Effects of Female Group Size on the Number of Males in Blue Monkey (*Cercopithecus mitis*) Groups

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Abstract

The number of males per group varies substantially in group-living primates, both between and within species. In blue monkeys (*Cercopithecus mitis*), males may temporarily join groups during annual mating seasons when sexually receptive females are present. A likely determinant of the number of males per group is female group size (the number of adult females in a group). To clarify the role of female group size in driving variation in the number of males per group, we expanded on earlier observations of a wild population in the Kakamega Forest, Kenya with a larger sample of groups that varied fivefold in female group size. We found considerable flexibility in social organization, with groups experiencing multimale episodes both during and outside mating seasons, some persisting over multiyear periods. The dichotomy between single- and multimale mating seasons was less distinct than previously reported, suggesting greater variation in multimale states. Across 65 group-specific conception periods, female group size strongly influenced how often multiple sexually active females and multiple males were present in a group. The number of sexually active females present on a given day related closely to the number of males in the group that same day, especially during conception periods. Results suggest that males join and remain in larger groups where mating opportunities are greater and costs of joining or staying may be lower than in smaller groups. This longitudinal study highlights intraspecific social variation within and across groups while confirming that female group size influences the number of males.

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Introduction

The number of males in a social group is a highly variable feature of primate social organization that influences mating systems, the exchange of social behavior, and the adaptive benefits of gregarious living for members of both sexes (Kappeler 2000, 2017). Early studies of social organization often focused on the distinction between single- vs. multimale groups in cross-species comparisons (Crook and Gartlan 1966; Eisenberg *et al.* 1972; Emlen and Oring 1977), but awareness of intraspecific variation has grown (Agnani *et al.* 2018; Díaz-Muñoz and Bales 2016; Silk and Kappeler 2017; Sterck and van Hooff 2000). Such variation can occur among populations, among groups within a population, and over time in a single group (Kappeler 2017).

Comparative cross-species analyses suggest that female group size (i.e., the number of adult females) is a major factor influencing the number of males per group (Altmann 1990; Carnes *et al.* 2011; Mitani *et al.* 1996; Nunn 1999), although there are exceptions (Robbins and Robbins 2018; van Schaik 1996). Female group size influences the number of sexually active females simultaneously present, the attractiveness of the group to males and thus male monopolization potential (Altmann 1962; Nunn 1999; Ridley 1986). Andelman (1986) concluded that primate groups with ≤5 females always included just 1 male, whereas those with ≥10 females included multiple males. Groups with an intermediate number of females included one or multiple males depending on ecological factors such as predation risk and habitat continuity, which affected group cohesion. These early findings that "males go where the females are" (Altmann 1990) have largely held true in primates (Kappeler and van Schaik 2002; Lindenfors *et al.* 2004; Mitani *et al.* 1996; Nunn 1999).

While cross-species comparisons are important for an evolutionary understanding of variation in male numbers, intraspecific comparisons offer insight into social flexibility and how it relates to environmental or demographic circumstances (Chapman and Rothman 2009; Robbins and Robbins 2018; Strier 2017). Several studies have demonstrated that intraspecific variation in the number of males per group also reflects variation in female group size (Pochron and Wright 2003; Srivastava and Dunbar 1996). The influence of sexually active females on male numbers is evident in temporary male influxes into groups that occur during the mating season in guenons (Cords 2002) and in other catarrhine monkeys (Hanuman langurs, *Semnopithecus entellus*: Borries 2000; bonnet macaques, *Macaca radiata*: Singh *et al.* 2006; Japanese macaques, *Macaca fuscata yakui*: Sprague 1991).

The nature of a causal link between male numbers and female sexual activity is not always clear. Socioecological models of primate societies, which focus on comparing species to explain the evolution of different social systems, assume the main determinants of the spatiotemporal distribution of females to be resource distribution and risk, which in turn affect male monopolization strategies (Nunn 1999). Phylogenetic analyses show changes in the number of females precede changes in the number of males in a group, thus also suggesting that female group size drives evolutionary changes in the number of males per group (Lindenfors *et al.* 2004). However, when there is variation in the number of males among groups of the same species or even over time in a single group, it can be challenging to determine whether female sexual activity attracts males to a group, or whether the presence of multiple males stimulates female sexual activity. In chimpanzees (*Pan troglodytes*), both mechanisms may act to maintain bisexual

parties: parties with more males attract cycling adult females, which in turn attract more adult and adolescent males (Matsumoto-Oda 1999). Furthermore, experimental studies provide physiological evidence related to both effects in nonprimate mammals: the presence of sexually receptive females stimulated testicular function, testosterone levels, and penile erection in male rodents (Folman and Drori 1969; Sachs *et al.* 1994; Vandenbergh 1977), whereas the introduction of males prompted estrus in female goats (*Capra aegagrus*: Rivas-Muñoz *et al.* 2007) and lordosis in female hamsters (*Mesocricetus auratus*: Lester and Gorzalka 1988). Reciprocal stimulation and attraction between the sexes may also occur in blue monkeys (*Cercopithecus mitis stuhlmanni*: Cords *et al.* 1986; Mugatha *et al.* 2007).

