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Female reproductive synchrony predicts skewed paternity across primates

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Recent studies have uncovered remarkable variation in paternity within primate groups. To date, however, we lack a general understanding of the factors that drive variation in paternity skew among primate groups and across species. Our study focused on hypotheses from reproductive skew theory involving limited control and the use of paternity “concessions” by investigating how paternity covaries with the number of males, female estrous synchrony, and rates of extragroup paternity. In multivariate and phylogenetically controlled analyses of data from 27 studies on 19 species, we found strong support for a limited control skew model, with reproductive skew within groups declining as female reproductive synchrony and the number of males per group increase. Of these 2 variables, female reproductive synchrony explained more of the variation in paternity distributions. To test whether dominant males provide incentives to subordinates to resist matings by extragroup males, that is, whether dominants make concessions of paternity, we derived a novel prediction that skew is lower within groups when threat from outside the group exists. This prediction was not supported as a primary factor underlying patterns of reproductive skew among primate species. However, our approach revealed that if concessions occur in primates, they are most likely when female synchrony is low, as these conditions provide alpha male control of paternity that is assumed by concessions models. Collectively, our analyses demonstrate that aspects of male reproductive competition are the primary drivers of reproductive skew in primates. *Key words*: limited control, paternity, primates, reproductive skew, reproductive synchrony. [*Behav Ecol* 19:1150–1158 (2008)]

The distribution of reproduction among members of a social group is a fundamental aspect of sociality, with implications for patterns of dispersal, genetic variation, and cooperation within groups. This partitioning of reproduction, or reproductive skew, has therefore attracted the attention of behavioral ecologists for some time (Altmann 1962), resulting in the development of mathematical models for how ecological and behavioral factors influence the distribution of reproduction within groups. Reproductive skew models can be broadly classified into 2 basic types (reviewed in Clutton-Brock 1998; Johnstone 2000). Transactional models propose that reproduction is controlled by the dominant individual and shared with subordinates as staying or fighting incentives (Keller and Reeve 1994; Clutton-Brock 1998; Johnstone 2000). One of these models, the concession model, predicts that the shared amount of reproduction varies according to the degree of relatedness between dominants and subordinates, with a smaller incentive provided to more closely related subordinates, based on the reasoning that they gain through indirect fitness benefits (Vehrencamp 1983; Reeve and Keller 2001). In contrast, limited control or compromise models assume that reproduction cannot be controlled completely by either dominants or subordinates. Consequently, the observed skew depends on the degree of control available to a dominant (Cant 1998; Reeve et al. 1998). Here, we tested predictions related to both types of models using comparative data on paternity in primate groups.

Empirical studies have provided mixed support for variants of both models in species of social insects, cooperatively breeding birds, and mammals (reviewed in Magrath and Heinsohn 2000; Clutton-Brock et al. 2001; Reeve and Keller 2001). Among mammals, for example, dominant individuals in dwarf mongoose and lion societies may allow subordinates to breed in order to retain helpers or coalition partners (Creel and Waser 1991; Packer et al. 1991; but see Clutton-Brock 1998), whereas limited control over reproduction has been proposed to drive reproductive partitioning in meerkats (*Suricata suricatta*, Clutton-Brock et al. 2001) and mountain gorillas (*Gorilla beringei*, Bradley et al. 2005).

With the growing knowledge that different models are supported in different species, new questions have emerged concerning the factors that drive these differences and, more generally, the ability of skew models to explain patterns of reproduction at broader evolutionary scales (Kutsukake and Nunn 2006 forthcoming). Indeed, because skew models aim to provide an integrative framework for understanding sociality, these models should account for variation both within and across species. A recent comparative study of male mating success in primates, for example, found evidence for the limited control model of reproductive skew (Kutsukake and Nunn 2006). This study demonstrated that broad phylogenetic approaches could be used to investigate patterns of mating within groups. Here, we apply a similar approach to investigate a more direct correlate of reproductive skew using measures of genetic paternity.

Predictions from limited control models that have been tested in primates are based on earlier research on group composition and mating skew (Emlen and Oring 1977; Vehrencamp and Bradbury 1984; Ridley 1986; Cowlshaw

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and Dunbar 1991; Nunn 1999b). Specifically, the monopolization potential of a dominant male (determining male reproductive skew) is predicted to be a negative function of the number of other males that are competing and the degree to which female estrous periods are synchronized (Ridley 1986; Cowlshaw and Dunbar 1991; Nunn 1999b). A conceptual forerunner of limited control models—the priority of access model (Altmann 1962)—also predicts a decline in reproductive skew with increasing female estrous synchrony but makes no predictions regarding the number of competitors (Kutsukake and Nunn 2006, forthcoming). These predictions have been supported in a handful of paternity studies within groups of mountain gorillas, common chimpanzees, mandrills, yellow baboons, and rhesus monkeys (Alberts et al. 2003; Widdig et al. 2004; Bradley et al. 2005; Charpentier et al. 2005; Boesch et al. 2006).

