylogeny by Purvis (1995). The second phylogeny was based on Smith and Cheverud (2002), with supplemental information of phylogeny among *Macaca* species from Morales and Melnick (1998) and Li and Zhang (2005). We found that the results did not differ qualitatively according to the phylogenies used in the analyses; thus, only the results from tests using Purvis and Webster (1999) are reported here.

We first tested whether the skew indices were correlated with phylogeny by using the test for serial independence (TFSI; Abouheif 1999). To implement the TFSI, we used the program Phylogenetic Independence (version 1.1; Reeve and Abouheif 1999). Statistical significance was assessed using simulations to generate a null distribution

($n=1,000$ simulations) as described in Abouheif (1999). Tests revealed a significant phylogenetic signal for lambda ($P=0.002$) and the maximum mating proportion ($P=0.03$). We therefore based our conclusions on phylogenetic tests. For completeness, we also ran nonphylogenetic tests using species values and report any differences from phylogeny-based analyses.

We ran diagnostic tests to ensure that the contrasts were properly standardized (Garland et al. 1992; Purvis and Rambaut 1995; Freckleton 2000). These tests revealed that log-transformed data and equal branch lengths best met the assumptions for the majority of variables. Confounding variables shared through common descent and violations of the assumptions of independent contrasts can produce outliers in contrast analyses (Price 1997; Purvis and Webster 1999; Harvey and Rambaut 2000; Nunn and Barton 2000, 2001). We therefore conducted analyses with and without outlying contrasts, where outliers were identified as contrasts with residuals more than 1.96 standard deviations (Jones and Purvis 1997). Removal of outliers helps to meet the assumptions of independent contrasts and avoids significant results that sometimes emerge from a single contrast with high leverage in the regression analysis. Results with outliers removed were therefore given precedence in this article. Analyses involving univariate analyses of discretely coded traits were run using the “BRUNCH” algorithm in CAIC (Purvis and Rambaut 1995).

We first conducted univariate analyses to test the influence of each independent variable separately. In addition to measures of demographic factors, female estrous overlap and male dispersal patterns, we tested the effect of the number of copulations observed in each study (provided in 71 of 84 studies; see “Electronic Appendix”) based on analyses from Kokko et al. (1998), which found that the lambda index was associated with the number of copulations in lekking species. Next, we ran analyses that investigated the influence of each independent variable in a stepwise multiple regression model that included demographic variables (number of males and number of females), female reproductive traits, number of copulations, and dispersal pattern. When investigating the effect of female reproductive traits, we had multiple measures available for estrous overlap available, but multiple regression models were run separately for each of these variables (rather than including all of them in one model). We did this because the estimates were biologically identical (e.g., the observed and the empirical probability of female receptive overlapping; Nunn 1999a). In addition, data were not available on all variables for the same set of species, resulting in exclusion of species when they were missing one or two of these variables.

A recent simulation study found that type I error rates can be inflated in phylogenetic comparative studies that use mean values based on few observations per species (Harmon and Losos 2005). We tested this possibility using ANOVA to investigate the proportion of variation that occurs between species. These results indicate that R^2 was 0.58 for the lambda and 0.55 for the maximum mating

proportion, which is very close to the recommended value of 0.60 in Harmon and Losos (2005). As noted above, we also paid close attention to outliers in the statistical analysis. If intraspecific variation is larger than the interspecific variation, these outliers are more likely to occur among contrasts of sister species (on the tips of the tree) with smaller sample sizes (Harmon and Losos 2005).

All statistical tests are two-tailed, and the alpha level was set as 5%. Because we conducted multiple analyses using different indices of mating skew and multiple estimates of female overlap, we used the sequential Bonferroni method to adjust the alpha level (Rice 1989).

Intraspecific analysis

We also performed one analysis within species to investigate whether the factors that produce interspecific variation in mating skew also account for variation within species. Only chimpanzees (*Pan troglodytes*) provide a large-enough sample size ($N=17$) to permit such an analysis, although only measures of expected estrous overlap were available for tests of female reproductive traits. Data were obtained from three studies of primates in the wild (Nishida 1983, 1997; Boesch and Boesch-Achermann 2000). A recent study has investigated patterns of male reproductive success in greater detail within one of these populations (Taï chimpanzees, Boesch et al. 2006).