This study contributes to an understanding of how demographic factors, especially female group size, influence male numbers within a single species, focusing on blue monkeys, a group-living primate with dynamic male group membership. Blue monkey groups typically include a single resident male, but additional males sometimes join the group during mating season "influxes." These extragroup males temporarily transform the group into a multimale social unit with fluid male membership (Cords 2002).

Summarizing observations made over 18 yr and 5 groups in the Kakamega Forest, Kenya, Cords (2000, 2002) reported that, during influx mating seasons, multiple males were present in the group on 50–94% of days and the mean number of males present on a single day ranged from 1.6 to 3.8. How long individual males remained in a group was variable, ranging from days to weeks (Cords 2000, 2002). By contrast, during noninflux seasons, multiple males were present far less often (4–28% of days), and the mean number of males per day was lower (1–1.3; Cords 2000, 2002). Field observations in more recent years suggested there is even greater variation in male numbers than previously reported, with groups retaining multiple males well outside of the mating season and sometimes for periods exceeding a full year. For example, before the start of this study, Tw group (parent group to Twn group and Tws group in the current study), retained ≥2 males (mean: 4, maximum: 9 per day) for 3.8 yr (July 2, 2001–April 20, 2005) before it fissioned. Observations such as these motivated our reexamination of variation in male numbers and female receptivity in relation to female group size.

We used a 9-yr data set encompassing more groups with a greater range of sizes than previously reported (Cords 2002) to evaluate factors that influence variation in the number of males. First, we examined variation in male numbers across the data set as a whole to see if a clear dichotomy between influx and noninflux years (Cords 2002) was still evident. Second, we tested the hypotheses that larger groups were more likely to contain multiple males and more likely to contain multiple simultaneously sexually active females during periods when conceptions were most likely. Third, to assess the relationship between number of males and female sexual activity on a daily basis, we first identified the specific time frame in which these variables were most closely associated and then examined how the number of sexually active females predicted the number of males present each day, and whether this association was stronger for conception vs. nonconception periods. Finally, to clarify the direction of the causal arrow linking the number of males in a group with the number of sexually active females, we examined how changes in male number from one day to the next predicted individual females' switching from sexually inactive to active.

Methods

Subjects and Study Site

Data came from a long-term study of blue monkeys conducted at the Isecheno study site in the Kakamega Forest, western Kenya (0°14′11″ N, 34°52′02″ E, 1580 m elevation, *ca.* 2000 mm mean annual rainfall; Mitchell *et al.* 2009). This site comprises mainly old secondary and near-natural mixed plantation forest (Cords 2012) and supports a fairly dense population of these arboreal monkeys (*ca.* 111–192 individuals/km^2; Fashing *et al.* 2012). The study population has been monitored since 1979, but data analyzed here came from a 9-yr period (2006–2014) during which there were close observations of multiple study groups (4–6 groups observed at any one time, eight groups total over the entire period, which included two group fissions; Fig. 1 in Klass and Cords 2015). The study groups (named Gs, Gsa, Gsaa, Gsb, Gsc, Gn, Twn, Tws) occupied adjacent home ranges averaging 49 ± SD 15 ha (Roth and Cords 2016).

Data Collection

Female and Male Presence

As part of the long-term study, an experienced field team, able to identify individual group members based on natural physical characteristics, made near-daily observations of each group (mean ± SD ranged from 0.94 ± 1.02 h/day for the smallest, Gsb, group to 7.13 ± 1.62 h/day in the large Gs group). Each observer recorded which group members were present each day. Because females are philopatric, we assumed they were in the group even on a day when they were not observed as long as they reappeared in the group in subsequent days. These records allowed us to determine daily adult female group size. Adult females account for about a third of total group members, with juveniles and the adult male(s) representing the remainder.

