

Reproductive seasonality is a poor predictor of receptive synchrony and male reproductive skew among nonhuman primates

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Abstract Among nonhuman primates, male reproductive skew (i.e., the distribution of reproductive success across males) appears to be affected primarily by receptive synchrony and the number of males per group. These factors have been assumed to depend on reproductive seasonality, with strong seasonality increasing receptive synchrony, which in turn reduces the strength of male monopolization associated with more males and lower skew. Here we tested the importance of reproductive seasonality for 26 populations representing 15 species living in multimale groups. We obtained data from the literature on paternity, number of males per group, receptive synchrony, and three measures of seasonality of reproduction. We analyzed these data using bivariate regressions and hierarchical regression by sets and controlled for the effect of evolutionary relationships using phylogenetic generalized least squares. As expected, alpha male paternity decreased as the number of males per group increased as well as with increasing female receptive synchrony. Reproductive seasonality did not explain variation in reproductive skew over and above the variation explained

by synchrony and the number of males. Reproductive seasonality alone only explained a small proportion of the variation in skew, and there was no strong association between reproductive seasonality and synchrony. The effects of receptive synchrony and reproductive seasonality as well as their link were reduced if we excluded captive populations. These results indicate that across primates male reproductive skew is related to the number of competitors in a group and that seasonality does not reliably predict synchrony or male reproductive skew.

Keywords Alpha paternity · Multimale groups · Nonhuman primates · Priority-of-access · Seasonality · Synchrony

Introduction

Among group-living animals, reproductive success is often unevenly distributed across group members, a phenomenon described as reproductive skew (Nonacs and Hager 2011). A group is said to exhibit high reproductive skew when one or a few individuals monopolize breeding, whereas low reproductive skew indicates a more even spread of reproduction (Johnstone 2000). Across animals, there is considerable variation in reproductive skew with the most extreme examples seen among eusocial species of Hymenoptera and Isoptera (Reeve et al. 1998). It has been argued that reproductive skew might be a critical factor important for the evolution of group living, and this idea led to the development of the reproductive skew theory (Nonacs and Hager 2011). At the same time, on a more proximate, mechanistic level, the question is what factors determine the level of reproductive skew within a group (Hager and Jones 2009). Within nonhuman primates, there is considerable variation in the amount of male reproductive skew, and high quality long-term data are available for a number of species across

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environments and a broad range of the phylogeny making them a suitable taxon to address this question. In addition, the primate order is characterized by a high proportion of species living in year-round associations of males and females (van Schaik and Kappeler 1997; Kappeler and van Schaik 2002), and the distribution of reproduction among group members represents an important byproduct of sociality and a potentially important cost of sociality.

Reproductive skew theory is composed of two broad categories of models describing reproductive shares of individuals living in groups: transaction and compromise models (Hager and Jones 2009; Port and Kappeler 2010). Transactional models emphasize the importance of group stability in defining the degree of reproductive skew, with reproduction traded as a means of maintaining group membership (Vehrencamp 1983; Reeve et al. 1998; Johnstone 2000; Buston et al. 2007; Buston and Zink 2009; Shen and Reeve 2010). Compromise models (encompassing tug-of-war or limited control and priority-of-access models), on the other hand, view the degree of skew as a function of a conflict between group members, in which there is a limit to each group member's ability to enforce its own optimum (Cant 1998; Reeve et al. 1998; Johnstone 2000; Hager and Johnstone 2004; Port and Kappeler 2010). Within the compromise models, limited control or tug-of-war models predict that with an increasing number of competitors for reproduction, the dominant's share of reproduction will decline (Port and Kappeler 2010). On the other hand, the priority-of-access model predicts that with increasing female receptive synchrony the dominant's ability to monopolize reproduction will decrease (Altmann 1962; Port and Kappeler 2010).

Many reproductive skew models are forced to make a number of assumptions that are not met in primates: that dominants have complete control over reproduction (Vehrencamp 1979), that dominants have complete control over group membership and subordinates have complete control over their reproductive share within the group (Johnstone and Cant 1999), that same sex group members decide their own reproductive partition and are not influenced by mate choice (Port and Kappeler 2010), an absence of incest avoidance (Cooney and Bennett 2000), and that individuals have perfect knowledge of their benefits if they stay in the group (Nonacs and Hager 2011). While these alternative models of the evolutionary process behind the evolution of reproductive skew are intriguing and have provided valuable insight into the evolution of cooperation, determining which of the reproductive skew models best explains the current distribution of reproductive success between different species has proven difficult (see Nonacs and Hager 2011 for discussion of the utility and limitations of reproductive skew theory and potential ways to test alternative models). Here we focus on the more proximate,

mechanistic level and attempt to determine what factors influence the level of reproductive skew within primate groups (Nonacs and Hager 2011).

Among primate species living in multimale–multifemale groups, variation in male reproductive skew seems primarily due to the variation in the number of females mating simultaneously (receptive synchrony) and secondarily due to the variation in the number of males per group (Ostner et al. 2008; Port and Kappeler 2010). Receptive synchrony could affect skew as stronger synchrony may decrease monopolizability of females (priority-of-access model; Altmann 1962). In other words, a dominant male may be able to monopolize access to one receptive female, but with an increasing number of receptive females, his ability to monopolize will decline and skew will decrease (Altmann et al. 1996; Boesch et al. 2006). The number of males might affect reproductive skew because more competitors may reduce a dominant male's ability to monopolize females (Cowlishaw and Dunbar 1991; Alberts et al. 2006; Boesch et al. 2006; for a more complex situation, see Launhardt et al. 2001).