Results

Mating skew among males

The distribution of mating was skewed among males in most cases. In 75.4% (43/57) of the studies for which it was possible to calculate the B index, statistical tests indicated significant mating skew (see “Electronic Appendix”). In 78.7% (59/75) of the studies with data on the proportion of mating by different males, the alpha male or the resident male achieved the highest mating success (species mean, 81.1%; standard error, 6.3).

Univariate analyses

In phylogenetic comparative tests, the lambda index and the maximum mating proportion decreased as the number of males increased (Fig. 1), as the number of females increased, and the number of observed copulations increased (Table 1). Similar results were obtained in nonphylogenetic tests. However, none of the female reproductive traits were correlated with indices of mating skew when using independent contrasts (Table 1). Results from nonphylogenetic tests (not shown) were generally consistent to those from the phylogenetic comparative tests. Outliers excluded in the phylogenetic tests included some contrasts at the tips of the phylogeny (Table 1), but these tips were not concentrated in species with only one

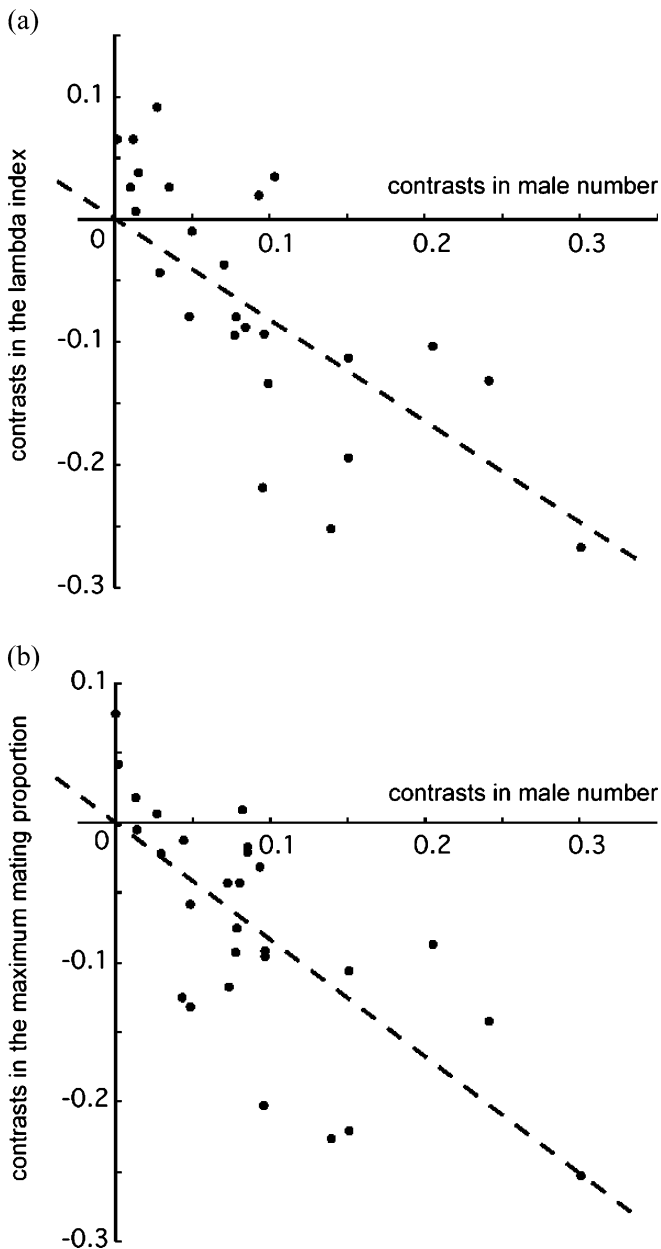


Fig. 1 Relationship between male number and mating skew indices. **a** Phylogeny-based comparative analysis using the lambda index (log-transformed); **b** phylogenetic comparative analysis on the maximum mating proportion (log-transformed)

observation. This suggests that the small sample sizes in our study were unlikely to result in elevated type I error rates (Harmon and Losos 2005). As found in a previous study (Kokko et al. 1998), the number of copulations also correlated with measures of skew. This variable was therefore included in the multivariate tests (see below).