For each day that a group was observed, we counted an adult male "present" if he interacted with a group member, or occupied an area <20 m outside the group's periphery, which we estimated as a line drawn around its other members (Cords *et al.* 1986). Adult males included in the study were full-grown nonnatal males. We did not count resident males from neighboring groups that sometimes appeared on the edge of a study group when their own group was nearby. The wide spatial dispersion of group members (especially in large groups, whose members could spread over several hundred meters) in a visually dense environment meant that observers may have overlooked adult males within groups. We assessed the likelihood of overlooking a resident male by assuming that resident males were present every day and then checking how often observers noted them as absent. Specifically, we examined tenures of 24 males that were the sole adult male in a group for an extended period (>6 mo), regardless of whether that period was preceded, followed, or interrupted by periods with additional males in the group. This procedure probably overestimated the chance of failing to detect a resident male that was present because 1) it assumed residents were present every day, even though observers occasionally witnessed them leave their groups for part of a day, and 2) many residents appeared to start or end their tenure with relatively many absences, in contrast to their near-daily presence mid-tenure, and

yet the analysis included all days in each tenure. Overall, residents were not detected on 5.0% of male-observation days ($N = 17,177$). Observers may have been more likely to miss influx males, whose presence in groups is more transient than that of residents, although group members often vocalized at influx males, attracting observer attention. Overall, these findings suggest that we may have slightly underestimated male numbers.

Female Sexual Activity

Blue monkey females do not exhibit cyclical morphological changes. Data on sexual activity came from records that were part of long-term monitoring. Specifically, observers prioritized conducting focal animal samples of adult females, but both during and between these samples, they noted all observed occurrences of sexual activity including copulation (mount-thrust with or without ejaculatory pause) and female proceptive behavior (lip-puckering, presenting hindquarters, and persistent following of a male). We counted any female >4 yr old (earliest age at birth: 4.6 yr) as "sexually active" if she engaged in any of the above behaviors or had semen on her vulva (indicating copulation). We also assigned her as sexually active on 1- or 2-day gaps (with no observed sexual activity or semen on vulva) between two copulations, and on 1-day gaps between a copulation and any form of proceptive behavior (Pazol 2003).

Data Analysis

Describing Influx and Noninflux Mating Seasons

We examined how well criteria that distinguished influx from noninflux mating seasons in prior analyses (such as proportion of days with multiple males and mean number of males per day; Cords 2002) applied to this dataset. To facilitate comparisons, we followed previous analyses in focusing on annual "mating seasons," the period from June 15 to October 31 when most mating occurs in the population as a whole (Cords 2002). Given that two group fissions occurred toward the end of the mating season (Gs on October 3, 2008; Gsa on October 11, 2009), we truncated the mating seasons for these two groups at the time they fissioned and did not include the remaining days in October as a mating season for the daughter groups.

Defining Group-Specific Conception Periods

Although births peak from January to March in the population (Cords and Chowdhury 2010) and correspond to a peak in mating 6 mo prior, there is variation among groups and years in the timing of conceptions and births. Our analyses of the relationships among female group size, female sexual activity, and male numbers therefore focused on group-specific conception periods. To specify the period when most conceptions occurred in each group, we began by determining the 29-day "conception window" for each infant born from 2006 to 2015. This window, 162–190 days before the birth date, represented the 95% confidence interval of the infant's conception date (Pazol *et al.* 2002), and we considered a female "conceptive" during this period. We then defined group conception periods as any period in which one or more females in the group were

conceptive, allowing gaps of up to 31 days. With this procedure, we identified one to two conception periods per group per year, or 65 group conception periods total.

Statistical Analysis

We ran statistical models in RStudio 1.3.959 (RStudio Team 2020). For each model, we verified that residuals were normally distributed using QQ plots; plots of fitted values vs. residuals showed no evidence of unequal variance, a lack of linearity, or outliers.

To test whether larger groups were more likely to contain multiple males and multiple sexually active females per day across group-specific conception periods, we used binomial-family generalized linear mixed models (GLMMs) with a logit-link function and group as a random effect. The predictor for these two models was mean daily female group size, and the dependent variables were the proportion of days per conception period when a group contained either multiple (≥ 2) males or multiple (≥ 2) sexually active females.

To analyze the relationship between female sexual activity and male numbers, we used data compiled on a daily basis. We began with a cross-correlation analysis (daily number of adult males and daily number of sexually active females, with all days during conception periods) to determine when the two variables were most strongly associated. Specifically, to explore whether there was a delay (lag) or an advance (lead) in the response variable (number of males) by 1 day or more, we asked if there was a significant cross-correlation between the time series of these two variables, and which of these correlations was strongest. Because it is biologically unlikely that extragroup males would respond to sexual activity after a long gap, we allowed lags and leads up to 14 days. For the most strongly correlated lag or lead, and additional lag/lead values up to 5 days on either side, we then ran individual Poisson-family linear mixed models (log-link function, group as random effect) to model how the number of females at a specific lag or lead value predicted the number of males (Liew 2004). We selected the best fit model, and thus the most appropriate lag or lead, by comparing Akaike information criterion (AIC) values.