Importantly, in mammals in general and nonhuman primates in particular, both of these factors have frequently been assumed to depend on the length of the mating season (Ridley 1986; Mitani et al. 1996; Paul 1997; Nunn 1999; Isvaran and Clutton-Brock 2007; Carnes et al. 2011), here called reproductive seasonality. In a comparative analysis, Paul (1997) suggested that seasonally breeding species had lower reproductive skew and a weaker effect of dominance on reproductive success, although he did not control for the effect of phylogeny and used broad categorical variables for reproductive skew and seasonality. Strong seasonality (a short mating season) is assumed to increase female receptive synchrony because there is a shorter window over which all conceptions will occur (Ridley 1986; Paul 1997; Isvaran and Clutton-Brock 2007). This in turn may reduce monopolizability of females and result in lower reproductive skew (Mitani et al. 1996; Nunn 1999) or in a higher number of extra-group paternities (birds: Birkhead and Biggins 1987; mammals: Isvaran and Clutton-Brock 2007). Thus, nondominant males may have increased access to females when reproduction is more seasonal. Strong seasonality is also predicted to increase the number of males in a group and thus lower the reproductive skew and has been suggested to act above and beyond the effect of the number of females in a group if reproductive synchrony is not accounted for (Nunn 1999; Carnes et al. 2011). These studies suggest that there is a strong relationship between reproductive skew and reproductive seasonality, with reproductive skew predicted to decrease with increasing reproductive seasonality.

This idea, however, has been criticized as even in highly seasonal taxa such as lemuroids from Madagascar with short mating seasons of 3 or fewer months, females may cycle

asynchronously (Pereira 1991; Mass et al. 2009). Thus, while seasonal breeding may increase the likelihood of synchronous cycling of females, the crucial measure is the probability of one or more females being receptive at the same time (Pereira 1998; Dunbar 2000; Pereira et al. 2000). However, thus far, only a limited number of studies have used receptive synchrony as a predictor variable for the number of males in a group or male reproductive skew (Nunn 1999; Kutsukake and Nunn 2006; Ostner et al. 2008; Carnes et al. 2011). Importantly, the interrelationship between synchrony and seasonality has not been empirically tested. Lastly, many studies have used dichotomous categorical variables (i.e., categorizing species as either seasonal or nonseasonal) when including seasonality in models (e.g., Ridley 1986; Paul 1997), unnecessarily reducing the power for phylogenetic comparative tests (Garland et al. 1993; Sokal and Rohlf 1995; Streiner 2002).

Here, we conducted a comparative analysis across non-human primates to investigate variation in male reproductive skew and to explicitly test three hypotheses about the effect of reproductive seasonality and its link to receptive synchrony. (1) We hypothesized that male reproductive skew is affected by the monopolizability of females, which might be driven by female receptive synchrony and the number of males in a group. Thus, we predicted that male reproductive skew decreases with increasing number of males and increasing female receptive synchrony in a group. This part of the study replicates a previous investigation (Ostner et al. 2008), but with an extended dataset and different phylogenetic comparative methods. (2) Based on the suggestions by Paul (1997) and Kutsukake and Nunn (2006), we hypothesized that male reproductive skew is affected by reproductive seasonality. Thus, we predicted that male reproductive skew decreases with increasing reproductive seasonality. This hypothesis and prediction implicitly makes the untested assumption that reproductive seasonality can serve as proxy for female receptive synchrony. Consequently, we predicted that reproductive seasonality is a strong, positive predictor of female receptive synchrony. (3) Lastly, we hypothesized that male reproductive skew is affected by reproductive seasonality over and above the effect of the number of males and female receptive synchrony (Paul 1997). Thus, we predicted that male reproductive skew decreases with increasing reproductive seasonality over and above the effect of a decrease with increasing female receptive synchrony. Because the data available for nonhuman primates are from a mix of captive as well as wild populations and captivity can affect female group size and hence monopolizability of females (de Ruiter and van Hooff 1993) as well as reproductive seasonality (Hendrickx and Dukelow 1995), we repeated the tests of most of our predictions excluding captive populations.

