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Group size but not dominance rank predicts the probability of conception in a frugivorous primate

Su-Jen Roberts · Marina Cords

Abstract In social mammals, within-group competition for food can drive variation in female fitness. Frugivores may face particularly strong competition because they use patchily distributed usurpable resources. Dominance rank and group size influence how a female experiences within-group competition. Both are predicted to affect access to food and, thus, reproductive success. We used 15 years of behavioral, demographic, and reproductive data from wild frugivorous blue monkeys to examine effects of rank and group size on the probability that a female conceived. We used generalized linear mixed models, controlling for potentially confounding maternal and environmental factors. Blue monkey females compete aggressively and disproportionately for fruits and exhibit linear dominance hierarchies, but neither rank index we tested significantly predicted the probability of conception. Although earlier studies found that group size effects on activity budgets were minimal, we found that group size had a quadratic relationship with the probability of conception, which peaked at around 31 members. The lack of a rank effect may reflect behavioral strategies (e.g., switching resources, spreading out during feeding, using cheek pouches) that minimize the strength of within-group competition, thus facilitating group-level cooperation in between-group contests. The significant quadratic effect of group size on reproduction may occur if individuals in small groups do not obtain the full benefits of group living (e.g., predator avoidance, increased foraging success, communal care for offspring) and those in large groups experience a lower quality diet or constrained feeding time. Ultimately, measures of reproduction are preferable to behavioral proxies for accurately assessing within-group competition.

Keywords Within-group competition · Female reproduction · Breeding success · Flexible feeding behavior

Introduction

In female mammals, reproduction depends on adequate nutrition (Wade and Schneider 1992), so factors limiting access to food are likely to exert a strong influence on behavioral strategies. In gregarious taxa, competition within and between groups may limit access to food, and therefore competition figures prominently in theoretical explanations of female social behavior and its reproductive consequences (Silk 2007; Clutton-Brock and Janson 2012). Socioecological models characterize this relationship, using ecological factors like food abundance and distribution to predict the strength and type of feeding competition and its consequences for social organization (Wrangham 1980; Sterck et al. 1997; Isbell and Young 2002; Archie et al. 2006; Snaith and Chapman 2007). Frugivores have been suggested to be especially likely to experience strong feeding competition because fruits are often preferred high-quality foods with limited availability, and because individual feeding sites are clumped in space and slowly depleted, making them usurpable (Pruetz and Isbell 2000; Vogel and Janson 2011).

Increasingly, behavioral ecologists are recognizing that there is marked variance in reproductive success in female mammals, even among plural breeders, and despite inevitable

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female-biased investment in young (Pusey 2012; Clutton-Brock and Huchard 2013). Such variance often, though not exclusively, reflects competition within or between groups (Silk 2007; Stockley and Bro-Jørgensen 2011). Within-group competition is commonly inferred when dominance rank or group size affects behavioral proxies or reproductive measures of fitness (Koenig 2002). While there has been a long-standing interest in how rank and group size affect behavior (reviewed in Koenig and Borries 2009; Schülke and Ostner 2012; Clutton-Brock and Huchard 2013), limited data are available to assess their direct effects on reproduction, especially in long-lived, slowly reproducing species (dolphins, Mann et al. 2000; elephant seals, McMahon and Bradshaw 2004; hyenas, Watts and Holekamp 2009; primates, Pusey 2012).

Theory predicts that higher ranking females should have priority of access when individuals compete directly for food (i.e., contest competition, Isbell 1991; Snaith and Chapman 2007). Many studies of social mammals support this prediction, showing that higher ranking females win more food-related contests, have higher energy intake rates, or spend a larger proportion of feeding time eating preferred foods (e.g., bison, Rutberg 1986; red deer, Thouless 1990; hyenas, Hofer and East 2003; chimpanzees, Wittig and Boesch 2003; mangabeys, Chancellor and Isbell 2009). However, evidence that rank affects more direct reproductive measures is mixed. Some studies found that higher ranking females began reproducing earlier, gave birth at a more advantageous time of year, had higher birthrates, higher infant survivorship, longer reproductive life-spans, or higher estimated lifetime reproductive success, while other studies found no relationship or even a negative relationship (reviewed in Ellis 1995; Stockley and Bro-Jørgensen 2011; Pusey 2012).

In the absence of rank effects and controlled for variation in habitat quality, negative correlations between group size and behavioral or reproductive proxies of fitness suggest the occurrence of indirect within-group competition (i.e., scramble competition). For instance, because larger groups deplete local feeding areas more quickly, each individual must travel farther to sustain itself (Chapman and Chapman 2000). Because travel imposes energetic costs, larger group size (beyond a theoretical minimum) may correspond with reduced reproductive success for all group members (Janson and Goldsmith 1995). The meta-analysis of primate studies of Majolo et al. (2008) indicated that larger groups generally did travel farther and their individual members spent more time feeding. As with rank, however, evidence for a relationship between group size and direct measures of female reproduction is more complex. In the same meta-analysis, the relationship between group size and female fecundity was significant and negative when the data set included studies of two social groups (i.e., one large and one small), but the relationship was not significant when the data set

included studies of four or more social groups. Conversely, the meta-analysis of Ebensperger et al. (2012) of 51 mammal species showed that the number of adults and the number of non-breeders in a group had modest, but significant, *positive* effects on fitness, which included group fecundity and survivorship measures; however, the effect was not significant for other measures of group size (e.g., total group size, number of males, number of females), or when female fecundity constituted the fitness measure.

The variable relationships between rank and reproduction and between group size and reproduction suggest that within-group competition is not universally important in explaining reproductive variance in social mammals and raise questions about additional social or environmental factors that determine its strength. These factors might include temporal or spatial variation in food availability (Pusey 2012); for example, studies limited to a period when food availability was low may be more likely to find a rank or group size effect because within-group competition was stronger than at other times of year (Woodroffe and Mac-Donald 1995; Beehner et al. 2006; Foerster et al. 2011). Alternatively, the strength of within-group competition may be related to temporal variation in female energetic demands, which may change with age (especially for young females who are still growing, Pusey 2012) or reproductive state (Dufour and Sauther 2002). To evaluate the importance of these variables, it is critical to compare studies that are sufficiently long term to capture general patterns (Stockley and Bro-Jørgensen 2011; Clutton-Brock and Huchard 2013) while controlling for traits like environmental seasonality, female age, and reproductive state.

Our study takes such an approach, drawing on a 15-year data set to evaluate how within-group competition affects the probability of conception in largely frugivorous blue monkeys. This data set allowed us to evaluate the effects of dominance rank and group size in a population that included groups of varying sizes and in which the existence of linear dominance hierarchies suggested strong contest competition. Blue monkeys are arboreal forest-dwelling guenons that occur in eastern, central, and southern Africa (Lawes et al. 2013). Females generally live in their natal groups for life, whereas males invariably emigrate from their natal groups during adolescence (Ekernas and Cords 2007). While groups typically contain one adult male, they sometimes experience temporary influxes of additional males during the mating season (Cords 2002c). Fruit is a major and preferred part of the blue monkey diet, which, however, also includes leaves, flowers, and invertebrates (Lawes et al. 2013).