In testing the prediction of the concession model, male dispersal was unrelated to any of the measures of mating skew. In analyses using phylogenetic comparative methods, we had only four contrasts in male dispersal, and corresponding contrasts in mating skew index were not significantly different from zero (*t* test, Table 1). Results also were not significant in nonphylogenetic tests.

Multivariate analysis

In phylogenetic analyses, only the number of males correlated significantly with the two indices of mating skew. This was true when using any of the five measures of female mating overlap (only results for variables that provided the largest sample sizes are provided in Table 2). The number of females and the number of copulations were generally no longer significantly correlated with either measure of mating skew after controlling for the number of males. Male dispersal pattern was not significantly correlated with measures of mating skew (Table 2). Results from nonphylogenetic tests (not shown) were generally consistent, with one exception—the duration of estrus was positively associated with both measures of mating skew (lambda: $b=0.16$, $t_{52}=3.14$, $P<0.003$; maximum mating proportion: $b=0.16$, $t_{59}=4.62$, $P<0.0001$) after controlling for the effects of male number (lambda: $b=-0.42$, $t_{52}=4.04$, $P<0.0002$; maximum mating proportion: $b=-0.47$, $t_{59}=-6.6$, $P<0.0001$) and the number of copulations (lambda: $b=-0.18$, $t_{52}=-3.33$, $P<0.0002$; maximum mating proportion: $b=-0.15$, $t_{59}=-4.5$, $P<0.0001$).

Intraspecific analysis in chimpanzees

Consistent with interspecific analyses, the number of males was negatively associated with both mating skew indices in a stepwise multiple regression model (lambda: $b=-0.18$, $P=0.004$; maximum proportion mating: $b=-0.17$, $P=0.002$; Fig. 2). Neither the number of females (lambda: $b=0.05$, $P=0.12$; maximum proportion mating: $b=0.045$, $P=0.11$) nor the expected estrous overlap (lambda: $b=0.02$, $P=0.11$; maximum proportion mating: $b=0.02$, $P=0.10$) was significant.

Discussion

Our comparative analyses revealed that across 31 species of primates, mating is significantly skewed among males in multimale groups, and in species with clear dominance relationships among males, the alpha male or resident male tends to mate more frequently. We tested two major models of reproductive skew and found support for the tug-of-war model, which predicts a decrease in mating skew with an increase in the number of males. Although mating skew decreased as female number increased, this association generally became nonsignificant after controlling for the effect of male number, which probably reflects that the number of males correlates with the number of females in primates (Mitani et al. 1996; Nunn 1999a; Lindenfors et al. 2004). Results involving the number of males were consistent when analyzing the comparative data with different measures of mating skew, in phylogenetic and nonphylogenetic tests, and when using different estimates of primate phylogeny. In addition, results were consistent when we examined within-species data from chimpanzees, where the number of males was also correlated negatively with measures of mating skew.

Table 1 Results of univariate analyses of the phylogenetic comparative methods on factors associating to mating skew indices

	Lambda index					Outlier ^a	Maximum mating proportion					Outlier ^a
	<i>b</i>	SE	<i>df</i>	<i>t</i>	<i>P</i>		<i>b</i>	SE	<i>df</i>	<i>t</i>	<i>P</i>	
Male number	-0.82	0.12	24	-6.91	>0.0001 ^b	2 (AB)	-0.84	0.10	27	-8.48	>0.0001 ^b	2 (GH)
Female number	-0.43	0.12	23	-3.47	>0.002 ^b	2 (AC)	-0.39	0.11	26	-3.56	0.002 ^b	2 (CI)
No. copulation	-0.30	0.09	20	-3.26	0.004 ^b	2 (AE)	-0.28	0.06	22	-4.39	0.0002 ^b	2 (IJ)
Breeding seasonality	0.20	0.17	20	1.17	0.26	2 (CD)	0.10	0.13	21	0.77	0.45	3 (CDI)
Duration of estrus	0.14	0.13	19	1.05	0.31	1 (C)	0.14	0.11	21	1.20	0.24	1 (C)
Expected estrous overlap	0.01	0.06	18	0.21	0.84	2 (CF)	-0.10	0.05	19	-1.80	0.09	3 (CFI)
Observed estrous overlap	0.07	0.11	18	0.62	0.54	1 (D)	0.01	0.09	18	0.07	0.95	2 (DI)
Synchrony index	0.24	0.26	11	0.91	0.38	1 (B)	-0.05	0.28	13	-0.16	0.87	0
Male philopatry/dispersal			3	-1.31	0.28				3	-1.42	0.25	