Methods

Sample and data selection

We searched the literature for data on male reproductive skew, reproductive seasonality, receptive synchrony, and number of males in multimale–multifemale groups of non-human primates (Supplementary Table 1). We began with the dataset used by Ostner et al. (2008) and added data that had become available since 2008 (*Cebus capucinus* from Lomas Barbudal, Costa Rica; *Macaca sinica* from Polonnaruwa, Sri Lanka; and *Pan troglodytes schweinfurthii* from Budongo, Uganda). Where possible, we recalculated all variables included in our analysis from the original source. In all cases in which discrepancies occurred with the dataset of Ostner et al. (2008), we used our new calculations after repeatedly re-checking our calculations. If inconsistencies between the datasets could not be explained, we cross-checked the calculated values with the author(s) of the original source (see Acknowledgments). The final dataset comprised 15 wild, four free-ranging, and seven captive populations representing 15 primate species including three strepsirrhine subspecies (*Eulemur fulvus rufus*, *Eulemur fulvus mayottensis*, *Propithecus verreauxi verreauxi*), two New World monkeys (*Alouatta seniculus*, *C. capucinus*), eight cercopithecines (*Macaca arctoides*, *Macaca fascicularis*, *Macaca fuscata*, *Macaca mulatta*, *M. sinica*, *Macaca sylvanus*, *Mandrillus sphinx*, *Papio cynocephalus*), one Asian colobine (*Semnopithecus entellus*), and three African apes (*Gorilla beringei beringei*, *P. troglodytes schweinfurthii*, and *Pan troglodytes verus*; Supplementary Table 1). We excluded genetic studies for which detailed demographic and male rank data were not available (*Brachyteles hypoxanthus* from Minas Gerais, Brazil, Strier et al. 2011; *M. fuscata* from Kyoto, Japan, Inoue et al. 1992; *M. sylvanus* from Gibraltar, Brauch et al. 2008; *Papio ursinus* from Moremi, Botswana, Moscovice et al. 2010; *Pan paniscus* from Lomako, DR Congo, Hohmann et al. 1999; *P. paniscus* from Lomako, DR Congo, Gerloff et al. 1999) and a study in which multimale groups had only one breeding female (Huck et al. 2005).

Number of males and alpha paternity

While numerous measures and indices of reproductive skew have been proposed to capture different aspects of the distribution of reproduction between group members (e.g., Vehrencamp 1983; Cant 1998; Kokko et al. 1999; Nonacs 2003), these have only been applied to a limited number of primate studies and are not broadly available for a comparative analysis. Thus, we followed Ostner et al. (2008) in using the percentage of total paternity monopolized by the alpha male as a measure of reproductive skew. While

including only paternity studies of multimale–multifemale groups, we also checked the demographic status of groups over the course of the studies. When groups were multimale for only part of the genetic studies (i.e., only one adult male was present in the group during a part of the paternity study), we only included data from those periods for which they were multimale (e.g., *M. sylvanus* from Rheine; Witt et al. 1981). For all studies, we calculated the average number of males in the multimale groups included in the paternity study (i.e., if group membership changed during the study, we calculated the average number of males present over the whole study period). We considered captive populations those that were located in zoos and laboratories or which were corral housed. Free-ranging populations were those that had confined housing in large outdoor enclosures or lived on islands.

From paternity data, we calculated the percent of within-group parentage of the alpha male (alpha paternity; Ostner et al. 2008). We did not attempt to further characterize reproductive skew (Nonacs 2000) because often the necessary data were lacking, which would have reduced the sample size.

Receptive synchrony and reproductive seasonality

Where possible ($n=13$), we calculated receptive synchrony as the proportion of mating season days, in which two or more females were observed mating on the same day (following Nunn 1999). For the remaining cases, we used the proportion of days in which two or more females were expected to mate, utilizing the following formula (data either from Ostner et al. 2008 or calculated here following Nunn 1999):

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

Where $P_{(Y \geq 2)}$ is the probability that two or more females (Y) are mating simultaneously, k is the number of females in the group rounded to the nearest integer value, and P is the probability that any given female in the group is mating. P can be calculated with information on the duration of mating per cycle (i.e., length of estrous, measured in days; m), the average number of cycles to conception (c), and the interbirth interval measured in days (I) using the formula:

$$P = \frac{(m \times c)}{I}$$

For macaque species, the cycles to conception was set to two (Nunn 1999; Ostner et al. 2008), while for all other species the number of cycles to conception came from values in the literature (following Ostner et al. 2008).

This measure of receptive synchrony reduces the information on receptive females to a dichotomous variable (more or less than two receptive females). Based on the priority-of-access model (Altmann 1962), it may be argued that the actual number of simultaneously receptive females may further affect reproductive skew. We were unable to incorporate such an approach into the current analysis because the data were not available from observational studies and our sample size precluded adding additional factors, such as the number of females in the group, to our models. Future studies may benefit from incorporating alternative metrics of female synchrony which also incorporate the number of females simultaneously receptive, as the number of females simultaneously receptive might affect the share of paternity that the alpha male can monopolize.

The description and measurements of reproductive seasonality vary in the literature, especially among studies of the effect of seasonality on the number of males and reproductive skew (Ridley 1986; Mitani et al. 1996; Paul 1997; van Noordwijk and van Schaik 2004). For example, some have reduced seasonality to a dichotomous categorical variable (i.e., categorizing a species as being either seasonal or nonseasonal; Paul 1997), while others have used the length of the breeding season as a continuous variable (Mitani et al. 1996; Nunn 1999). Both of these approaches do not contain information about the narrowness of the birth distribution and may be strongly affected by the number of births included in the analysis (for discussion of sensitivity of the different metrics to small sample sizes, see Janson and Verdolin 2005). To take these various approaches into account, we estimated reproductive seasonality using three measurements: (1) the percentage of months of the year during which births occurred ($n=26$; Mitani et al. 1996); (2) the r -statistic, a measure from circular statistics describing the mean vector length of all births considered as vectors of length 1, each with an angle equivalent to the month of the year it occurred (where January=30°, February=60°, etc.), which ranges from 0 (nonseasonal) to 1 (highly seasonal; $n=24$; Batschelet 1981; Janson and Verdolin 2005); and (3) the percentage of births during the three consecutive months with the highest number of births ($n=24$; van Noordwijk and van Schaik 2004). Both the r -statistic and the percentage of births during the three consecutive months with the highest number of births are robust to differences in the number of births in the sample. In addition, both metrics capture aspects of the shape of the birth distribution that the percentage months of the year during which births occurred does not capture (Janson and Verdolin 2005). When available, we used months of birth data from the specific population of interest ($n=21$), but when data from the specific population were deficient (i.e., less than ten birth dates known with an even sampling effort over a minimum of a year), we used birth data from another geographically close