Aggression among female blue monkeys occurs mostly and disproportionately in the context of feeding, and especially disproportionately when females feed on fruits (Cords 2000; Pazol and Cords 2005; Foerster et al. 2011). Linear dominance hierarchies are detectable (Klass and Cords

2011), with high-ranking individuals directing and low-ranking individuals receiving agonism at the highest rates (Cords 2000; Foerster et al. 2011). Prior studies, however, have generally failed to identify rank-related differences in feeding behavior or reproduction, including time spent feeding and proportion of feeding time devoted to different food types (Cords 2000; Pazol and Cords 2005; but see Foerster et al. 2011), fruit intake rate, and rate of producing offspring that survived to 1 year (Cords 2002b).

Although groups vary considerably in size, these differences also appear to have unexpectedly few effects on behavior. For instance, there were no differences in the group's daily path length, individual travel distance, or daily area used among groups differing in size by a factor of 2, even after accounting for variation in habitat quality (Cords 2012). Additionally, a comparison of reproductive parameters following group fission showed no differences in female birthrates and offspring survival between the large pre-fission and smaller post-fission groups (Cords 2012).

In this study, we used detailed long-term behavioral, demographic, and reproductive data to evaluate how within-group competition affected reproduction, specifically the probability of conception. We chose this reproductive parameter because unlike measures of fertility like interbirth interval, which spans an entire year or more, the probability of conception, a particular event, can be related to fine-scale variation in social and ecological parameters (Wolff and Dunlap 2002; Beehner et al. 2006). Ultimately, the probability of conception also determines interbirth intervals and therefore is a more direct measure of fertility. Our goal was to evaluate the importance of within-group competition by determining whether dominance rank and group size affected the probability of conception.

Methods

Study site and population

The study population of blue monkeys (*Cercopithecus mitis stuhlmanni*) inhabits the Isecheno area of the Kakamega Forest, a rainforest in western Kenya (0° 19′ N, 34° 52′ E; elevation 1,580 m; mean annual rainfall (1997–2011) 1,942 mm). Rainfall is variable across years (range 1,343–2,334 mm, 1997–2011) and falls seasonally, with the wettest period typically in April and May and a smaller peak from August through October (Mitchell et al. 2009). The study site supports a dense population of blue monkeys, with 192 individuals per km^2 in areas of natural forest (Fashing et al. 2011). Like other guenons (Butynski 1988), the Kakamega blue monkeys reproduce seasonally, with 64 % of births occurring from January to March (Cords and Chowdhury 2010), a period that includes or immediately follows the 2

months (January–February) of peak ripe fruit availability (Foerster et al. 2012; MC, unpublished data).

Data on demographic events and social behavior were recorded as part of a long-term research project on blue monkey behavior and reproduction that began in 1979 (Cords 2012). Here, we used data from 92 reproductive females observed from 1997 to 2011, when near-daily monitoring generated detailed records of group membership and social behavior. In 1997, the study population included two groups, but four fission events between 1999 and 2009 resulted in six study groups by the end of 2011 (Cords 2012). Members of the study groups were habituated and distinctive in body and facial features, allowing individual recognition.

Demographic data

Observers recorded births, deaths or disappearances, and the presence and identity of adult males. We used these data to infer conception dates, assess age, and calculate group size.

Birthdates

We used birthdates to infer conception dates for the 264 infants conceived during the study period (see below). Most birthdates (69 %) were known to the day. When a birthdate was known to a 2-day period (19 %), we assigned it to the first day. If the range of possible birthdates spanned a longer period (3–14 days, 12 %), we assigned the infant's birthdate to the midpoint of the range.

Maternal birthdates were more uncertain, as some mothers were older juveniles or adults when first identified, before the study period began. Long-term records allowed us to estimate the birthdates of such females with various degrees of precision. Fifty-nine (64 %) of the mothers had birthdates known to ≤2 months (37 known to 1 week). For the remaining 33, all born before 1997, we estimated birthdates to the nearest year based on body size changes during their juvenile years (N=20) or to a range of 4–20 years, based on general appearance, for those first identified as adults (with pendulous nipples; range of 4–10 years, N=11; range of 20 years, N=2). For the 33 birthdates known only to the year or to a period of several years, we generally set the birthdate to February 15 of the year in the middle of the assigned range, as that day corresponds with the middle of the peak birth month of the population (Cords and Chowdhury 2010).

Deaths and disappearances

We rarely found carcasses that allowed us to confirm that an individual died; thus, we usually inferred deaths from

permanent disappearances. Female blue monkeys are strictly philopatric, so we presumed that all females that disappeared from the group were dead. Natal males emigrate around 7 years old (Ekernas and Cords 2007) and we no longer considered them to be group members after they permanently left the group.

Female reproductive parameters

We aimed to identify the factors affecting whether a female conceived in a given month. To do so, we assigned each month of an adult female's life to one of four categories corresponding to whether she conceived, was pregnant, gave birth, or none of those three. We identified months in which a female gave birth from observational records. We identified the month in which she conceived by subtracting 176 days, the mean gestation length (Pazol et al. 2002), from the infant's birthdate. Inferring conceptions from subsequent births excludes conceptions that end in miscarriage. In wild baboons, miscarriage occurs after 13 % of conceptions (Beehner et al. 2006); however, in the absence of visual cues of conception or hormonal data, our study was limited to conceptions that resulted in birth (live or stillbirth). We assigned all months between conception and birth as pregnant and all remaining months as none of the above.

All females that were reproductive in January 1997 were included in the data set beginning in that month. Females that became reproductive after January 1997 were included beginning with the month after their first conception. We excluded months in which females had their first conceptions because these months had missing values for some of the variables (e.g., time since last conception), which excluded them from the statistical analysis. In addition, the timing of first conceptions is likely to be strongly influenced by developmental and genetic factors (Zehr 2005; Charpentier et al. 2008). We were unable to control for these factors, providing additional justification for excluding these months.

For females that died during the study, the last month included in the data set was the month of their last known birth or the month that was 7 months before their deaths, whichever was later. Truncating the data this way allowed us to exclude months in which the female may have conceived but the conception was undetectable because the female died before giving birth. Similarly, females that were alive at the end of the study (December 2011) must have survived one gestation length into the following year to be included in the final month of the data set. We were interested in the probability of conception, so we removed all months in which a female was pregnant (and therefore unable to conceive) from the final data set.