Whereas recent studies supported the notion that dominants have limited control over reproduction in a group, no evidence was found for alpha males to concede paternity to subordinates (Altmann et al. 1996; Bradley et al. 2005; Boesch et al. 2006; Kutsukake and Nunn 2006). The lack of support for transactional sharing may arise because when testing the transactional models, these studies investigated the prediction that skew changes with relatedness among males (but see Robbins A and Robbins M 2005).

Because male relatedness is difficult to calculate (Csillery et al. 2006) and can be low even in male philopatric species (Lukas et al. 2005), we developed a new prediction to investigate situations in which concessions may occur. Specifically, we focus on threats from outside the group by proposing that skew within groups declines as the risk of extragroup paternity (EGP) increases. This prediction is based on the reasoning that the proportion of offspring that the alpha male sires overall will decrease if paternity is lost to outside males. If subordinates receive incentives to fend off extragroup males that want to mate with females in the group, these concessions will result in lower within-group paternity by the alpha male. The conceded paternity share has to be smaller than the dominant's paternity loss to outside males to make it a worthwhile strategy to the alpha male; indirect fitness benefits to the alpha can be neglected because male relatedness in primate groups is generally low (Lukas et al. 2005). The degree of EGP varies across mammalian species, with a maximum value of 80% and is predicted by female group size and breeding seasonality in a sample of predominately single-male groups (Clutton-Brock and Isvan 2006; Isvan and Clutton-Brock 2007). Increasing numbers of coresident males have been shown to reduce the amount of paternity lost to outside males in Hanuman langurs (*Semnopithecus entellus*, Launhardt et al. 2001), which supports the rationale underlying this new prediction.

Thus, by taking a broad comparative perspective that links genetic and behavioral data, our study extends previous work on reproductive skew to test 2 fundamental hypotheses in primate sociality. Based on the idea that control over reproduction is incomplete, we predict that reproductive skew within a group will decrease with an increasing number of males and increasing female estrous synchrony; the latter association would also be consistent with the priority of access model (Altmann 1962). With regard to concessions of paternity, we predict that in populations where males from outside the group pose a measurable risk (i.e., rates of EGP >0), reproductive skew among males within the group will be lower, as compared with species where EGP has not been documented (EGP = 0). In addition, we investigate for the first time how skew, estrous synchrony, and the number of males influence patterns of EGP in primates.

MATERIALS AND METHODS

We systematically searched the literature for data on the distribution of paternity among males in multimale groups of primates. In addition, we compiled information on female estrous synchrony, the number of resident adult males, and estimates of EGP, that is, the proportion of offspring sired outside the social group. In total, we obtained data on 43 different primate groups, sometimes from a single study of multiple groups in a population. We used the average alpha male paternity across groups from the same population as the population value of male reproductive skew in the analyses presented here. This "populations" sample comprised 27 populations from 19 species in 11 genera. Data on EGP were obtained for 17 of the 27 populations. The data set includes 3 Prosimian species, 3 Neotropical primate species, 9 Old World monkey species, and 4 species of great apes (Table 1). Subspecies were treated as distinct populations. If 2 paternity studies were available from the same geographic locality, we treated them as 2 populations if different groups had been studied or observation periods were exclusive of one another. Our analysis of independent contrasts avoids unjustified sample inflation in this case. For example, if 2 groups in a population had the same value, this would yield a zero contrast and the variation would be carried to the next level (i.e., differences among populations or species).

We also ran analyses that aggregated the data by groups or species as data points, and these analyses produced largely congruent results. We therefore present the population-level analyses here.

Measures

Reproductive success was based on published records of genetic paternity studies. Nineteen studies used DNA microsatellite analyses with on average 8.5 ± 3.8 primers and subsequent paternity exclusion analyses. Eight studies used DNA fingerprinting and/or polymorphisms in serum proteins, blood types, isozymes, and enzymes. Reported paternity exclusion probability averaged $96 \pm 4\%$. We defined "alpha male paternity" as the proportion of offspring sired within the group by the alpha male and used it as our measure of reproductive skew. Hence, lost reproduction due to high levels of EGP was not taken into account by this measure, which is solely a function of a male's reproductive success within a group. We did not use alternative indices of reproductive skew (Nonacs 2003) because original work often did not provide the distribution of paternity among subordinates. "EGP" was expressed as the proportion of offspring sired by males outside the social group, that is, when all within-group males could be excluded from paternity. This data set was limited to 17 populations with potential for EGP, hence wild and free-ranging populations only (Table 1).