population of the same species and with similar group sizes ($n=5$; Janson and Verdolin 2005). To achieve normality and reduce heteroscedasticity and skewness of the variables, male reproductive skew, receptive synchrony, the percentage of months of the year during which births occurred, and the r -statistic were arcsine-transformed while the number of males was inverse-transformed (Sokal and Rohlf 1995).

Data analyses

All statistical analyses were conducted in R 2.14.2 (R Development Core Team 2012). To account for non-independence due to shared evolutionary history, we used phylogenetic generalized least squares (PGLS; Felsenstein 1988). Two R packages, *APE* (Paradis et al. 2004) and *CAPER* (Orme et al. 2011), were used to conduct the comparative analysis. Specifically, we used the function PGLS, which estimates Pagel's lambda, a measure of the phylogenetic signal in the data, and fits a PGLS model to the data that accounts for the non-independence of the data points due to phylogeny using the estimate of lambda (Pagel 1999; Freckleton et al. 2002; Orme et al. 2011).

To generate a phylogeny for the taxa in our dataset, we modified a consensus tree from the 10kTrees project (Arnold et al. 2010; Fig. 1). If a specific species was not available in the phylogeny due to a lack of genetic data, we used a well agreed upon sister taxon that excluded all other species in the analyses to place the species in the phylogeny and infer branch length (e.g., *Gorilla gorilla*

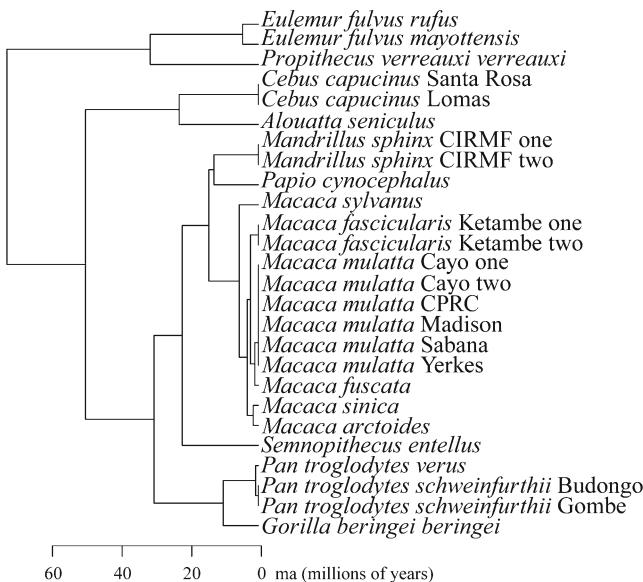


Fig. 1 Phylogeny of primate populations included in the comparative analyses modified from a consensus tree from the 10kTrees project (Arnold et al. 2010). If a specific species was not available, we used a well agreed upon sister taxon (see text for details). Branch lengths are corresponding to millions of years (ma)

gorilla was used in place of *G. beringei beringei*). The macaque phylogeny of the 10kTrees project was modified based on recent Alu-sequence data (Li et al. 2009) combined with divergence times estimated from mtDNA and Y-chromosome data (Tosi et al. 2003). To incorporate data from multiple populations of the same species, populations were added to the phylogeny as polytomies at the tips of the species branches and these polytomies were then randomly resolved prior to analysis.

We conducted bivariate PGLS regressions of synchrony and number of males on skew as well as a multiple PGLS regression including both factors (hypothesis 1). We also conducted bivariate PGLS regressions of reproductive seasonality on skew and on receptive synchrony (hypothesis 2). These bivariate analyses were also run on the dataset while excluding captive populations to examine any potentially confounding influence of captivity on synchrony, number of males, and reproductive seasonality. In addition, we conducted multiple regressions explaining variance in reproductive skew with the three metrics of seasonality and the number of males (hypothesis 2). To test our third hypothesis, we conducted PGLS hierarchical regression by sets building three models: (1) beginning with number of males, (2) beginning with synchrony as suggested by the priority-of-access model (Altmann 1962), and (3) beginning with seasonality (Paul 1997). Following Sokal and Rohlf (1995), we tested the significance of the incremental change in R^2 with the addition of each set and always report adjusted R^2 values.

Results

Male reproductive skew was significantly related to both the number of males ($F_{s(2, 24)}=27.15, P<0.001, \lambda < 0.001$) and receptive synchrony ($F_{s(2, 24)}=17.76, P<0.001, \lambda < 0.001$; Table 1). Skew decreased with increasing number of males and with increasing reproductive synchrony (Fig. 2). The individual predictors explained 51.1 % (number of males) or 40.1 % (synchrony) of the variability in reproductive skew. A PGLS multiple regression including both predictors was significant ($F_{s(3, 23)}=20.05, P<0.001, \lambda < 0.001$) and explained 60.4 % of the variability in reproductive skew. Both predictors contributed significantly to this effect (number of males: $T=3.64, P<0.001$; synchrony: $T=2.57, P<0.05$; Table 1).