Predictor variables

We evaluated the effects of group size and dominance rank on the probability of conception in a given month. We controlled for additional variables that may affect female reproduction (Table 1).

Group size

Group size was equal to the number of individuals in a group each day, averaged over the month. Because we were not always able to achieve a complete group census on each day of the month, we initially calculated group size separately for adult females plus juveniles (i.e., "female/juvenile group size") and for adult males (i.e., "male group size") because the sexes differ in the duration and stability of social bonds. Female/juvenile group size is relatively stable, with changes occurring only when an individual was born or died, a natal male emigrated, or a group fission or fusion occurred. Because of this stability, if an adult female or juvenile was not seen on one or a few days but was subsequently observed in the group, we presumed that she or he was present but unobserved on the missing days. One exception involved an adult female that was not observed for 42 consecutive days: the length of this period suggested that we had not simply overlooked her, so we assumed she was away from the group during this period and excluded her from the group count.

The number of adult males in a blue monkey group is more variable than the number of females, especially during the breeding season when multi-male influxes may occur (Cords 2002c). We calculated male group size directly from daily observations, making no presumptions that males were present if they were not observed. Three periods in 1997 and early 1998 were exceptions to this practice. During these periods, groups were not observed for 1.5 to 5.5 months, making it impossible to assign a monthly male group size based on observations alone. Each observation gap occurred outside the mating season at times of the year when male influxes are generally rare, and the same resident male was alone in the group before and after each gap. We therefore presumed that there was only one male in the group during the gaps. We added the average female/juvenile group size (mean±SD=36.4±14.1; range=7–64.6) to the average male group size (1.5±1.1; range 0.1–8.5) for each month to obtain the total group size (43.8±12.8; range=7.9–69.2).

We also tested an alternative measure of group size—the number of females over age 5 (17.9±5.5; range=4–29)—to determine if individuals in the same age/sex class were particularly important competitors. Five is the age at which females approach adult size and begin to behave like adults (e.g., participate in intergroup encounters, exhibit sexual

Table 1 Variables included in the analysis

Variable	Type	Description
Dependent		
Conception[a]	Categorical (yes/no)	Did the female conceive?
Independent		
Fixed effects		
Group size[a, b]		
Total group size	Continuous	Average number of individuals in the group in a month
Female group size	Continuous	Average number of females over age 5 in the group in a month
Group size^{2c}	Continuous	Group size squared
Dominance rank[a, c]		
Standardized rank	Continuous (0–1)	The proportion of group females who outrank a given female (highest ranking female in the group is 0, lowest ranking is 1)
Ordinal rank	Ordinal (1–N)	The value for the highest ranking female is 1; the value for the lowest ranking female is the number of adult females in the group (N)
Age[a]	Continuous	Female's age calculated to the nearest month
Age^{2a}	Continuous	Female's age squared
Time since last conception[a]	Continuous	Number of months since the month of the female's last conception
Lactation stage[a]	Ordinal (very high, high, mid, low, none)	Reflects whether the female's last offspring is present and suckling; very high to low lactation as offspring ages; if last offspring was dead or older than 32 months, the female was classified as "no lactation"
Rainfall[a]	Continuous	Measured in millimeters
Time of year[a]	Categorical (4 groups)	Three-month groups defined based on the availability of major blue monkey foods; groups: December–February, March–May, June–August, and September–November
Interactions		
Time since last conception × lactation stage[a], time since last conception × age, time since last conception × rank, time since last conception × group size, lactation stage × rank, lactation stage × group size, age × rank, age × group size, rank × group size, time of year × rank		
Random effects		
Female identity[a], year[a], group		

[a] Variables included in the final model

[b] Only one alternative measure was included in each model

[c] Variable had an inconsistent effect on the probability of conception. It was included in the models with total group size and not in the models with female group size

behavior, engage in prolonged grooming) and are likely to become important participants in within-group competition.

Dominance rank

To compute female dominance rank, we used records of dyadic agonistic behavior (supplant, chase, attack, lunge, bite, hit, avoid, cower, flee, gecker, trill, and scream) from ad lib and focal samples, carried out as part of long-term monitoring of the population (Cords 2012). We included interactions between females age 5 and older for reasons noted above. We included only interactions in which there was a clear winner and loser (i.e., only one individual showed submissive behavior).

We compiled data on agonism for 1-year periods to compute dominance hierarchies using MatMan 3.2 (Noldus Information Technology). We chose 1-year periods because

they capture rank changes while minimizing the number of unknown relationships in the data matrix, which can cause unstable rank output (Klass and Cords 2011). Blue monkeys show agonism at low rates, necessitating data collation over 1-year periods to detect linear hierarchies (Cords 2000; Klass and Cords 2011). Females that interacted agonistically with fewer than three partners during the year were excluded from the data set because they could not be placed reliably in the hierarchy. For each hierarchy, MatMan calculates a directional consistency index (DCI), which is a measure of dyadic outcome predictability. The DCI equals the total number of dyadic encounters with an outcome in the main direction for that dyad minus the number of encounters with outcomes in the opposite direction, divided by the total number of interactions; thus, 0 indicates that the outcome of an encounter is unpredictable based on earlier encounters and 1 indicates that all encounters have the same directionality (van Hooff

and Wensing 1987). The hierarchies included in this analysis had a DCI of 0.88±0.06 (mean±SD; range=0.68 to 0.98; $N=54$), indicating that dyadic outcomes were generally very consistent.

MatMan implements the I&SI method of ranking, minimizing the number and strength of inconsistencies within an ordinal hierarchy (de Vries 1998). For 8 of the 54 hierarchies, we extended the period of data collation 1 to 6 months before and after the calendar year in question to increase sample size and achieve a stable hierarchy. In these cases, some agonism data were used to construct more than one hierarchy. Fifty-two of the hierarchies (96 %) were significantly linear. Thirty-seven (69 %) produced stable rankings over 10 MatMan runs; the remaining 17 included blocks of two to seven females that were variously placed relative to one another in repeated MatMan runs. In these cases, we assigned the median rank to all females in a block.

Researchers commonly code dominance as ordinal rank (e.g., Wittig and Boesch 2003; Beehner et al. 2006; Chancellor and Isbell 2009; Cafazzo et al. 2010) or as ordinal rank standardized by group size (i.e., standardized rank; e.g., Clutton-Brock et al. 1986; Hofer and East 2003; Fedigan et al. 2008; Foerster et al. 2011). We tested both rank indices to account for uncertainty in how individual blue monkeys experience rank. MatMan produced ordinal ranks from 1 (highest) to N (lowest), where N is the number of females aged ≥5 years in the group. In our data set, N varied from 4 to 29. Standardized rank (ranging from 0 to 1) reflects the proportion of group females that ranked higher than a given female. As rankings were compiled annually, a female's rank was the same for all months in a given year.