Measures of "reproductive synchrony" from wild primates are difficult to obtain, and previous studies therefore used several proxies for synchrony (Nunn 1999b). One widely used estimate is reproductive seasonality (i.e., duration of birth season, Ridley 1986; Mitani et al. 1996), based on the assumption that females will overlap to a greater degree when the breeding season is shorter. This assumption is known to be violated in some species, for example, when females of highly seasonal species breed asynchronously (Pereira 1991). We therefore instead used the proportion of days in which 2 or more females were observed to be mating on the same day (relative to observation days during the mating season). Female primates mate outside their short ovulatory periods, which may allow for increased polyandry leading to paternity confusion and subsequent protection from infanticide (van Noordwijk and van Schaik 2000). This suggests that male information about the timing of female fertile phases is

Table 1

The “populations” data set: alpha male paternity (percentage of paternity within a group), number of males per group, degree of reproductive synchrony, EGP, and total alpha male paternity for 27 groups or populations of primates living in multimale groups

Species	Population	Status	Alpha paternity within group (%)	Number of males	Synchrony	EGP (%)	Alpha paternity total (%)	Sources
<i>Alouatta seniculus</i>	Hato Masaguaral	Wild	100.0	2.3	2.5 ^a	0.0	100.0	(Pope 1990)
<i>Cebus capucinus</i>	Santa Rosa	Wild	87.5	2.9	15.8 ^a	0.0	87.5	(Jack and Fedigan 2006; Kutsukake and Nunn 2006)
<i>Eulemur fulvus mayottensis</i>	Strasbourg	Captive	80.0	2.0	0.0 ^a	NA	80.0	(Gachot-Neveu et al. 1999)
<i>Eulemur fulvus rufus</i>	Kirindy	Wild	87.5	3.3	35.0 ^a	0.0	87.5	(Wimmer and Kappeler 2002; Ostner J, Kappeler P, unpublished data)
<i>Gorilla beringei</i>	Karisoke	Wild	78.0	3.0	4.7 ^a	0.0	78.0	(Watts 1990; Bradley et al. 2005; DFGF Int. ^b)
<i>Macaca arctoides</i>	Wisconsin	Captive	95.0	4.0	13.3	NA	95.0	(Smith 1984; Bauers and Hearn 1994)
<i>Macaca fascicularis Ketambe 1</i>	Ketambe 1984–1986	Wild	75.3	5.0	66.6 ^a	0.0	75.3	(de Ruiter and van Hooff 1993; de Ruiter et al. 1994; Kutsukake and Nunn 2006)
<i>Macaca fascicularis Ketambe 2</i>	Ketambe 2000	Wild	67.0	5.0	61.8	0.0	67.0	(Engelhardt et al. 2006)
<i>Macaca fuscata Kyoto</i>	Kyoto	Captive	29.5	8.0	59.0 ^a	NA	29.5	(Inoue et al. 1992)
<i>Macaca fuscata Yakushima</i>	Yakushima	Wild	50.0	14.5	62.2 ^a	33.0	33.0	(Soltis et al. 2001)
<i>Macaca mulatta Cayo 1</i>	Cayo Santiago 1988	Free ranging	29.0	11.0	84.9	36.0	18.0	(Berard et al. 1993, 1994)
<i>Macaca mulatta Sabana Seca</i>	Sabana Seca	Captive	27.0	21.0	97.0	NA	27.0	(Bercovitch and Nürnberg 1996)
<i>Macaca mulatta Madison</i>	Madison Zoo	Captive	20.0	7.0	34.4	NA	20.0	(Curie-Cohen et al. 1983)
<i>Macaca mulatta Yerkes</i>	Yerkes	Captive	21.0	8.0	74.2	NA	21.0	(Duvall et al. 1976)
<i>Macaca mulatta CPRC</i>	CPRC	Captive	41.2	3.3	84.8	NA	41.2	(Smith 1981)
<i>Macaca mulatta Cayo 2</i>	Cayo Santiago 1997	Free ranging	20.0	46.0	100.0 ^a	36.7	12.0	(Widdig et al. 2004)
<i>Macaca sinica</i>	Polonnaruwa	Wild	49.0	3.0	51.2	12.0	43.0	(Keane et al. 1997; Dittus 1998; van Noordwijk and van Schaik 2004)
<i>Macaca sylvanus</i>	Rheine	Captive	64.0	3.0	98.5	NA	64.0	(Witt et al. 1981)
<i>Mandrillus sphinx CIRMF 1</i>	CIRMF 1996–2003	Free ranging	69.0	5.0	34.0 ^a	NA	69.0	(Setchell et al. 2005)
<i>Mandrillus sphinx CIRMF2</i>	CIRMF 1987–1991	Free ranging	76.0	6.0	34.0 ^a	NA	76.0	(Dixson et al. 1993)
<i>Pan paniscus</i>	Lomako	Wild	21.0	6.0	88.0	11.0	19.0	(Gerloff et al. 1999; Stumpf 2007)
<i>Pan troglodytes schweinfurthii</i>	Gombe	Wild	36.0	12.3	42.3	0.0	36.0	(Constable et al. 2001)
<i>Pan troglodytes verus</i>	Tai	Wild	46.5	5.2	56.8	20.0	38.0	(Vigilant et al. 2001; Boesch et al. 2006)
<i>Papio cynocephalus</i>	Amboseli	Wild	81.0	5.0	25.0 ^a	0.0	81.0	(Altmann et al. 1996; Altmann 2000)
<i>Propithecus verreauxi</i>	Kirindy	Wild	100.0	2.5	12.5 ^{a,c}	0.0	100.0	(Brockman and Whitten 1996; Kappeler and Schäffler 2006)
<i>Saguinus mystax</i>	EBQB	Wild	92.0	2.5	0.0 ^a	0.0	92.0	(Huck et al. 2005)
<i>Semnopithecus entellus</i>	Ramnagar	Wild	77.5	4.0	30.2 ^a	34.0	52.0	(Launhardt et al. 2001; Borries C, Koenig A, unpublished data)