All three of the reproductive seasonality metrics were significant predictors of skew; however, they explained only a relatively small proportion of the variance (<24 %). Multiple regressions including the number of males and one of the reproductive seasonality metrics were all highly significant and explained more than 52 % of the variance in skew (Table 2). However, while all of these multiple regression

Table 1 Bivariate and multiple PGLS regressions for male reproductive skew (expressed as alpha paternity) predicted by the number of males and receptive synchrony

Independent variable(s)	Overall model			
	R ²	λ	F _{s(df)}	P
Bivariate regressions				
N males***	0.511	<0.001	27.15(2, 24)	<0.001
Synchrony***	0.401	<0.001	17.76(2, 24)	<0.001
Multiple regression				
N males*** + synchrony*	0.604	<0.001	20.05(3, 23)	<0.001

Significance factors in the models are indicated with *** ($P<0.001$) and * ($P<0.05$). P values indicate overall model significance

models had number of males as a significant factor, seasonality was nonsignificant in all three cases ($T<1.86$, $P>0.1$, Table 2). All three metrics of seasonality were strong predictors of one another ($R^2>0.81$, Table 3) with the r -statistic and percentage of births during the three consecutive months with the most births having the strongest relationship ($R^2>0.95$). Two of the reproductive seasonality metrics (the r -statistic and percentage of births during the three consecutive months with the highest number of births) were significant predictors of receptive synchrony; however, variance explained was not as large as for the other explanatory factors discussed above (<27 %, Table 3).

The hierarchical regressions by sets showed that seasonality did not explain significantly more variance in reproductive skew beyond what was explained by the number of males and synchrony (Table 4). In model 1, starting with the number of males, the addition of synchrony explained a

significant amount of variance (9–16 %) in reproductive skew in addition to what was explained by the number of males. Similarly, for model 2 starting with synchrony, the addition of the number of males explained a significant amount of variance in skew on top of what was explained by synchrony (20–23 %). In both models 1 and 2, seasonality did not explain significant amounts of variance in skew above and beyond synchrony and number of males, explaining only an additional 1 % of the variance in skew or in the case of percentage of births during the three consecutive months with the highest number of births, reducing the amount of variance explained. In model 3, only two of the three seasonality metrics were significant predictors of skew. The addition of the number of males was highly significant in all cases, while synchrony was a significant factor for two of the three metrics of seasonality (Table 4).

When PGLS bivariate analyses were run on the dataset excluding captive studies, we found a stronger inverse relationship between reproductive skew and the number of males ($R^2=0.758$, $F_{s(2, 18)}=57.53$, $P<0.001$, $\lambda < 0.001$). The relationship between reproductive skew and synchrony was similar (albeit weaker) to that found when captive populations were included in the analysis ($R^2=0.429$, $F_{s(2, 17)}=14.55$, $P<0.001$, $\lambda = 0.328$). When captive populations were excluded, the relationship between reproductive skew and the percent of the year during which births occurred approached significance ($R^2=0.102$, $F_{s(2, 17)}=3.05$, $P=0.074$, $\lambda = 0.914$), while the relationship between reproductive skew and the r -statistic was not significant ($R^2=-0.039$, $F_{s(2, 17)}=0.316$, $P=0.582$, $\lambda = 0.778$) and neither was the relationship between reproductive skew and the percentage of births during the three consecutive months with the highest number of births ($R^2=-0.032$, $F_{s(2, 17)}=0.436$, $P=0.653$, $\lambda = 0.807$). The

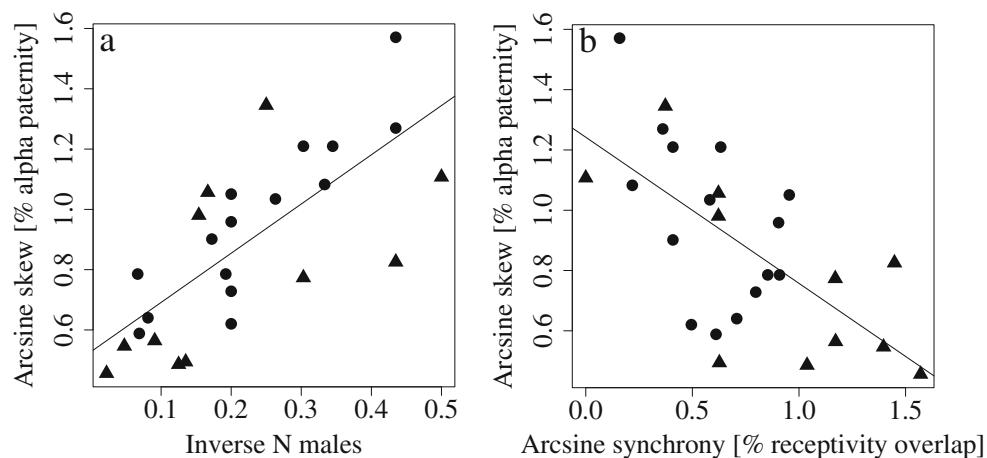


Fig. 2 Male reproductive skew as predicted by **a** the number of males and **b** female reproductive synchrony. Male reproductive skew is expressed as percent alpha paternity (arcsine-transformed). The number of males was inverse-transformed, which reverses the relationships between skew and number of males (increasing number of males in a

group corresponds to decreasing trend in reproductive skew). Data on percent receptivity overlap were arcsine-transformed. Circles indicate wild populations and triangles represent captive and free-ranging populations. Solid lines represent the results of the PGLS regression