Maternal traits

Age, time since last conception, and lactation stage provided information about a female's reproductive state and history. We calculated a female's age to the nearest month using known or estimated birthdates as described above (mean±SD=176.3±70.8 months; range: 41–405). We also calculated time since last conception to the nearest month (mean±SD=20.0±11.3 months; range 5–90). We coded lactation stage as an ordinal variable with each category being assigned an integer from 1 (no lactation) to 5 (very high lactation). We distinguished these categories based on the presence and age of the female's last infant, combined with population-wide frequencies of infant suckling behavior. Infants less than 5 months old spent the most time suckling and the least time away from their mothers (Foerster and Cords 2002), so we classified mothers of infants less than 5 months as "very high lactation." We classified females as "high lactation" if their infants were 5 to 9 months old, "mid lactation" if their infants were 10 to 14 months old, and "low lactation" if their infants were 15 to 32 months old. The low lactation range

is large because while all infants over 15 months old suckled rarely, some were observed to suckle until they were 32 months old. Finally, we classified females as "no lactation" if their last infant was older than 32 months or dead.

Seasonality

Two variables—rainfall and time of year—provided information about seasonality. We used rainfall matching each month of our study (mean±SD=170±88 mm; range 0–399) to indicate environmental change. Time of year also tracked environmental change, as fruit availability is known to vary across months. We identified four 3-month categories from changes in the availability of major foods eaten by blue monkeys (Foerster et al. 2012; MC, unpublished data), grouping together December–February, March–May, June–August, and September–November. Generally, fruit is most available in December–February and June–August, and least available in March–May.

Data analysis

To test whether the probability of conception related to the predictor variables, we used R Project Software version 2.15.0 (R-Development-Core-Team 2012) to conduct a mixed-effects logistic regression with the lme4 package (Bates and Maechler 2009). We used maximum likelihood estimation, a binomial error structure, and the logit link function. We tabulated the data in 1-month windows, and the dependent variable was whether a female conceived during a given month. We were primarily interested in the effects of rank and group size on conception, so we included these variables as fixed effects. High correlation values for the two measures of rank (Pearson correlation coefficient=0.85) prevented us from including alternative measures in the same model. We thus constructed two similar models: one for ordinal rank and one for standardized rank. We controlled for other factors that could influence conception by including age, time since last conception, lactation stage, rainfall, and time of year as additional fixed effects (Table 1). We also ran these models substituting female group size for total group size.

We tested 11 two-way interactions by including them in the model as fixed effects (Table 1). These included interactions between time since last conception and (1) lactation stage, (2) age, (3) rank, and (4) group size because we predicted that females might require extended recuperation time between conceptions if they were nursing an infant, very young or very old, low-ranking, or living in a large group. We included interactions between lactation stage and (5) rank and (6) group size because we predicted that females that were nursing an infant might benefit most from reduced within-group competition associated with high rank or small group size. We included interactions between age and (7)

rank and (8) group size because we predicted that young females simultaneously investing in growth and reproduction might benefit most from the reduced within-group competition associated with high rank and small group size (Pusey 2012). We included the interaction between (9) rank and group size because we predicted that conception by low-ranking females might be more strongly affected by group size than conception by high-ranking females (Takahata et al. 2008). We included the interaction between (10) time of year and rank because we predicted that priority of access associated with high rank might be particularly advantageous during certain times of year, specifically periods of low fruit availability (Foerster et al. 2011). Finally, we included the interaction between (11) time of year and rainfall because we predicted that conception might be more likely only in conception seasons with particular rainfall characteristics.

Before fitting the models, we standardized all fixed effects to improve model convergence and to allow us to compare the relative importance of the various predictors (Gelman 2008). We included quadratic transformations of the age and group size variables as additional fixed effects. We included the age quadratic because studies of other primate species indicated that age has a curvilinear relationship with the probability of conception (e.g., Beehner et al. 2006). We included the group size quadratic because groups of intermediate size may be most likely to maximize the difference between the costs and benefits of group living (Sterck et al. 1997; Courchamp et al. 1999). Standardizing both age and group size before transformation reduced the correlation between the linear term and its quadratic so both could be included in the model (Schielzeth 2010).

We included year, female, and group as random effects to control for repeated sampling. Group did not contribute to variance in the dependent variable and we removed it from the final models.

We present the parameter estimates and standard errors from the full models because the full models minimize bias to effect size estimates and p values, and provide a balanced representation of all hypotheses tested (Forstmeier and Schielzeth 2011). We did not use stepwise methods to minimize the probability of erroneously rejecting the null hypothesis of no effect (type I error) (Whittingham et al. 2006; Mundry and Nunn 2009). We did, however, remove nonsignificant ($p > 0.05$) interaction terms to allow for the interpretation of the estimates, standard errors, and p values of the main effects (Engqvist 2005). This process eliminated ten interactions, leaving only the interaction between time since last conception and lactation stage. Thus, the full model of the probability of conception included ten fixed effects (rank, group size, group size^2, age, age^2, time since last conception, lactation stage, the interaction of time since last conception and lactation stage, rainfall, and time of year) and two

random effects (female identity and year). To confirm the overall significance of the one categorical variable (i.e., time of year), we used a log-likelihood ratio test to compare the full model to the model without this variable.
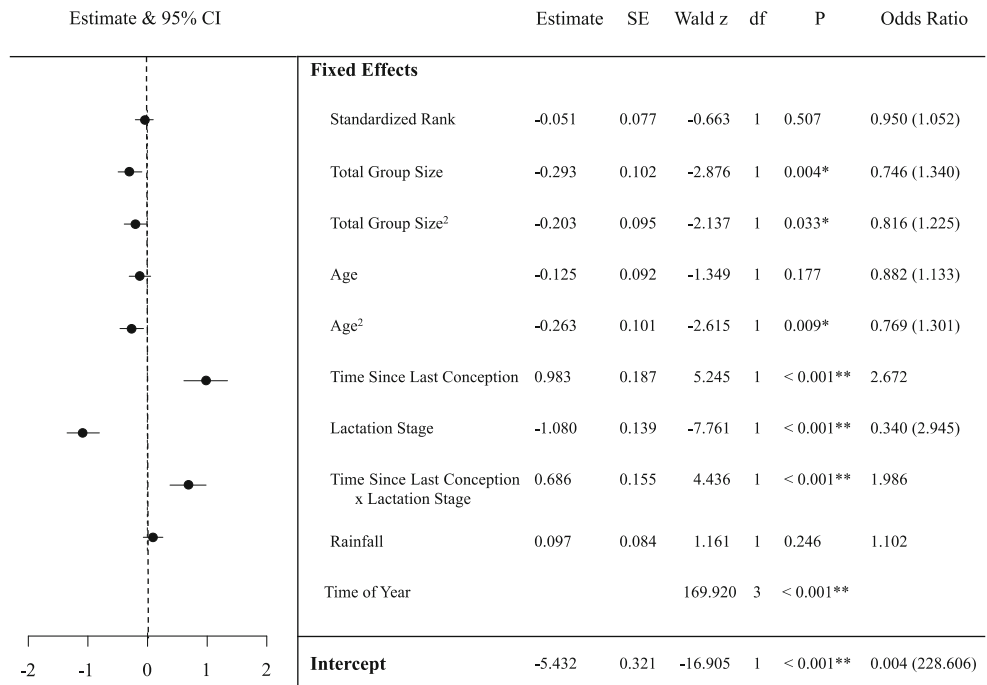
Multicollinearity was low for most predictor variables (variance inflation factors ranged from 1.02 to 1.63 for the model with total group size and standardized rank; VIFs were similar for other models). VIFs were somewhat higher for time since last conception and the one significant interaction retained in our final models (7.41 for both), but values below 10 suggest that multicollinearity was not a problem (Chatterjee and Price 1991; Zuur et al. 2009). We plotted normalized residuals against each predictor variable and confirmed that there was no systematic pattern in residual spread. To determine if the whole set of predictor variables influenced conception, we conducted a log-likelihood ratio test using the ANOVA function in R to compare the full models to the null model (including only random effects). We also conducted a log-likelihood ratio test to compare the full models to a model that contained all control variables (all except rank, group size, and group size^2) to assess the joint significance of the variables of interest. We used odds ratios to assess the relative importance of the fixed effects.