^aRemoved outlier(s) and sample size for each species (shown in parenthesis). A, *Lemur catta* (3) vs *Eulemur fulvus* (2); B, *Alouatta palliata* (2) vs *A. seniculus* (2); C, *Pan troglodytes* (17) vs *Pan paniscus* (2); D, *Ptilocolobus badius* (1) vs *Procolobus verus* (1); E, *P. verus* (1) vs *Semnopithecus entellus* (1); F, *Cercopithecus ascanius* (1) vs *C. mitis* (2); G, *L. catta* (3) vs *E. fulvus* (4); H, *Macaca radiata* (2) vs *M. arctoides* (1); I, *Chlorocebus aethiops* (2) vs *Erythrocebus patas* (1); J: (*P. badius* and *P. verus*) vs *S. entellus* (1); J: (*A. palliata* and *A. seniculus*) vs *Brachyteles arachnoides* (4); outliers in block letters indicate the contrasts of sister species with only one sampling for each species.

^bSignificant after sequential Bonferroni correction.

The results of Cowlshaw and Dunbar (1991) revealed that male dominance rank correlates positively with mating success. Our study expanded on this previous study in several ways. First, we updated information on male mating skew by adding studies published since Cowlshaw and Dunbar conducted their study and by using measures of skew that permitted inclusion of additional species. Second, we controlled for the effect of phylogeny by using independent contrasts. Finally, we investigated the influence of male dispersal pattern and multiple female reproductive traits (although like us, Cowlshaw and Dunbar 1991 also investigated seasonality). With our updated data set and methodological approach, we confirmed that dominant males have an advantage in mating with estrous females (Altmann 1962). As was also found by Cowlshaw and Dunbar (1991), our analyses revealed no significant effect of female number on patterns of male skew—a result that was also consistent in our intraspecific analysis of chimpanzees (Fig. 2).

We found little support across species for an effect of female reproductive traits on male skew. Similarly, reproductive skew was not significantly associated with female estrous synchrony in rhesus macaques (Widdig et al. 2004). In contrast, negative relationships between female receptive synchrony and skew among males have been reported in nonprimates [Ims 1988; Moller and Ninni 1998; domestic cats (*Felis catus*) Say et al. 2001] and in primates (priority-of-access model; Altmann 1962). A recent analysis of long-term data from a single population of chimpanzees at Tai found evidence for an effect of both the number of males and female synchrony on male reproductive success (Boesch et al. 2006). This difference is likely to reflect that Boesch et al. (2006) used data that were collected in a consistent way at the same site over many years, and that more refined estimates of female overlap and genetic estimates of paternity were available (e.g., Widdig et al. 2004 estimated synchrony from births rather than matings). This discussion suggests that the

Table 2 Results of stepwise multivariate multiple regression models investigating associations between mating skew and the demographic variables, female reproductive traits, and male dispersal pattern

	Lambda index					Maximum mating proportion				
	<i>b</i>	SE	<i>df</i>	<i>t</i>	<i>P</i>	<i>b</i>	SE	<i>df</i>	<i>t</i>	<i>P</i>
Female mating overlapping										
Breeding seasonality	0.06	0.12	15	0.48	0.64	0.05	0.11	16	0.46	0.65
Expected estrous overlap	0.03	0.04	15	0.79	0.44	0.04	0.04	16	0.99	0.34
Other variables ^a										
Male number	-0.6	0.15	16	-4.1	<0.001*	-0.8	0.14	17	-5.6	<0.001 ^b
Female number	-0.1	0.16	15	-0.6	0.58	0.01	0.16	16	0.06	0.95
No. copulation	0	0.1	15	-0.3	0.78	-0.1	0.08	16	-1.7	0.11
Male dispersal pattern ^c	0.15	0.09	15	1.73	0.10	0.14	0.09	16	1.55	0.14

Multivariate analyses were run separately for each of the measures (see “Methods”).