Table 2 Bivariate and multiple PGLS regressions for male reproductive skew (expressed as alpha paternity) predicted by reproductive seasonality

	Independent variable(s)	Overall model		
		R ²	λ	F _{s(df)}
Bivariate regressions				
%months with births**		0.233	0.938	8.61(2, 24)
r-statistic*		0.140	0.925	4.74(2, 22)
max % births in 3 months*		0.117	0.923	4.05(2, 22)
Multiple regressions				
N males*** + %months with births		0.556	<0.001	16.6(3, 23)
N males*** + r-statistic		0.522	<0.001	13.6(3, 21)
N males*** + % births in 3 months		0.526	<0.001	13.8(3, 21)

Significance factors in the models are indicated in italics

P values indicate overall model significance. ***P<0.001, **P<0.01, and *P<0.05

relationship between synchrony and the percent of the year during which births occurred was not significant ($R^2=-0.019$, $F_{s(2, 17)}=0.668$, $P=0.527$, $\lambda = 0.695$) nor was the relationship between synchrony and the *r*-statistic ($R^2=0.052$, $F_{s(2, 17)}=1.995$, $P=0.167$, $\lambda = 0.674$) or the relationship between synchrony and percentage of births during the three consecutive months with the highest number of births ($R^2=-0.021$, $F_{s(2, 17)}=0.634$, $P=0.542$, $\lambda = 0.692$).

Discussion

Number of males, receptive synchrony, and male reproductive skew

As predicted, male reproductive skew was strongly affected by the monopolizability of females confirming the results of a previous study (Ostner et al. 2008). With increasing number of males and increasing receptive synchrony, the dominant male of a group appears to be unable to monopolize access to females and consequently his share of the reproduction declines. This finding supports the idea of the priority-of-access model (Altmann 1962) as well as the influence of the number of competitors on the reproductive share a male can receive (Cowlishaw and Dunbar 1991; Alberts et al. 2006; Boesch et al. 2006), thereby supporting

an extended version of the priority-of-access model (Kutsukake and Nunn 2006).

Contrary to Ostner et al. (2008), who found receptive synchrony to have the strongest effect, we found that the number of males explained more variance in the bivariate regressions (see also results for mating skew in Kutsukake and Nunn 2006). Similarly, in a multivariate analysis, Ostner et al. (2008) found that only synchrony was a significant factor, while our multivariate model contained both factors with the number of males as the stronger factor. Differences in the results may lie in part in the use of independent contrasts by Ostner et al. (2008), which is identical to PGLS techniques utilized here while assuming a lambda of one (Garland and Ives 2000). Additionally, our analysis comprised some different taxa and some different values for individual populations, which may explain differences in the results of the two studies.

Importantly, however, the relationship between reproductive skew and the number of males became much stronger when captive populations were excluded from the analysis, while the relationship between reproductive skew and synchrony became weaker. This might suggest that captivity has an effect on the monopolizability of females, and consequently, levels of reproductive skew may differ between wild and captive populations. Inspection of Fig. 2 shows that in captive studies all ranges of synchrony from low to

Table 3 Bivariate PGLS regressions for receptive synchrony and reproductive seasonality

Dependent variable	Predictor variable	Bivariate PGLS regression results			
		Synchrony	%year with births	r-statistic	% births in 3 months
Synchrony	Synchrony	–	$R^2=0.051$, $\lambda = 0.549$, $F_{s(2, 24)}=2.34$, $P=0.118$	$R^2=0.269$, $\lambda = 0.768$, $F_{s(2, 22)}=9.47$, $P=0.001$	$R^2=0.146$, $\lambda = 0.718$, $F_{s(2, 22)}=4.93$, $P=0.017$
	%year with births	–		$R^2=0.819$, $\lambda = 0.409$, $F_{s(2, 22)}=105.1$, $P<0.001$	$R^2=0.911$, $\lambda < 0.001$, $F_{s(2, 22)}=235.9$, $P<0.001$
	r-statistic	–		–	$R^2=0.949$, $\lambda < 0.001$, $F_{s(2, 22)}=429.2$, $P<0.001$
	% births in 3 months	–			–

Table 4 Hierarchical regression by sets for three models explaining variance in male reproductive skew (expressed as alpha paternity). Each row of the table represents models built with a different metric of seasonality of reproduction (see superscript)