We excluded paternity studies if they were on species/groups living in pairs (fat-tailed dwarf lemur *Cheirogaleus medius* [Fietz et al. 2000] and fork-marked lemur *Phaner furcifer* [Schülke et al. 2004]), in a dispersed social organization (gray mouse lemur *Microcebus murinus* [Andrès et al. 2001] and orang-utan *Pongo pygmaeus* [Utami et al. 2002]), or in one-male multifemale groups (chimpanzee *Pan troglodytes* [Sugiyama et al. 1993] and Patas monkey *Erythrocebus patas* [Ohsawa et al. 1993]), studies that did not relate reproductive skew to rank in a way that allowed to extract the alpha male's share of paternity within a group (e.g., Barbary macaque *Macaca sylvanus* [Kümmerli and Martin 2005]), and species for which information for estrous synchrony could not be calculated from the literature (e.g., sooty mangabey *Cercocebus torquatus* [Gust et al. 1998]). NA, not available.

^a Observed estrous synchrony.

^b Dian Fossey Gorilla Fund International (unpublished data).

^c Mating data from Beza Mahafali.

incomplete, and thus, the overlap of estrous periods among several females determines the degree to which alpha males can control reproduction within groups. For the majority of populations, we succeeded in obtaining observed estrous overlap values from the literature (15 out of 27 populations). In the remaining cases, we calculated the expected proportion of days in which 2 or more females are mating using a formula based on breeding season duration, number of females, interbirth interval, estrous duration, and number of cycles to conception in the study group/population (Nunn et al. 2001). More specifically, we used the following formula:

$$P_{(Y \geq 2)} = \frac{k!}{Y!(k-Y)!} P^Y (1-P)^{k-Y},$$

where $P_{(Y \geq 2)}$ is the probability that 2 or more females (Y) are mating simultaneously, k is the number of females in the group rounded to the nearest whole number, and P is the probability that any given female is mating. With information on the duration of mating per cycle in days (m), the number cycles to conception (c), and the interbirth interval measured in days (I), the probability of a female mating is $P = (m \times c) / I$. This formula applies to nonseasonally breeding species, where females mate throughout the year. Breeding seasonality was incorporated by multiplying I by the proportion of the year in which mating can take place, which was calculated as the duration of the breeding season in Mitani et al. (1996) divided by 365. Number of cycles to conception was set conservatively to 2 for all macaque species, and actual numbers of females present during conceptions were used in all expected synchrony calculations.

Analyses

As noted above, we conducted analyses at 3 levels of variation: at the group level, population level, and species level. At each of these levels of data aggregation, we performed all tests on 2 data sets: the complete set and a reduced set with data on EGP. The latter included only studies on free-ranging or wild populations and hence controls for artifacts that might arise in captive conditions, such as limited opportunities for dispersal. In addition to the phylogenetic tests described below, we also provide nonphylogenetic tests because some authors have questioned the use of phylogeny-based analyses under certain conditions (Price 1997; Harvey and Rambaut 2000) and many readers prefer to see the results of both phylogenetic and nonphylogenetic analyses. In addition, the methods sometimes produce different results (e.g., Carvalho et al. 2006), and the analyses presented here included populations as well as true species (rather than a pure cross-species analysis). For nonphylogenetic tests, we treated each population value as an independent data point, and the number of males was log transformed to meet statistical assumptions. Nonphylogenetic statistical tests were performed in STATISTICA 7, with the best model selected by whole-model R^2 value.