The results of the cross-correlation analysis led us to model the daily number of adult males in a group as a function of the daily number of sexually active females on the same day (lag or lead of zero). We used a Poisson-family GLMM with a log-link function, group as a random effect, and included daily number of sexually active females and whether the day was part of a group conception period (yes/no) as predictors, along with their interaction. We ran this model using R package MASS 7.3-51.4 (Venables and Ripley 2002) with a Penalized Quasi-Likelihood algorithm (function glmmPQL). We accounted for the temporal nonindependence of consecutive daily records by including a continuous-time first-order autocorrelation structure (R package MASS, function corCAR1). This correlation structure also tolerated temporal gaps in the data, such as those resulting from occasional nonobservation days.

To assess whether an increase in the number of males in a group triggered individual females to become sexually active, we compiled a data set in which male numbers either increased, decreased, or stayed the same from one day (day X) to the next (day X + 1), and in which we knew individual female sexual activity status for the same 2 days. We excluded days when male numbers changed from 0 to 1 or from 1 to 0, as these

were likely cases when observers failed to detect a group's resident male. We included only those females that were not sexually active on day X. To increase the independence of data points, we thinned the data, ensuring that each group contributed data not more than once every 7 days (mean: 7.1 days, $N = 2398$ intervals between consecutive dates). We used mixed effects logistic regression to model whether females became sexually active (yes/no) from one day to the next as a function of whether male numbers increased, decreased, or stayed the same. We included conception period (yes/no) as a second fixed effect, and female identity and group date as random effects.

Ethical Note

All data collection was noninvasive. Research protocols complied with the legal requirements of Kenya, Columbia University's IACUC, and the IPS Code of Best Practices for Field Primatology. The authors declare that they have no conflict of interest.

Data Availability Our datasets are available on Dryad (https://doi.org/10.5061/dryad.kkwh70s31).

Results

Describing Variation in the Number of Males Across Groups

For all groups combined, 15% of all 16,719 group observation days (2006–2014) were multimale days, but there was considerable intergroup variation: the proportion of multimale days per group ranged from 0.003 (Gsb, $N = 1857$) to 0.332 (Tws, $N = 3269$; Table I). Some groups included multiple males (with few exceptions) for prolonged periods that extended beyond the mating season (Fig. 1). For example, Twn group's mean number of males was 2.6 (with a maximum of seven) over the 2006 calendar year (84% of 357 observation days with ≥2 males). Over a 2-yr period from 2006 to 2007, this group included multiple males on 72% of the 718 observation days.

Overall, 21% of the 47 group-mating seasons (mid-June to October) included multimale influxes and 64% were noninflux seasons, according to previously established nonoverlapping criteria (Cords 2002). However, 15% of the group-mating seasons showed an intermediate pattern in which the maximum number of males per day was 5, the mean number was 1.3 to 1.6 males per day, and the proportion of multimale days was 0.21 to 0.39 (Fig. 2).

Mating season influxes, whether intermediate cases or adhering to previously established criteria, did not occur in two of the smallest groups (Gsb, Gsc), whereas the largest group experienced influx or intermediate mating seasons every year (Tws, $N = 9$ seasons; Table I). Intermediate seasons occurred only in two of the largest groups (Gn, Tws). Across all groups, mean female group size correlated closely with how frequently influx mating seasons occurred (Table I; $r_{(df=5)} = 0.79$, 2-tailed $P = 0.035$).

Table I Summary statistics per group, ordered by female group size (mean daily number of adult females), including proportion of multimale days across entire observation period and during group conception periods, and proportion of mating seasons (June 15–October 31, except for one season each for Gs and Gsa; see text) that adhered to previously established criteria distinguishing influx from noninflux seasons

Group	Mean female group size	Total observation days	Proportion of multi-male days[b]	N of mating seasons	Proportion of influx[a] and intermediate mating seasons (the rest being noninflux)	Total group-specific conception period days[b]	Proportion of conception period days with multiple males
Tws	17.2	3269	0.332	9	1.00	1253	0.50
Gs	16.8	994	0.178	3	0.33	336	0.24
Gn	13.7	3266	0.124	9	0.44	1111	0.18
Gsaa	10.8	1878	0.086	5	0.20	767	0.16
Gsa	9.0	371	0.073	1	0	70	0.07
Gsc	8.4	1828	0.019	5	0	523	0.03
Twn	7.8	3256	0.197	9	0.22	667	0.12
Gsb	3.4	1857	0.003	6	0	196	0

[a] Following Cords (2002), mating seasons were classified as "influx" if multiple males were present on ≥50% of observation days, with a mean of ≥1.6 males per observation day.