Model 1			Model 2			Model 3		
Set 1: N males	Set 2: + synchrony	Set 3: + seasonality	Set 1: synchrony	Set 2: + N males	Set 3: + seasonality	Set 1: seasonality	Set 2: + N males	Set 3: + synchrony
$F_{\text{sk}^2_{24}}=27.15$, $R^2=0.511***$	$F_{\text{sk}^1_{23}}=5.40$, $R^2=0.604*$	$F_{\text{sk}^1_{22}}=0.51$, $R^2=0.613 \text{ ns}^a$	$F_{\text{sk}^2_{24}}=17.76$, $R^2=0.401***$	$F_{\text{sk}^1_{23}}=11.79$, $R^2=0.604**$	$F_{\text{sk}^1_{22}}=0.512$, $R^2=0.613 \text{ ns}^a$	$F_{\text{sk}^2_{24}}=8.61$, $R^2=0.233***^a$	$F_{\text{sk}^1_{23}}=16.73$, $R^2=0.556***$	$F_{\text{sk}^1_{22}}=3.24$, $R^2=0.613 \text{ ns}$
$F_{\text{sk}^2_{22}}=27.07$, $R^2=0.531***$	$F_{\text{sk}^1_{21}}=11.47$, $R^2=0.697***$	$F_{\text{sk}^1_{20}}=0.05 R^2=0.697 \text{ ns}^b$	$F_{\text{sk}^2_{22}}=20.74$, $R^2=0.462***$	$F_{\text{sk}^1_{21}}=16.29$, $R^2=0.697***$	$F_{\text{sk}^1_{20}}=0.052$, $R^2=0.697 \text{ ns}^b$	$F_{\text{sk}^2_{22}}=4.74$, $R^2=0.140**^b$	$F_{\text{sk}^1_{21}}=16.78$, $R^2=0.522***$	$F_{\text{sk}^1_{20}}=11.51$, $R^2=0.697**$
$F_{\text{sk}^2_{22}}=27.07$, $R^2=0.531***$	$F_{\text{sk}^1_{21}}=11.47$, $R^2=0.697***$	$F_{\text{sk}^1_{20}}=-0.68$, $R^2=0.686 \text{ ns}^c$	$F_{\text{sk}^2_{22}}=20.74$, $R^2=0.462***$	$F_{\text{sk}^1_{21}}=16.29$, $R^2=0.697***$	$F_{\text{sk}^1_{20}}=-0.680$, $R^2=0.686 \text{ ns}^c$	$F_{\text{sk}^2_{22}}=4.05$, $R^2=0.117**^c$	$F_{\text{sk}^1_{21}}=18.12$, $R^2=0.526***$	$F_{\text{sk}^1_{20}}=10.19$, $R^2=0.686***$

Significance tests are of the change in R^2 with the addition of each set, with significance indicated by *** ($P<0.001$), ** ($P<0.01$), and * ($P<0.05$). For regressions including the r -statistic or percent births in 3 months, fewer data points are available than for percent months with births

^a ns not significant

^b r -statistic

^c Percent births in 3 months

high were present, but high values of synchrony were particularly frequent, thus “causing” the negative slope of the regression. This might either indicate more receptivity overlap in captivity due to larger groups or increased social facilitation of synchrony (Lindburg 1987; Fürtbauer et al. 2011). In addition, due to artificial group composition, captivity might affect reproductive skew through female choice, and space restrictions in captivity could change options for alternative male reproductive strategies (Lindburg 1987; Setchell 2008) and thereby change reproductive skew.

This difference in captive and wild studies has implications for the interpretation of proximate causes of male reproductive skew. It suggests that receptive synchrony, together with female group size, is primarily driving the number of males in primate groups (Nunn 1999; Carnes et al. 2011) similar to what has been observed in other animals (Emlen and Oring 1977; Ims 1988). Concerning male reproductive skew, however, receptive synchrony seems to be less important. Receptive synchrony is certainly affecting male reproductive skew in some groups or populations of primates (Altmann et al. 1996; Boesch et al. 2006) and it will be important to consider why the effects are different across populations. As such, it will be important to investigate what factors are acting in specific groups, populations, or species. However, across all species, the number of males seems to be the more important factor responsible for the variation in male reproductive skew. However, given the reduced sample size for wild studies, clearly more data are required to support this interpretation.

Seasonality, synchrony, and male reproductive skew

To test the suggestion of a relationship between seasonality and male reproductive skew, we used three different measures of seasonality. As predicted, male reproductive skew decreased with increasing reproductive seasonality regardless of the metric, but the variance explained was small. Multivariate models including the number of males and seasonality contained only the number of males as a significant factor, suggesting that seasonality explains little variance in addition to what is explained by the number of males. This is in contrast to multivariate models including the number of males and synchrony, in which both factors were significant. Lastly, when testing skew, synchrony, and seasonality together, reproductive seasonality added little to almost nothing to the variance explained. Thus, we found very little to no support for the suggestion that reproductive seasonality is one of the most important factors determining male reproductive skew among nonhuman primates (Paul 1997). Instead, it appears that the crucial measure is receptive synchrony as has been suggested earlier (Pereira 1998; Dunbar 2000; Pereira et al. 2000). A similar point has been made by Nunn (1999) and Kutsukake and Nunn (2006),

who showed that the number of males or the mating skew in primate groups is much more accurately predicted by observed mating overlap of females than by seasonality.

This finding has repercussions for the use of proxies for reproductive synchrony in animal behavior studies. Among avian studies, the use of seasonality as a proxy for synchrony is uncommon, likely because measures of synchrony are more easily obtained by monitoring nests and using the timing of egg-laying as measure of receptive synchrony (Stutchbury and Morton 1995; Schwagmeyer and Ketterson 1999). In contrast, among primates and other mammals, reproductive seasonality has been used as proxy for receptive synchrony to investigate a number of hypotheses, for example, the influence of seasonality on the number of males, extra-group paternity, or testis size (Ridley 1986; Mitani et al. 1996; Isvaran and Clutton-Brock 2007; Iossa et al. 2008). However, Nunn's (1999) and our results clearly show that the underlying assumption that seasonality equals synchrony is likely too simplistic and seasonality seems not to be a good proxy for synchrony especially when considering reproductive skew.