For phylogenetic tests, we based our analyses on Purvis (1995) composite estimate of primate phylogeny. To add populations to this tree, we included them as branches emanating from the species tips; polytomies were thus created for species with more than 2 populations in the data set. Using the program Physigm (Blomberg et al. 2003), we calculated phylogenetic signal for the 3 main traits in the largest analysis—percentage of within-group paternity by the alpha male, log number of males, and synchrony—to investigate whether more closely related lineages have more similar trait values (see also Blomberg and Garland 2002). The mean square error of the actual data was always significantly less than for permuted data ($P \leq 0.001$ for all traits), consistent with strong phylogenetic

signal in these traits. In addition, we used this program to calculate the K statistic (Blomberg et al. 2003). A value of K less than one indicates departures from Brownian motion evolution such that species are less similar than one might expect based on their phylogenetic relationships; a value of K greater than 1 indicates greater similarity than expected based on the Brownian motion model of evolution. The K statistic ranged from 1.08 (number of males) to 1.32 (reproductive skew), further indicating that the traits show phylogenetic signal and evolved according to a Brownian motion model of evolution with the branch lengths and data transformations used here (see below). These results justify the use of phylogeny-based comparative methods, and we therefore base our primary conclusions on results from these tests.

Purvis' (1995) phylogeny provides branch length estimates that could be used for the species-level data set. However, we found some violations of statistical and evolutionary assumptions when using these estimates to calculate independent contrasts (Garland et al. 1992; Nunn and Barton 2000), and we needed to estimate branches for the other data sets. We therefore explored other branch length transformations using the computer program Mesquite (version 1.12, Maddison W and Maddison D 2006) and based our decision on the ability of the transformation to meet the assumptions of independent contrasts (Garland et al. 1992). For all data sets, we found that branch lengths based on a constant rate birth–death process best met the key assumptions of independent contrasts, implemented as “branch length method of Nee” in Mesquite. This method calculates branch lengths by dating nodes, with the distance from the tips to the current node equal to the \log_{10} of the number of tips descending from that node (Purvis 1995). We also found that log transformation of the data on the number of males helped to meet the phylogenetic assumptions; other variables were not transformed.

We ran tests for correlated evolution (independent contrasts) using the PDAP module (Midford et al. 2005) within Mesquite (Maddison W and Maddison D 2006). The test of the concessions model involved a discrete variable, involving presence or absence of EGP. We analyzed the presence of EGP in 2 ways: using independent contrasts and with Maddison's method of paired comparisons (Maddison 2000), as implemented in Mesquite (Maddison W and Maddison D 2006). In the former test, we treat EGP as a 2-state dummy variable using standard implementation of independent contrasts (Midford et al. 2005). The paired comparisons test has lower statistical power because the degrees of freedom are limited to the number of transitions in categorical coding of EGP, with significance assessed by a sign test. Analyses of independent contrasts and associated statistical tests were taken from Mesquite and, in some cases, recalculated in JMP 5.0.1 and STATISTICA 7.

When assessing the possibility for collinearity among predictor variables in a multiple regression, we used variance inflation factors (VIFs, Petraitis et al. 1996). In multiple regression models using R^2 for model selection, we found significant (or nearly significant) associations between predictor variables. In phylogenetic tests, for example, the log number of males was positively correlated with the degree of female synchrony ($r = 0.37$, $P = 0.064$ for the full data set and $r = 0.52$, $P = 0.038$ for the data set restricted to extrapair paternity). In all cases, however, VIFs were less than 3, well below the cutoff of >10 that indicates problems with collinearity (Petraitis et al. 1996). The alpha level for rejecting the null hypothesis was set to 0.05 using 2-tailed tests.

RESULTS

Among the 27 data points in the populations data set, we found considerable variation in reproductive skew and the factors

Table 2
Results of bivariate analyses of factors influencing reproductive skew

Data set		N	Log number of males			Synchrony		
			R^2	t	P	R^2	t	P
Full	Nonphylogenetic	27	0.52	-5.26	<0.001	0.58	-5.86	<0.001
	Phylogenetic	26	0.12	-1.84	0.078	0.34	-3.61	0.001
With EGP	Nonphylogenetic	17	0.62	-4.97	<0.001	0.75	-6.71	<0.001
	Phylogenetic	16	0.48	-3.69	0.002	0.70	-5.97	<0.001

Phylogenetic tests are based on independent contrasts regressed through the origin, as calculated in PDAP module of Mesquite (Midford et al. 2005; Maddison W and Maddison D 2006), and "with EGP" refers to the data set restricted to having data on EGP. Table shows t statistics, with the direction of the effect indicated by the sign of the t statistic. N refers to the number of studies in the population data set as well as independent contrasts among those. P values are from 2-sided tests.

that we predicted to be associated with skew. Thus, alpha male paternity within groups ranged from 20% to 100%, with an average of 60%. Groups contained 2–46 adult males (mean = 7.4), and female synchrony ranged from 0% (total asynchrony) to 100% of days with more than one female in estrus (mean = 47%). Across 17 populations, EGP varied between 0% and 36.7%, and extragroup males sired an average of 10.8% of offspring within a group.

Nonphylogenetic tests

Bivariate analyses revealed that the log number of males and female synchrony were significant predictors of the percentage of alpha male reproductive success within a group (Table 2). Similar results were obtained when the analyses were restricted to species with data on EGP (Figure 1).