^aThe results of statistics for other variables were identical between two separate analyses on the breeding seasonality and on the expected estrous overlap.

^bSignificant after sequential Bonferroni correction.

^cWe used CRUNCH to analyze the effect of male dispersal pattern, although it is a discrete variable (Purvis and Rambaut 1995).

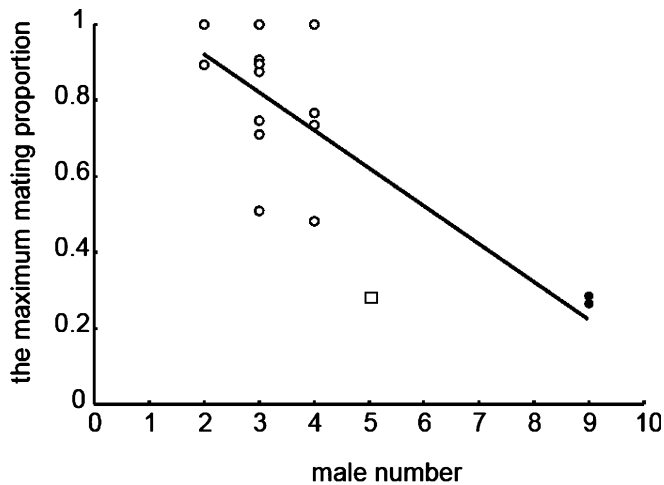


Fig. 2 Relationship between the number of males and the maximum mating proportion in chimpanzees. We only show the graph of the maximum mating proportion because the graph of the lambda index was nearly identical. *White circles* are from Nishida (1983); *black circles* are from Nishida (1997); white square is from Boesch and Boesch-Achermann (2000)

effects of estrous synchrony are either not universal to all primate species or its effects are difficult to quantify, both of which would hinder our ability to detect a significant association in comparative analyses. In addition, we only considered multimale groups. Thus, it appears that female receptive synchrony affects the number of males when looking across single-male and multimale groups combined (Nunn 1999a), but not the distribution of mating among males in multimale groups.

Regarding female traits, recent socioecological models suggest that the females adopt anti-infanticide strategies to confuse paternity of offspring through promiscuous matings and concealed ovulation (van Schaik et al. 1999). This factor, along with sperm competition more generally (Harcourt et al. 1981), will tend to decrease mating skew, but other factors associated with infanticide can also increase reproductive skew. Even in promiscuous species, for example, females might attempt to concentrate the paternity of offspring in higher-ranked males by copulating with the dominant male during periods in which the probability of fertilization is high (van Noordwijk and van Schaik 2004; Nunn 1999b). Similarly, the high-ranked male may concentrate mating effort on times when fertilization is highly likely (Engelhardt et al. 2004; but see Heistermann et al. 2001). In this study, we tried to control for the “blurring” effects of paternity confusion by focusing on copulations during the fertile period and using data most linked to fertilization (see “Methods” and “Electronic Appendix”). Although many studies have shown that mating frequency predicts reproductive success (Smith 1981; Pope 1990; Ohsawa et al. 1993; de Ruiter et al. 1994; Paul and Kuester 1996; Soltis et al. 1997), other studies did not find such links (Curie-Cohen et al. 1983; Shively and Smith 1985; Inoue et al. 1991, 1993). Genetic information on actual reproduction in groups would clarify these issues and allow reproductive skew to be examined more directly, but such data are not

yet sufficiently available to test the predictions in a comparative context.

Interpreting analyses of the concession model

As a test of the concession model, we investigated whether mating skew is higher in species with male philopatry, but we found no evidence for this prediction. Based on these results, it is tempting to conclude that our study supports the tug-of-war model more than the concession model. However, a variety of factors would weaken such a conclusion. With the goal of developing stronger comparative tests of the concession model in primates and other taxa in the future, in what follows, we consider these factors in greater depth.

First, our analyses were based on discrete variables involving dichotomous codes of male philopatry. The power of these comparisons is therefore likely to be low, with only four evolutionary transitions in reconstructed values in male philopatry. Using the computer program G Power, for example, we found that the power of this test was only 5.7% ($d=0.20$, small effect size, and an alpha level of 0.05). Future tests that make use of quantitative data on dispersal would increase the power of this test substantially (Garland et al. 1993; Purvis and Rambaut 1995; Nunn and Barton 2001).