Synchrony versus seasonality

The apparent question is why seasonality is not a good proxy for receptive synchrony. In previous studies, numerous measures of seasonality have been utilized, but to our knowledge these metrics of seasonality have not been empirically compared nor has their relationship to synchrony been investigated. Although the use of circular statistics and the *r*-statistic has the strongest mathematical and theoretical support of the three metrics of seasonality investigated here and appears to be well suited for comparative studies (Batschelet 1981; Janson and Verdolin 2005), we found, as one might expect, strong positive relationships between all three measures ($R^2 > 0.81$). In addition, although the associations between synchrony and two of the seasonality measures were significant, the variance explained was small. Importantly, the relationship between seasonality and synchrony disappeared when captive populations were excluded. The latter may be in part due to a reduced sample size, but may also reflect an influence of captivity on the relationship between seasonality and synchrony, as captivity may reduce reproductive seasonality (Brockman and van Schaik 2005). In any case, our results indicate a weak (if any) link between receptive synchrony and reproductive seasonality. Several factors may be responsible for this weak relationship.

First, seasonality is primarily a measure of duration, which is unaffected by factors that potentially influence mating overlap. For example, ovarian synchronization has been reported in a number of human (McClintock 1971; Weller and Weller 1993) and primate populations (Wallis 1985; French and Sibley 1987), although the results are

inconclusive and methods have been criticized (Clarke et al. 2012; see discussion in Fürtbauer et al. 2011). Still, if mechanisms for ovarian synchronization or desynchronization would exist, this would affect the degree of mating overlap, but would not necessarily affect the length of the mating season. In addition, the duration of receptive periods is likely to have an impact on the ability of a dominant male to monopolize a female (Kutsukake and Nunn 2006). Longer receptive periods should lead to more mating overlap per unit time, but again this measure is likely independent of the length of the mating season. Rather the length of the receptive period has been related to the number of males in a group (Borries et al. 2001; see also discussion in van Schaik et al. 1999).

Second, variation in receptive synchrony could relate to the different types of breeding seasonality such as income and capital breeders (Drent and Daan 1980; Jönsson 1997). In income breeders, which primarily use acquired energy for reproduction, the beginning of the mating season is typically set by external cues such as the photoperiod (van Horn 1975; overview for primates in Brockman and van Schaik 2005). This could result in many females simultaneously becoming receptive and ultimately high levels of synchrony. Capital breeders, which primarily use stored energy for reproduction, rely instead on internal, endogenous cues (Jönsson 1997; Brockman and van Schaik 2005). The use of such non-acute signals like fat reserves (van Schaik and van Noordwijk 1985; Koenig et al. 1997) could increase variation in the onset of receptivity resulting in lower synchrony. As strict income breeders usually have tightly limited mating and birth seasons, it is tempting to assume that such short seasons indicate high synchrony. However, as has been shown for one strict income breeder, the ring-tailed lemur, female cycles may still be asynchronous (Pereira 1991).

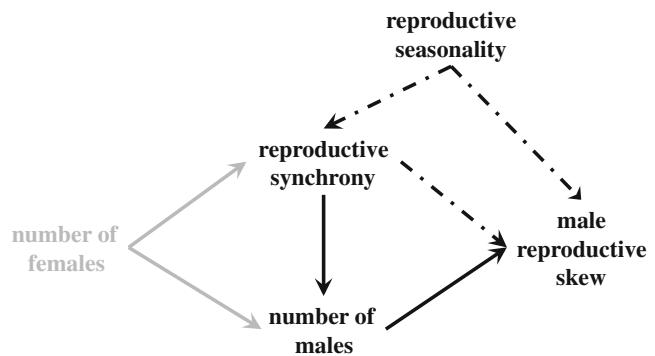


Fig. 3 Hypothesized relationships between the number of females, the degree of reproductive synchrony, the number of males, reproductive seasonality, and male reproductive skew. Gray lines represent previous hypotheses tested by Nunn (1999), solid black lines represent relationships strongly supported by the present study, while dashed lines represent hypothesized relationships for which only limited to no support was found

Lastly, life history, more specifically speed of reproduction, is likely an important factor as well, as it can influence the operational sex ratio in a group. Males in groups in which females are breeding annually must compete for all adult females every year, while in species with interbirth intervals of 2 or more years only a fraction of the females will mate each year. All else being equal, this suggests that males in annually breeding species may be less likely to monopolize all females in a group than in other species. However, while measures such as observed or expected mating overlap (Nunn 1999) take these differences across species or populations into account, seasonality does not.

Thus, while theoretically receptive synchrony might be linked to reproductive seasonality, in practice the relationship appears to be very weak in nonhuman primates; it might, in fact, be nonexistent.

Conclusions

The results of this study suggest that variance in male reproductive skew among primates is related to variation in the number of males in a group and to a lesser degree to receptive synchrony (results summarized in Fig. 3). Reproductive seasonality explains only a small proportion of variance in male reproductive skew. Both the effects of receptive synchrony and of reproductive seasonality are diminished if only wild populations are considered. Thus, while reproductive seasonality seems to affect receptive synchrony to some degree, its predictive power is weak and it appears to be an insufficient proxy for synchrony.

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