[b] Tally of observation days that fell within group-specific conception periods.

Female Group Size, Multimale Days, and Female Sexual Synchrony Across Conception Periods

Across the 65 group conception periods, mean female group size predicted the proportion of multimale days (Fig. 3, GLMM, $\beta = 0.021$, 95% CI [0.007, 0.034], $P =$
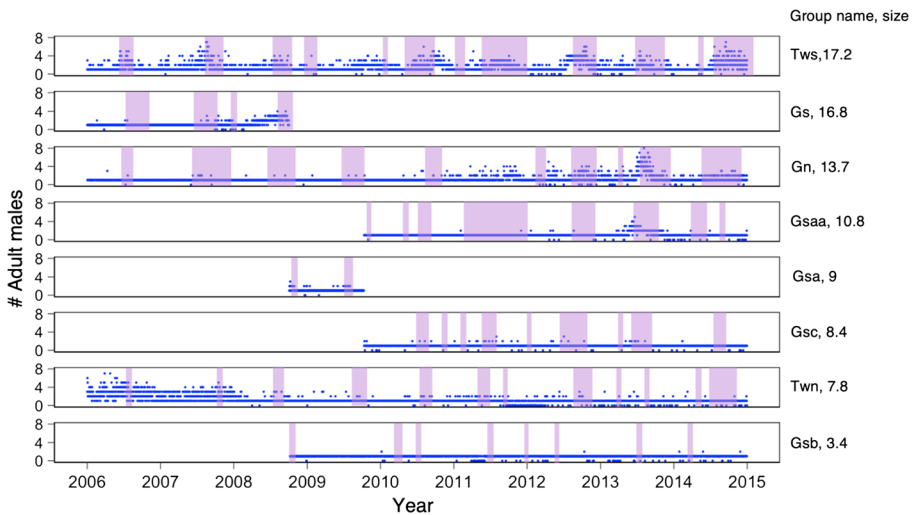

Fig. 1 Variation in the number of adult males in eight blue monkey groups in Kakamega Forest from 2006 to 2014, with group-specific conception periods (shaded blocks, pink) shown. Each horizontal panel represents one group, arranged from top to bottom by descending mean daily female group size (number of adult females, right margin). Each point represents the number of males on a given day, and each year label denotes January 1 of that year.
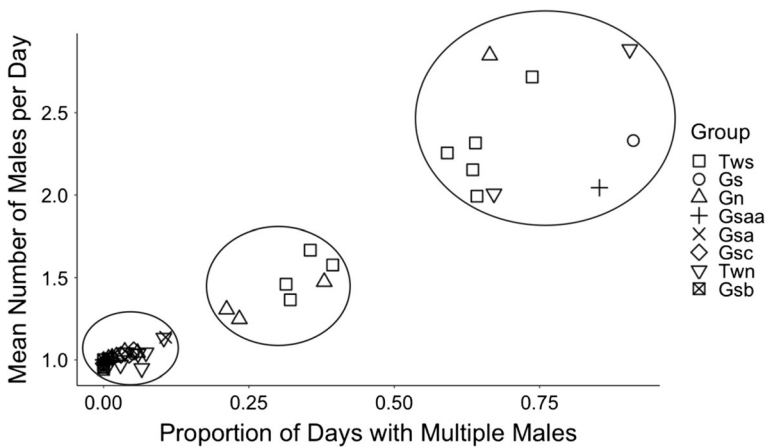
Fig. 2 Characteristics of influx mating seasons of Kakamega blue monkeys (2006–2014). Axes show the proportion of days with multiple males and mean number of males per day in mid-June to October group-mating seasons, as these features distinguished influx from noninflux seasons in previous research. Each point denotes one group in 1 yr ($N = 47$). In the legend, groups are listed according to decreasing female group size. We applied previously defined criteria (Cords 2002) to indicate periods that qualified as influx (upper right ellipse) or noninflux (lower left ellipse). Points in the middle ellipse were intermediate.