In line with predictions based on concession models, skew among males of the same group decreased in populations with a measurable loss of paternity to extragroup males ($EGP > 0$), as compared with populations experiencing no EGP ($80.4 \pm 18.8\%$ alpha male paternity within group in 10 populations without EGP and $40.9 \pm 20.4\%$ in 7 populations with EGP, $t = 4.02$, $P < 0.001$).

Using quantitative data on EGP, we found a significant positive correlation between EGP and log number of males ($r = 0.66$, $N = 17$, $P < 0.001$) and also between EGP and estrous synchrony ($r = 0.61$, $N = 17$, $P < 0.001$). Thus, significant effects of EGP on paternity skew could reflect a confounding

effect of synchrony. We investigated this possibility with a multivariate model. In a multiple regression model with log number of males and synchrony as predictor variables, both factors were significant and the full model explained 67% of the variance (Table 3). The effect sizes of predictors representing log number of males and synchrony were indistinguishable, based on the similarity of standardized beta values. Adding EGP as a third continuous factor produced a statistically significant overall model with higher explanatory power ($R^2 = 0.79$). In this model, however, the only significant predictor was female estrous synchrony (Table 3).

Phylogenetic tests

Bivariate analyses revealed that contrasts in the log number of males and synchrony each explained significant variation in percentage of paternity gained by the alpha male of a group (Table 2). As compared with the number of males, synchrony explained nearly 3 times as much variation in alpha paternity. These results were replicated when analyzing only those populations with data on EGP.

In phylogenetic tests that treated presence/absence of EGP as a dummy variable, we found a negative association between contrasts in EGP presence and contrasts in within-group reproductive skew ($t_{15} = -2.22$, $P = 0.044$; Figure 2). When using Maddison's (Maddison 2000) method of paired comparisons, only 5 contrasts were available, and this produced a nonsignificant result (30 possible pairings for 17 taxa; 4 of these

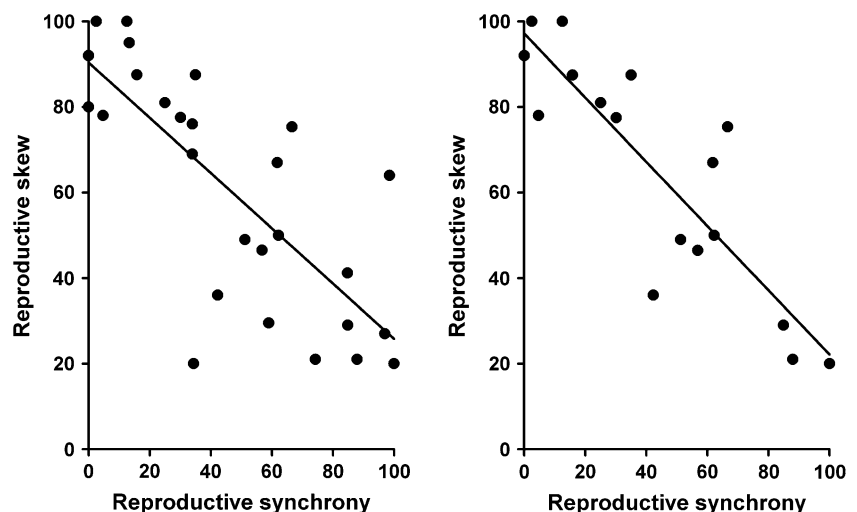


Figure 1
Male reproductive skew (alpha male paternity) within the group regressed on female reproductive synchrony (proportion of mating season with more than one female being estrus on the same day) in 27 primate populations (left) and a subset of 17 populations with data on EGP (right; for references, see Table 1).

Table 3
Results of multiple regression models

Data set		N	Whole model		Log number of males		Synchrony		EGP	
			R ²	P	Standardized β	P	Standardized β	P	Standardized β	P
Full	Nonphylogenetic	27	0.67	<0.001	-0.40 ± 0.15	0.014	-0.50 ± 0.15	0.003		
	Phylogenetic	26	0.36	<0.005	-0.15 ± 0.17	0.390	-0.53 ± 0.17	0.006		
With EGP	Nonphylogenetic	17	0.79	0.001	-0.28 ± 0.22	0.220	-0.62 ± 0.21	0.009	-0.05 ± 0.17	0.77
	Phylogenetic	16	0.76	<0.001	-0.28 ± 0.16	0.10	-0.67 ± 0.17	0.002	-0.04 ± 0.15	0.80

Results are given for the full population data set as well as the EGP selection of populations. *P* values are from 2-sided tests.

contrasts were always in the predicted direction, $P = 0.19$). In line with the results from nonphylogenetic tests, the continuous measure of EGP exhibited a trend to be associated with estrous synchrony when using independent contrasts ($r = 0.45$, $P = 0.07$), and 14 of 16 contrasts showed a positive association between these 2 traits (sign test, $P = 0.004$). However, EGP was no longer significantly correlated with the log number of males ($r = 0.29$, $P = 0.26$).