Results

With the probability of conception as the dependent variable, log-likelihood ratio tests indicated that full models including total group size and one measure of rank differed significantly from the null model including only random effects (log-likelihood ratio tests: standardized rank, $\chi^2 = 456.26$, $df = 12$, $p < 0.001$; ordinal rank, $\chi^2 = 457.55$, $df = 12$, $p < 0.001$) and from models including only control variables (log-likelihood ratio tests: standardized rank, $\chi^2 = 9.75$, $df = 3$, $p = 0.021$; ordinal rank, $\chi^2 = 11.04$, $df = 3$, $p = 0.012$). Results were similar for both models, so for simplicity, we present the results of the model with standardized rank only (Fig. 1; results of model with ordinal rank is Online Resource 1). Regardless of the index used, rank was never a significant predictor of conception. However, there was a significant quadratic relationship between group size and the probability of conception. The probability of conception peaked at a group size of 30.5 members in the model with standardized rank (Fig. 2) and 31.5 members for the model with ordinal rank.

When we substituted female group size for total group size, the results were again similar for the models with standardized and ordinal rank and again we present only the model with standardized rank (Fig. 3; results of model with ordinal rank is Online Resource 2). With female group size as a predictor, the quadratic transformation of the

Fig. 1 Results of the logistic regression in which *total group size* and *standardized rank* were entered as fixed effects and female identity (variance=0.117) and year (variance=0.279) as random effects. The figure on the *left* is a plot of the coefficient and 95 % CI for each fixed effect; variables with CIs that do not cross 0 are significant predictors of conception. The corresponding table includes the estimate, standard error (SE), Wald score, degrees of freedom (*df*), significance (*p*), and odds ratio (e^estimate) for each fixed effect. If the odds ratio was less than 1, we presented the inverse *in parentheses* to ease comparisons among fixed effects

	Estimate	SE	Wald z	df	P	Odds Ratio
Fixed Effects						
Standardized Rank	-0.051	0.077	-0.663	1	0.507	0.950 (1.052)
Total Group Size	-0.293	0.102	-2.876	1	0.004*	0.746 (1.340)
Total Group Size^2	-0.203	0.095	-2.137	1	0.033*	0.816 (1.225)
Age	-0.125	0.092	-1.349	1	0.177	0.882 (1.133)
Age^2	-0.263	0.101	-2.615	1	0.009*	0.769 (1.301)
Time Since Last Conception	0.983	0.187	5.245	1	<0.001**	2.672
Lactation Stage	-1.080	0.139	-7.761	1	<0.001**	0.340 (2.945)
Time Since Last Conception x Lactation Stage	0.686	0.155	4.436	1	<0.001**	1.986
Rainfall	0.097	0.084	1.161	1	0.246	1.102
Time of Year			169.920	3	<0.001**	
Intercept	-5.432	0.321	-16.905	1	<0.001**	0.004 (228.606)

number of adult females was not significant. Removing the quadratic term did not significantly change model fit (log-likelihood ratio test: standardized rank, $\chi^2=2.30$, $df=1$, $p=0.129$; ordinal rank, $\chi^2=2.15$, $df=1$, $p=0.142$), so we reran the models without this term to test for a linear effect of number of females. In the final models, the number of females was not a significant predictor of the probability of conception (Fig. 3, Online Resource 2). The models also indicated that dominance rank was not a significant predictor of conception. The models including female group size were significantly different from models including only random effects (log-likelihood ratio tests: standardized rank, $\chi^2=450.66$, $df=11$, $p<0.001$; ordinal rank, $\chi^2=452.23$, $df=11$, $p<0.001$). However, they were not significantly different from the model including only control variables (log-likelihood ratio test: standardized rank, $\chi^2=4.15$, $df=2$,
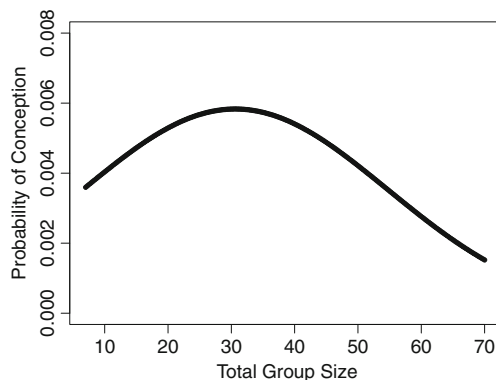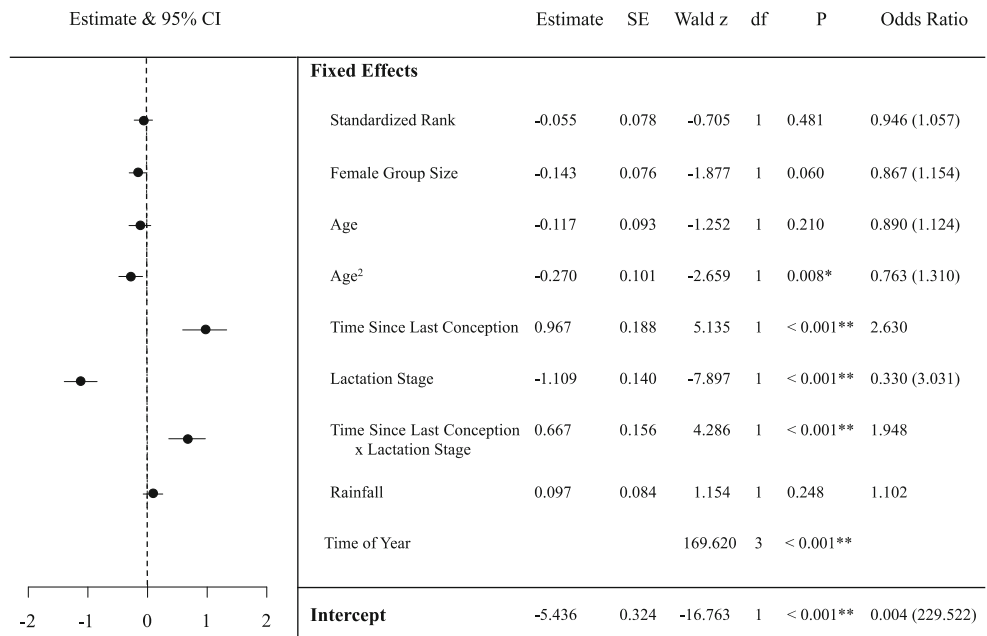