Another issue involves our assumption that genetic relatedness is higher among members of the philopatric sex. Previous studies provided mixed results concerning the relationship between male philopatry and relatedness among males. In two studies of chimpanzees, within-group relatedness among males is no greater than among females (Constable et al. 2001; Vigilant et al. 2001; but see Morin et al. 1994; reviewed in Lukas et al. 2005). Similarly, a study of wild long-tailed macaques reported a nonsignificant difference in within-group relatedness among males and females (de Ruiter and Geffen 1998). Because within-group relatedness can be affected by various factors (Lukas et al. 2005), the relatedness among males in male philopatric species sampled in our study may have deviated from the level that we expected. Moreover, concessions can be given to individual males on a pairwise basis within groups, regardless of overall relatedness among males in the group (Vehrencamp 1983a,b). To test this possibility, quantitative estimates of dyadic relatedness based on molecular biological methods are needed.

The aim of future studies should be to generate predictions from different versions of concession models. In primates, for example, it would be worth exploring the application of queuing models and models with multiple subordinate members (Kokko and Johnstone 1999; Ragsdale 1999; Johnstone et al. 1999; Reeve and Emlen 2000). These models may be more appropriate because social primates commonly live in groups with three or more males (see “Electronic Appendix”), and subordinates in these groups may queue for the dominant position (Alberts et al. 2003; van Noordwijk and van Schaik 2004; Robbins and Robbins 2005). Importantly, these models predict

weaker effects of relatedness on reproductive skew as compared to the “classic” concession model that we considered here (Kokko and Johnstone 1999; Ragsdale 1999; Johnstone et al. 1999; Reeve and Emlen 2000). Thus, if these other models are more appropriate, weak effects of relatedness on reproductive skew may have been difficult to detect in our study.

A final factor that can account for nonsignificant tests of the concession model involves the many assumptions that underlie this skew model and its variants, which can lead to different models applying to different species. Indeed, recent developments in modeling reproductive skew suggest that the transactional and compromise models are not mutually exclusive, with the compromise model potentially regarded as a special case of the transactional model (Johnstone 2000). It can be that cross-species differences in social systems and ecological opportunities for reproduction outside the group result in different models being appropriate for different species (Hager 2003). Thus, the concession model may apply to particular primate species even if it is not a general explanation for patterns of skew across primates. For example, males are tolerant to group males and share copulations with receptive females in some species of primates [e.g., muriquis (*Brachyteles arachnoids*), Strier et al. 2002; wild chimpanzees in Ngogo, Nishida 1983; Watts 1998]. It would be interesting to investigate whether high tolerance among males is associated with ecological, social, and genetic factors in empirical studies on a single species; however, a comparative approach may have difficulty discerning effects when they vary among species in the data set.

Conclusions

In summary, we documented a positive association between measures of mating skew and the number of males in multimale primate groups, thus providing evidence consistent with a tug-of-war model. The concession model was not supported, possibly due to weaknesses of the tests enumerated above. In addition, proxy variables for the degree of female overlap were largely nonsignificant predictors of mating skew among males. Reproductive skew models have been regarded as a unifying framework for understanding the diversity of social systems seen in animals (Keller and Reeve 1994; Bennett and Faulkes 2000). Several studies have introduced this framework in primate studies (Hager 2003; Widdig et al. 2004; Bradley et al. 2005; Robbins and Robbins 2005) and have discussed the importance of interspecific comparisons (Nonacs 2000). To our knowledge, however, this is the first study to use phylogenetic comparative methods to test predictions from reproductive skew models in a broad phylogenetic context. Application of similar approaches to other groups of animals such as insects and birds is likely to give important insights to understanding broad evolutionary patterns of reproductive skew. More generally, comparative methods provide a means to investigate how demographic

and other factors influence patterns of skew, including factors not considered here such as female choice (Widdig et al. 2004), reproductive queuing (Alberts et al. 2003), alliances (Noe 1992; Watts 1998), and alternative reproductive strategies by males (Berard et al. 1994). Many of these details are not presently easy to obtain, but they may prove key insights in future comparative studies and for empirical studies on a single species.

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