A multiple regression model that included both contrasts in log number of males and synchrony as predictor variables produced significant results for the full model (Table 3). In contrast to nonphylogenetic tests, we found that only synchrony had a significant effect, and this effect was much larger than for number of males (based on standardized beta coefficients). Adding contrasts in EGP as a third continuous predictor variable yielded a highly significant model that explained 76% of the variation in the alpha male's share of paternity within a group. Again, synchrony had the strongest effect. EGP was not statistically significant in this model.

Analyses using groups or species as data points instead of populations produced largely congruent results: all relationships were in the same direction; all analyses revealed that reproductive synchrony was a better explanation than the number of males; phylogenetically controlled analyses were

better at distinguishing effect sizes; and EGP had an effect in bivariate analyses only.

DISCUSSION

Our analyses of paternity in primates support predictions in line with limited control models of reproductive skew. Bivariate analyses yielded significant negative associations involving reproductive skew and both the number of males and the estrous synchrony. Of these 2 predictors, estrous synchrony turned out to have a stronger effect in bivariate and multivariate models. In the phylogenetically controlled multivariate analyses, the number of males had no independent explanatory value. Thus, reproductive skew was solely explained by estrous synchrony, which is in accordance with the original version of the priority of access model (Altmann 1962). The priority of access model was first developed for primates. It can be viewed as a special case of the more general compromise models of reproductive skew because it also aims at explaining the partitioning of paternity in social groups and because some of the models' predictions are similar (Kutsukake and Nunn forthcoming).

A recent nonphylogenetic comparative study on a smaller sample of reproductive skew in male primates found that the number of males had a stronger effect than both the number of females per group and the birth seasonality (van Noordwijk and van Schaik 2004). Likewise, a comparative study on EGP in mammals also found that number of females and mating seasonality were predictors of EGP (Isvaran and Clutton-Brock 2007). Number of females and reproductive seasonality are, however, indirect measures of female estrous overlap because a large number of females without strict birth seasonality may produce low estrous synchrony. In the present study, we used a more direct and biologically meaningful measure of estrous overlap and found a consistent pattern of synchrony predicting both reproductive skew within groups and EGP.

Another comparative study used several measures of estrous synchrony and found none of them to be significant predictors of skew in primate mating frequency (Kutsukake and Nunn 2006). However, the risk of infanticide may impact patterns of mating and reproductive skew differently, with females attempting to confuse paternity by mating promiscuously, while potentially concentrating actual paternity in the alpha male (Nunn 1999a). Reproductive skew models that investigated the effectiveness of infanticide in concentrating reproduction in the dominant suggest that infanticide is a viable strategy freeing subordinates from restraining their reproduction if offspring are cheap to produce (Johnstone and Cant 1999; Hager and Johnstone 2004). However, offspring are not cheap to produce in primates. In fact, primates are more vulnerable to infanticide than other mammals due to their long lactation period relative to gestation (van Schaik 2000); early infanticide terminates costly lactation and speeds up subsequent conception and will thus open new breeding opportunities.

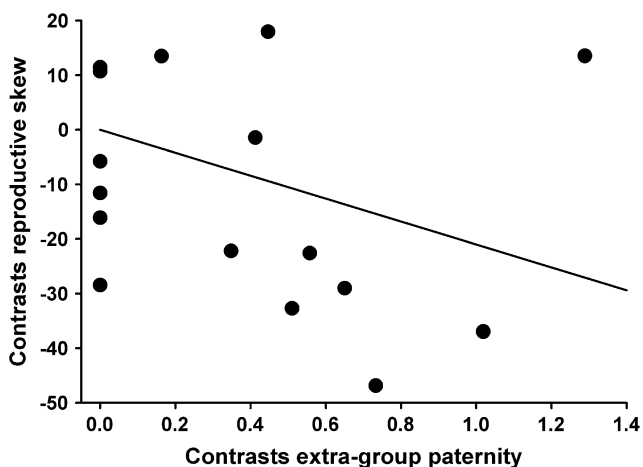


Figure 2
 Independent contrasts of male reproductive skew within a group regressed on contrasts of categorical measures of EGP in the populations data set (for references, see Table 1). Outlier data point in the upper right corner represents the contrast between the 2 chimpanzee populations, *Pan troglodytes schweinfurthii* and *Pan troglodytes verus*. Contrasts in EGP can be greater than one when the sum of the branch lengths is less than one, as this sum is used to standardize the contrasts.

Consequently, female primates probably benefit greatly by mating with all males in a group as a means to confuse paternity and decrease the risk of infanticide (van Noordwijk and van Schaik 2000). Even low levels of offspring discrimination are likely to promote infanticide as a means of increasing skew (Hager and Johnstone 2004). Thus, the higher the number of males in a group the more mates a female has to seek out. The number of males may therefore have a stronger effect on mating skew compared with reproductive skew, which will be more affected by reproductive synchrony.