Fig. 2 Probability of conception as a function of group size as determined by the predicted values from the logistic regression including total group size and standardized rank

$p=0.123$; ordinal rank, $\chi^2=5.72$, $df=2$, $p=0.057$), indicating that removing the nonsignificant group size and rank terms did not reduce model fit.

In all models, five of the six control variables were important predictors of conception. Specifically, the three maternal traits, the interaction, and time of year were significant predictors, but rainfall was not (Figs. 1, 3). There was a quadratic relationship between age and the probability of conception with the probability of conception peaking at 13 years in all models (see Online Resource 3 for probability curve for model with total group size and standardized rank). Predictably, the probability of conception increased if more time had passed since a female's last conception and if she did not have a dependent infant. The significant interaction indicated that the probability of conception for non-lactating females was much higher than the probability of conception for lactating females; however, the difference between these groups decreased with time. Time of year was a significant predictor of conception, as expected, with females most likely to conceive between June and November.

The odds ratio allowed us to assess the relative contribution of each continuous or ordinal fixed effect, with greater departures from unity indicating greater contribution. For all models, the odds ratios indicated that time since last conception, lactation stage, and their interaction were more important predictors of conception than either dominance rank or group size (Figs. 1, 3). The odds ratio of the age quadratic was similar to that of group size, suggesting that the predictive value of the two variables is about equal.

Fig. 3 Results of the logistic regression in which *female group size* and *standardized rank* were entered as fixed effects and female identity (variance=0.144) and year (variance=0.301) as random effects. The figure on the *left* is a plot of the coefficient and 95 % CI for each fixed effect; variables with CIs that do not cross 0 are significant predictors of conception. The corresponding table includes the estimate, standard error (SE), Wald score, degrees of freedom (*df*), significance (*p*), and odds ratio (e^estimate) for each fixed effect. If the odds ratio was less than 1, we presented the inverse *in parentheses* to ease comparisons among fixed effects

Estimate & 95% CI	Estimate	SE	Wald z	df	P	Odds Ratio
Fixed Effects						
Standardized Rank	-0.055	0.078	-0.705	1	0.481	0.946 (1.057)
Female Group Size	-0.143	0.076	-1.877	1	0.060	0.867 (1.154)
Age	-0.117	0.093	-1.252	1	0.210	0.890 (1.124)
Age^2	-0.270	0.101	-2.659	1	0.008*	0.763 (1.310)
Time Since Last Conception	0.967	0.188	5.135	1	< 0.001**	2.630
Lactation Stage	-1.109	0.140	-7.897	1	< 0.001**	0.330 (3.031)
Time Since Last Conception x Lactation Stage	0.667	0.156	4.286	1	< 0.001**	1.948
Rainfall	0.097	0.084	1.154	1	0.248	1.102
Time of Year			169.620	3	< 0.001**	
Intercept	-5.436	0.324	-16.763	1	< 0.001**	0.004 (229.522)

(x-axis: -2 -1 0 1 2)

Discussion

Rank and the probability of conception

Blue monkeys prefer and consume contestable foods like fruit, compete aggressively and disproportionately for this food category, and exhibit linear dominance hierarchies based on highly asymmetric agonistic relationships in which high-ranking females have priority of access to feeding sites (Cords 2000; Pazol and Cords 2005; Foerster et al. 2011). This suite of behaviors suggests that they experience high within-group contest competition and high-ranking animals should have a reproductive advantage (Isbell 1991; Snaith and Chapman 2007). We found, however, that rank did not affect the probability that a female conceived. While surprising from a theoretical perspective, our results support previous research on the study population, which documented limited, inconsistent, or no rank effects on feeding behavior (Cords 2000; Pazol and Cords 2005; Foerster et al. 2011), energetic stress (Foerster et al. 2011), or the rate of producing offspring that survived to 1 year (Cords 2002b). Together, these findings suggest that individuals actually experience low within-group contest competition.

Flexible feeding behavior may offer a proximate explanation for the discordance between theoretical predictions and our results. For example, feeding individuals may avoid contests by maintaining large interindividual distances, thereby mitigating rank effects on behavioral and reproductive proxies of fitness (Vogel and Janson 2007). In ring-tailed coatis, another mammal with linear dominance hierarchies, individuals increase the distance to neighbors when feeding on contestable fruit relative to uniformly distributed insects (Hirsch

2007). While similar resource-related adjustment of interindividual spacing does not seem to occur in blue monkeys (Cords 2002a), group members do spread out over large distances (mean group spread=109 m, range=60–190 m, N=35 measurements of one group with 45 members, Cords 1987; mean group spread=65.6 m, range=6–321 m, N=3162 measurements of six groups, Plumptre 2000) and individuals often feed alone in a tree crown (39 % overall, 13–40 % of fruit-feeding time while in trees large enough to hold several monkeys) or feed in trees that could accommodate others (76 % of feeding time; Cords 2002a). Given the potential costs of spreading out, such as increased predation risk (Cheney et al. 2004) and inefficient transfer of information (Di Bitetti and Janson 2001), individuals that adopt such behavior should obtain substantial benefits, and the reduction of within-group contest competition is likely to be one of them.

Morphological adaptations may also reduce within-group contest competition. Blue monkeys have an enlarged caecum and colon, which allows them to ferment leaves in the hindgut and permits a flexible diet that can include large proportions of either fruit or leaves (Lawes et al. 2013). The ability to eat diverse items, and to readily switch among them on short time scales, may allow individuals to avoid contests over foods that are in high demand (Lambert 2002). Additionally, cheek pouches may reduce contest competition by allowing individuals (particularly low-ranking individuals) to store food, even if they are quickly displaced from feeding sites (Lambert 2005; Smith et al. 2008).