0.015). Compared to smaller groups, larger groups had more multimale days. Mean female group size also predicted the proportion of days in which ≥2 females were sexually active (Fig. 3, GLMM, $\beta = 0.010$, 95% CI [0.002, 0.018], $P = 0.017$): during conception periods, female sexual synchrony (i.e., temporal overlap) was more common in larger groups. The mean number of simultaneously sexually active females was $2.7 \pm$ SD 1.2 (range: 2–10, $N = 1017$) on days when there was more than 1 female.

Daily Male Numbers and Female Sexual Activity

The strongest correlation between the daily number of adult males and the daily number of sexually active females during conception periods occurred when there was no lag or lead in the days assessed (female lag or lead = 0, Table II), but relatively strong correlations (≥0.175) occurred for lags up to −8 (females counted
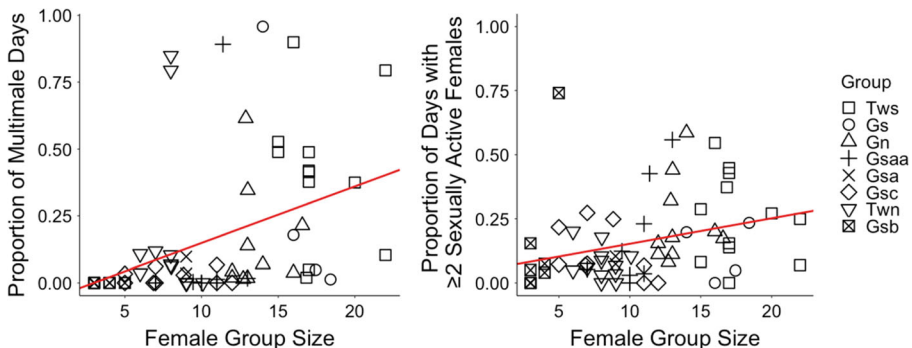

Fig. 3 Relationship of female group size and the proportion of multimale days (left) or the proportion of days with ≥2 sexually active females (right) across 65 group conception periods of Kakamega blue monkeys (2006–2014). Lines indicate slope and intercept from respective GLMMs.

Table II Cross-correlation function, and beta estimate (and 95% confidence interval), AIC, and ΔAIC values from linear mixed models in which the daily number of sexually active females per group, measured up to 8 days previously or 5 days later, predicted the daily number of males in a group during conception periods

Female lag (−) or lead (+)	Correlation	Estimate	95% CI	AIC	Δ AIC
−8	0.175	0.065	0.047–0.084	11,100.2	43.7
−7	0.175	0.065	0.046–0.084	11,100.3	43.8
−6	0.175	0.065	0.046–0.085	11,100.1	43.6
−5	0.179	0.067	0.047–0.086	11,098.2	41.7
−4	0.176	0.066	0.046–0.085	11,099.9	43.4
−3	0.167	0.061	0.042–0.080	11,105.6	49.1
−2	0.173	0.064	0.044–0.083	11,102.2	45.7
−1	0.187	0.070	0.051–0.089	11,093.0	36.5
0	**0.235**	**0.091**	**0.072–0.110**	**11,056.5**	**0**
1	0.190	0.072	0.052–0.090	11,091.4	34.9
2	0.163	0.059	0.040–0.079	11,107.9	51.4
3	0.177	0.066	0.046–0.085	11,099.7	43.2
4	0.170	0.062	0.043–0.082	11,103.9	47.4
5	0.157	0.057	0.037–0.076	11,111.1	54.6

All models included $N = 4339$ data points, and all were statistically significant ($P < 0.001$). AIC values show that a lag of zero was the best model of the data (bolded).

up to 8 days before males) and leads up to +3 (females counted up to 3 days after males). In regression models in which the number of sexually active females, with lags of −8 to leads of +5, predicted the number of males, the lag/lead of zero corresponded with the biggest regression coefficient and (by far) the lowest AIC (Table II). That is, the relationship between the daily number of sexually active females and the daily number of adult males appeared to be strongest when both were measured on the same day. Accordingly, we proceeded to use counts of males and sexually active females on the same day in analyzing the data across days.

In both conception and nonconception periods, the number of males in the group on a given day related positively to the number of sexually active females on that day (Fig. 4). This relationship was stronger for days that were part of conception periods compared with days that were not. In other words, there was a significant interaction between the type of day (part of conception period or not) and the number of sexually active females ($β = 0.146$, 95% CI [0.127,0.165], $P < 0.0001$). For approximately every 10 sexually active females, groups had one more adult male during conception periods than during nonconception periods.