Field studies have uncovered mixed results concerning the effect of synchrony on reproductive success. In chimpanzees, for example, the dominant's share of reproduction declined with increasing overlap of female estrous periods, indicating that the alpha male had limited control over reproduction (Boesch et al. 2006). In contrast, a study on rhesus macaques on Cayo Santiago Island reported that estrous synchrony was not significantly correlated with reproductive skew (Widdig et al. 2004). However, the level of synchrony was very high in the rhesus macaque study—100%, according to our estimation procedure—and this could reduce the power to identify associations between synchrony and reproductive skew. From the high consistency of our results, the marked differences in effect sizes, and the explanatory power of our regression models, we conclude that female estrous synchrony is the strongest predictor of male reproductive skew across primates.

In using data that combine data from groups, populations, and species into a phylogenetic analysis, we are making the assumption that rates of evolution above and below the species level are similar. Empirically for our data set, this appears to be a valid assumption, for the following reasons. First, we repeated analyses with both more aggregated data (species level) and less aggregated data (groups), and this produced congruent results. Second, we were careful to check the assumptions of independent contrasts and to transform the data and branch lengths in ways that meet the assumptions, as described above. Lastly, we conducted nonphylogenetic analyses, which also produced largely congruent results.

Correlates of EGP

Both of our main predictors—number of males and female synchrony—were correlates of EGP. EGP was positively correlated with number of males in the nonphylogenetic test. Because females of all species included here mate polyandrously, subordinate males can be expected to protect their paternity share against outside males. Thus, it seems counterintuitive that more males within a group were not better at controlling females and reducing EGP. In contrast, a study of Hanuman langurs found that an increased number of males reduced the rate of EGP (Launhardt et al. 2001). However, in our phylogenetic analysis, the correlation was no longer significant, indicating that evolutionary changes in the number of males are not significantly associated with evolutionary changes in EGP.

By comparison, synchrony correlated positively with the rate of EGP in nonphylogenetic comparative tests and approached significance after controlling for phylogeny. In another comparative study on 13 populations with estimated rates of EGP, EGP was strongly linked with reproductive seasonality (van Noordwijk and van Schaik 2004). The positive relationship of EGP and breeding seasonality holds also across mammals (Isvaran and Clutton-Brock 2007). This result concurs with our finding of a positive relationship between synchrony and EGP, indicating that the loss of reproduction to extragroup males may be caused by limited control over simultaneously fertile females.

Room for concessions?

Whereas transactional models (Reeve and Keller 2001) generally predict that the subordinates' paternity share is related to breeding opportunities for subordinates outside the group, we predict that incentives are given to subordinates when the dominant perceives a threat from outside the group and subordinates help to avoid this threat. We conceptualized this threat as the risk of paternity lost to extragroup males and predicted within-group reproductive skew to be lower when EGP was present. This concession prediction was unable to account for general patterns of reproductive skew across primate species. It has been pointed out, however, that a single model may not hold for all species or across different ecologies (e.g., Johnstone 2000). Thus, despite the general support for limited control models across primates found in this and other studies, patterns of skew in some populations or species may also be explained by concession mechanisms. A promising approach to identify viable candidates for skew-related concessions is to investigate situations in which 2 conditions are met: control by the dominant male is possible because synchrony is low, but nevertheless skew within a group is low. In those situations, dominant males may concede paternity to increase group productivity by avoiding paternity loss to outside males.

The threat may also take the alternative form of aggressive takeover with subsequent eviction of resident males from the group (Crockett and Sekulic 1984; Ostner and Kappeler 2004), promoting cooperation between males and potentially leading to concession by the alpha male (Ostner and Kappeler 2004). Regardless of the actual threat, either EGP or takeover, its avoidance by concessions to subordinates will lead to an increase in group productivity, as implied in all transactional skew models (Clutton-Brock 1998; Johnstone 2000). Previous theoretical work on male primates has taken a different perspective by analyzing the partitioning of reproduction within the group as a zero sum game (Pandit and van Schaik 2003). Generating proxies for the actual threat from extragroup males and integrating threat from within and outside the group will be next steps in promoting our understanding of reproductive skew in males living in stable, large multimale groups like most primates, including humans.

CONCLUSIONS

Collectively, our comparative analysis of reproductive skew revealed that variation in paternity across primates is accounted for mainly by lack of control by the dominant male. Female estrous synchrony consistently turned out to be the main predictor of paternity distribution among male group members, indicating that synchrony is the main factor driving male monopolization potential. The number of males per group less consistently predicted the degree of skew, and EGP was not an independent predictor of reproductive skew. A concession model was not supported as a general explanation for paternity skew in primates. Explaining the deviation from this general pattern of synchrony driving reproductive skew, for example, due to concessions by the dominant male, should ultimately increase our understanding of the relative roles of alternative mechanisms of paternity distribution in mammalian evolutionary ecology.

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