In species with low within-group contest competition, high rank may not confer an energetic advantage. Foerster et al. (2011) tested this hypothesis in the same population by measuring fecal glucocorticoids (fGCs), an indicator of

energetic stress (Sapolsky et al. 2000). Controlling for other factors that could influence fGC levels, they found a significant relationship between rank and fGCs in one of two groups studied. Many of the females in this group were lactating during a period of low fruit availability, suggesting that rank effects may appear only during periods when energetic demand is high and particularly when it is difficult to meet this demand. Indeed, among lactating females, fGC levels were always lower for higher ranked versus lower ranked individuals. Based on these earlier findings, we tested the interactions between rank and lactation stage (a proxy for energetic demand) and rank and time of year (a proxy for fruit availability) predicting that high rank would be particularly important during periods of energetic stress. These interactions, however, were not significant predictors of the probability of conception. Our results build on those from Foerster et al., suggesting that subtle rank-related differences in energetic stress do not translate into differences in the probability of conception. However, this conclusion should be confirmed by evaluating the relationship between direct measures of food availability and the probability of conception.

We focused on the reproductive effects of *within*-group contest competition; however, this mode of competition can interact with *between*-group competition to affect behavior. For example, if social cohesion increases the likelihood of winning between-group contests, selection may favor behavioral strategies (e.g., flexible feeding behavior) that increase tolerance among group members, allowing them to remain a cohesive team (Vehrencamp 1983; Sterck et al. 1997). The importance of group cohesion in the presence of strong between-group competition is supported in some primates whose between-group aggressive encounters are followed by a spike in within-group allogrooming (Perry 1996; Cords 2002b; but see di Sorrentino et al. 2012), a behavior that has been proposed to relieve stress and solidify cooperative relationships among allies (Cheney and Seyfarth 2009).

If increased social tolerance results in a relatively relaxed dominance hierarchy within the group, we may expect few or no rank effects on feeding behavior or reproduction, as we observed. Blue monkey groupmates jointly defend feeding territories (Cords 2002b, 2007), suggesting that group-wide cooperation is important to secure access to resources. The need to cooperate may provide an ultimate explanation for the lack of a rank effect on reproduction. However, the social consequences of strong between-group competition generally remain poorly understood (Schülke and Ostner 2012), and evidence for a link between success in between-group contests and social tolerance, facilitated by low levels of within-group contest competition, is required to substantiate this hypothesis.

Our results are consistent with an earlier report from our study population that rank did not affect the rate of producing offspring that survived to 1 year (Cords 2002b). Rank,

however, may affect other measures of reproduction, such as age at first reproduction, reproductive life-span, or infant survival. Indeed, across primate species and populations, rank effects on different components of reproductive success appear to vary in strength and prevalence, and recent reviews of rank and female reproduction do not agree on which components show the most consistent rank effects (Pusey 2012; Majolo et al. 2012). To some extent, this variation likely reflects which studies were included and the way in which comparisons were made. For example, in a recent meta-analysis, controlling for phylogeny affected the relationship between dominance rank and fecundity; a significant positive effect on rank on fecundity was evident only in the analysis in which phylogeny was not controlled (Majolo et al. 2012). These complex results highlight the value of additional high-quality data.

Group size and the probability of conception

We found that total group size had a significant quadratic relationship with the probability of conception, which peaked at a medium group size. Individuals in intermediate-sized groups are expected to have the highest fitness if they experience the maximal difference between the benefits of group living, such as predator avoidance and success in between-group contests, and its costs, such as within-group competition (Wrangham 1980; Van Schaik 1983; Sterck et al. 1997) and the "social time" commitment required to maintain a cohesive unit (Lehmann et al. 2006). In addition, when group size is regulated via group fission, as in all cercopithecine monkeys, it is likely that both the smallest and the largest groups in a population will exhibit suboptimal breeding success (Sterck et al. 1997). This pattern occurs because groups that have exceeded the optimal size may have to grow even larger to reach a point at which fission would produce new groups of a viable minimum size. These new groups—minimal but also not optimal in size—could then grow toward the optimum size. Thus, in a population at any one time, intermediate-sized groups should exhibit greater breeding success than those at the extremes of the size range.

Our models with total group size supported these predictions: while group size ranged from 7 to 70 individuals, the probability of conception was highest for groups with about 31 members. The humped relationship between group size and reproductive performance also occurs in other social mammals in which behavioral evidence suggests that intermediate group sizes are optimal (macaques, Takahata et al. 1998; baboons, Hill et al. 2000; ring-tailed lemurs, Takahata et al. 2006; lions, Vanderwaal et al. 2009).

A remaining question is why conception probability is lower in the smallest and largest groups. At low population density (i.e., in smaller groups), the positive relationship between population density and growth rates known as the

Allee effect may occur through several mechanisms (Courchamp et al. 1999). In social mammals, cooperation among group members may increase fitness if group living allows individuals to avoid predation, increase foraging success, or obtain assistance in caring for offspring (reviewed in König 1997; Krause and Ruxton 2002). Living in small groups may limit these density-dependent benefits. In our study population, we have noted previously that small group size can be disadvantageous when groups form through fission and divide up the original home range. In all five fissions we observed, the smaller daughter group ended up with a much smaller portion of the original territory (Cords 2012), which may have influenced the energetic balance, and hence conception probability, of females. A careful examination of diet quality in small and large groups would be needed to test this hypothesis.

In larger groups, enhanced feeding competition appears to affect many primates, which consequently invest in greater foraging effort, moving farther or increasing the time spent searching for food (Majolo et al. 2008). The guenons, however, do not appear to follow such patterns: group size shows no consistent relationship to daily travel distance or feeding time (Isbell 1991; Windfelder and Lwanga 2002; Cords 2012). In the study population, travel distance of individuals and entire groups was not correlated with group size, even when it differed by a factor of 2, and habitat differences were accounted for (Cords 2012). These findings suggest that individuals in larger groups have strategies to reduce within-group scramble competition. The same behavioral and morphological traits that reduce within-group contest competition, namely spreading out and feeding flexibly, may serve this purpose. Several studies of other guenons have reported that although there is no group size effect on daily travel distance, larger groups spread out over a wider area than smaller groups, thereby allowing individuals to feed without incurring additional energetic costs of travel (reviewed in Isbell 2012).