Individual females were more likely to become sexually active from one day to the next when the number of males increased relative to when it stayed the same (odds ratio: 1.37, 95% CI [1.002,1.88], $P = 0.048$, $N = 32,242$). There was no evidence that a decrease in the number of males had a similar effect (odds ratio: 1.19, 95% CI [0.86,1.64], $P = 0.293$). As expected, the odds of becoming sexually active from one
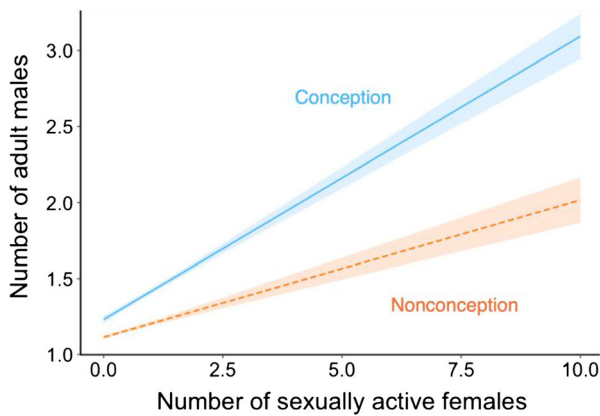
Fig. 4 Interaction plot showing the relationship between daily number of sexually active females and number of adult blue monkey males of Kakamega Forest from the 2006–2014 study period separated by conception and nonconception periods (N = 16,719 observation days). Shading shows 95% confidence intervals.

day to the next also increased during conception periods (odds ratio: 1.84, 95% CI [1.50,2.25], $P < 0.001$).

Discussion

Across eight study groups and 9 yr, we found substantial variation in the number of males present in blue monkey groups. Overall, our data show more variation in male numbers than previously reported for this population (Cords 2000, 2002). Specifically, some groups experienced predominantly multimale states for periods of one to almost 4 yr, which included periods outside the main population-wide mating season and group-specific conception periods. In addition, the dichotomy between single- and multimale mating seasons, in terms of mean number of males per day and proportion of days with multiple males, was less distinct than previously reported, suggesting greater continuity between primarily single- vs. multimale states.

Female group size had a strong effect on the number of adult males. During conception periods, groups with more adult females experienced more days with multiple males and more days with multiple sexually active females. The correlation between the daily number of males and sexually active females was strongest on the same day, though sexually active female numbers correlated significantly with male numbers with time lags and leads of up to 5 days. On a daily basis, the number of males in a group was positively associated with the number of sexually active females, but more strongly during conception periods than nonconception periods. Individual females were more likely to become sexually active from one day to the next if the number of males in their group increased.

Flexibility in Social Organization

The variable adult male numbers that we documented show that the nonoverlapping criteria that clearly differentiated influx from noninflux mating seasons in earlier reports (Cords 2000, 2002) are less distinct with additional data. Including the intermediate

values we observed as influx seasons, we would broaden the definition of an "influx" season to allow more variability in the proportion of mating season days with multiple males (0.25–0.94) and the mean number per day (1.3–3.8). Thus, influxes can vary more than previously documented in terms of the number of males involved. In addition, including such intermediate years as influxes increased the proportion of mating seasons characterized as influxes: whereas previous estimates suggested that 23% of annual mating seasons were characterized by influxes (Cords 2002), the present data including intermediate years substantially increase this figure to 36%. Most likely this higher estimate reflects the larger sample of groups included in this study, as well as the fact that some groups were larger than those previously studied.

On a broader level, these findings highlight intraspecific flexibility in primate social systems, with a nominally "one-male" species showing dynamic male membership and long periods—more than a year—when (large) groups contain multiple males. Group size is an important driver of this variation. We also emphasize the value of studying multiple groups over many years to discover and document intraspecific social flexibility, and to understand why it occurs (Chapman *et al.* 2017; Strier 2017).

Female Group Size Predicts the Number of Males and Sexually Active Females

Larger female groups should be more attractive to males because they offer more potential mates (Clutton-Brock 1989). Female group size also influences breeding synchrony, which in turn should affect the effectiveness of male mate guarding (Nunn 1999). In larger groups of blue monkeys, it was more likely for multiple females to be sexually active at once, and there was also considerably more variation in male numbers than in smaller groups, which were more consistently single male. The fact that nonresident males are more likely to sire an infant that is conceived when multiple females are conceptive (Roberts *et al.* 2014) provides an ultimate explanation for why larger groups are especially attractive to male intruders.