If larger group size does not stimulate greater foraging effort, why does it lower the probability of conception? One possibility is that females in larger groups have lower quality diets. This reduction in quality could be a consequence of readily switching from fruits to leaves; in other words, dietary flexibility, while reducing within-group competition in larger groups, may not entirely eliminate the competitive pressure of many individuals traveling together. Alternatively, reduced diet quality could result from more intensive use of the home range in larger groups. In a saturated population, groups may be unable to expand their home range as they grow, with the result that larger groups have a proportionately smaller resource base than smaller ones, and therefore must use less energy-rich foods (Dunbar 1987). Consistent with this hypothesis, Kakamega Forest supports a high density of blue monkeys and all forested areas in the vicinity of

our study groups are inhabited by other groups, potentially limiting opportunities for home range expansion. Again, a careful assessment of diet quality in groups of different size would be needed to test this idea.

Another possible explanation for the lower conception probability in larger groups is that time constrains an individual's ability to obtain and process the food required to meet its physiological needs (Dunbar 1992). If time is constrained, animals in larger groups might be unable to increase feeding time to compensate for the lower density of resources they experience without taking time away from other essential activities like socializing, territorial defense, or parenting (reviewed in Pollard and Blumstein 2008; Dunbar et al. 2009). This time constraint could thus place an upper limit on group size (Lehmann et al. 2006; Pollard and Blumstein 2008; Grove 2012). In our study population, group size appears not to affect individual activity budgets, suggesting that blue monkeys may face constraints that prevent them from increasing feeding time (Cords 2012). The large amount of time they spend resting (36–45 % depending on food availability and individual position in the hierarchy; Pazol and Cords 2005) may be deceptive, if resting time is necessary for thermoregulatory or digestive processes (Herbers 1981; Korstjens et al. 2010) or to conserve energy when processing low-quality food (Milton 1980).

A third possibility, in principle, is that individuals in larger groups experience more social stress, which suppresses reproduction (Wingfield and Sapolsky 2003). Rate of aggression is sometimes used as a proxy for social stress (Creel et al. 1996; Pride 2005) and some social vertebrates have higher rates of agonism in larger groups (Johnson 2004). In our study population, however, rates of agonism given, received, and both given plus received are not correlated with glucocorticoid levels (Foerster et al. 2011), suggesting that these rates are poor proxies for social stress in blue monkeys. A thorough examination would involve the comparison of physiological measures of stress across groups of different size, while carefully controlling for differences in energetic stress that may also correlate with group size.

When substituted for total group size, female group size was not a significant predictor of conception. The different effect of these two measures indicates that the presence of juveniles and males affects the costs and benefits of group living for adult females. The difference may occur because everyone, regardless of age/sex class, competes for food resources and so total group size reflects the overall strength of within-group scramble competition better than female group size. Overall, the difference emphasizes the importance of including all individuals when considering group size effects.

As with rank, group size might affect other measures of reproduction differently. A comparison of birth rate and infant survival before and after a group fission in our study

population revealed no group size effect on either reproductive parameter (Cords 2012). These results, however, were based on 4–6-year windows before and after each fission, which may not be long enough to document a group size effect in a species with 2–3-year interbirth intervals. More generally, studies have documented negative relationships between group size and fertility (e.g., voles, Boyce and Boyce 1988; macaques, van Noordwijk and van Schaik 1999) as well as positive relationships (e.g., horses, Pacheco and Herrera 1997; macaques, Suzuki et al. 1998), while still others found no relationship (e.g., macaques, Hsu et al. 2006; warthogs, White and Cameron 2011). Variable results have also been found for the effect of group size on infant survival (e.g., badgers, Woodroffe and MacDonald 1995; dolphins, Mann et al. 2000). Additionally, some studies that investigated the effect of group size on both fertility and infant survival have found that group size affects one reproductive parameter but not the other (hyenas, Watts and Holekamp 2009; snub-nosed monkeys, Zhao et al. 2011). These variable results may be caused in part by the fact that different studies sample the range of group sizes incompletely and reveal only one sector of an overall quadratic relationship. Discrepant group size effects on alternative measures of breeding success in a single population, however, are more likely to reflect the multiple ways in which group size contributes—either positively or negatively—to different parts of the reproductive process. For example, while enhanced energetic stress in larger groups may limit fertility in females, infant survival may be higher in such groups because of greater anti-predator protection.

Effects of control variables

Three control variables (time of year, lactation stage, time since last conception) and the interaction (lactation stage × time since last conception) had a predictably strong effect on the probability of conception. Over half of the conceptions occurred during July or August and including time of year in the model controlled for the marked reproductive seasonality in our subjects. Seasonal change in food availability is the most likely driver of seasonal reproduction in animals (Ims 1990; Brockman and van Schaik 2005). A study of fGC concentrations in female blue monkeys further suggested that there is a fitness advantage to reproduce at times of year when certain foods are available, as females experienced peaks in energetic stress when preferred foods were least available (Foerster et al. 2012).

Not surprisingly, the variables that tracked a female's reproductive status—lactation stage, time since last conception, and their interaction—had a strong effect on the probability of conception because they served as proxies for a female's energetic reserves. Females that were lactating or those whose last conceptions were relatively recent had a very low probability of conception. The probability of conception was a quadratic function of female age; a similar pattern of peak reproductive performance in prime-aged females also occurs in other mammals (e.g., goats, Côté and Festa-Bianchet 2001; primates, Pusey 2012). In our study population, the highest probability of conception occurred around 13 years of age. Lower fertility may affect young females because they are investing in both growth and reproduction and old females because of general body senescence (Pusey 2012).

Conclusion

These results indicate that the existence of a dominance hierarchy does not necessarily mean that high-ranking animals have a reproductive advantage. Rank may not predict success in feeding competition in species with flexible diets and foraging strategies. The behavioral and morphological adaptations allowing such flexibility may reduce the strength of within-group contest competition and could confer a fitness advantage if socially cohesive groups have greater success in between-group competition. More generally, behavioral options for mitigating within-group competition may be important in social species, even (and perhaps especially) in those with identifiable dominance hierarchies.

Total group size had a significant quadratic effect on the probability of conception, suggesting that groups of intermediate size are best able to maximize the benefits and minimize the costs of group living. Although behavioral evidence suggests that larger groups do not incur greater travel costs, diet quality or constraints on feeding time may explain the group size effect on the probability of conception. Although total group size was a significant predictor of the probability of conception, female group size was not, suggesting that the presence of juveniles and males affects the costs and benefits of living in a group. Finally, variables that tracked seasonality and a female's reproductive status were strong predictors of the probability of conception, emphasizing the importance of including these controls in analyses of reproduction.

Overall, we recommend that researchers not assume that behavioral proxies of within-group competition, such as linear dominance hierarchies or the lack of a group size effect on activity budget, have corresponding effects on reproduction (Koenig 2002; Koenig and Borries 2009). Rather, one should examine directly the relationship between rank or group size and reproduction to better understand whether and how animals experience within-group competition.

Ethical standards All research presented here was conducted in accordance with the laws of the Republic of Kenya.

Conflict of interest The authors declare that they have no conflict of interest.

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