Extragroup males are also probably more successful in joining larger groups. Their greater group spread seems to make it easier for a male to sneak in without the resident male noticing (Overduin-de Vries *et al.* 2015), and to reproduce (Hayakawa and Soltis 2011; Roberts *et al.* 2014). If larger groups contain more males, there is also likely to be more male–male competition that disrupts effective mate guarding (Roberts *et al.* 2014). In addition, the presence of multiple males in large groups could create a collective action problem that makes it easier for additional males to join. That is, conflicting interests among the coresiding males in larger groups may increase each male's reluctance to repel extragroup males (van Schaik 1996).

The Number of Sexually Active Females Predicts the Number of Males

During group conception periods, the number of sexually active females each day was positively related to the number of males in blue monkey groups. This relationship also held true during non-conception periods, though the effect was smaller. Mating does occur during nonconception periods, but males may be less motivated to join a group if nonconceptive females are less sexually attractive. It is also possible that males are more active in seeking out opportunities to join groups when females are conceiving, and that they have the ability to distinguish sexually active females that are conceptive from those

that are not. Previous studies of the same population suggest that males can distinguish between sexually active females that are conceptive vs. nonconceptive (Roberts *et al.* 2014; Schembari and Cords 2019). Studies of chemical signaling could add to an understanding of female cues that influence the number of males in blue monkey groups.

Do Males Respond to Females or Vice Versa?

Although there was a clear association between the daily number of sexually active females and the daily number of males in a group, and the strongest relationship occurred when these variables were measured on the same day, there were relatively strong correlations with various lags and leads as well. The strongest correlations included a greater number of lags (number of sexually active females measured up to 8 days *before* number of males) than leads (up to 4 days after), which could be taken as evidence supporting the hypothesis that males generally respond to sexually active females by joining groups. At the same time, an increase in male numbers predicted individual females becoming sexually active concurrently, which is consistent with the view that females also respond to the arrival of new males. In supporting both effects, our results match previous reports that the number of sexually active females and the number of adult males influence each other (Epple and Katz 1980; Mugatha *et al.* 2007; Vandenbergh and Drickamer 1974). Additional experimental studies could help to demonstrate such effects and reveal their underlying physiological mechanisms.

Why Do Blue Monkey Males Join Groups of Females?

The fact that blue monkey groups attract additional males when females are sexually active supports the conclusion that males enter groups to mate, as their behavior also suggests (Cords 2002; Mugatha *et al.* 2007; Roberts *et al.* 2014). Yet some groups retained multiple males beyond periods in which females were conceptive. These results suggest that male blue monkeys may enter and remain in groups not only to mate, but for other reasons as well.

Males may join or remain in groups to gain a survival advantage that solitary living does not offer. Group living is often viewed as a mechanism to decrease predation risk (Isbell 1994; Shultz *et al.* 2004; van Schaik and Hörstermann 1994), and it is possible that blue monkey males—which do not form all-male bands—can find such protection only in heterosexual groups. However, it is not obvious that the protection offered by groupmates is an improvement on the exceedingly cryptic lifestyle that lone blue monkey males adopt (Struhsaker and Leakey 1990). Unfortunately, there are no direct data from the Kakamega Forest blue monkeys to assess male risk when alone vs. in a group. While some studies in similar forests indicated that adult males as a whole face greater predation risk than other age–sex classes, and attributed this elevated risk to the fact that adult males often live alone, other interpretations are possible (McGraw *et al.* 2006; Struhsaker and Leakey 1990).

Males might also join groups to assess and perhaps to begin to challenge the resident male, even outside of the mating season. In groups with coresiding males, agonism between the males is generally common, with resident males reacting aggressively to newcomers. However, some group takeovers are gradual: in such cases, the original resident male sometimes lingered on for up to 6 mo in an uneasy truce with a new male, with neither male clearly dominant to the other (e.g., Gsaa, May–November 2013; Tws,

September–December 2010). In other cases, a new male successfully challenged the resident but appeared to allow the resident to remain in the group in a clearly subordinate status before finally dropping out (e.g., Gn, September–November 2011). A former resident may be motivated to stay to protect the offspring he has sired from infanticide by the new male (Cords and Fuller 2010). We suspect that males' tolerance in these situations reflects their assessment of the risks of engaging in decisive aggressive encounters. The outcome of escalated contact aggression in the trees appears highly unpredictable (M. Cords, *pers. obs.*), which may lead males that have failed to intimidate opponents with less risky threats and chases to tolerate them for some time.

Male blue monkeys are unlikely to benefit in other ways from tolerating other males in their groups, as shown in other primates. For example, in geladas (*Theropithecus gelada*) and red-fronted lemurs (*Eulemur fulvus rufus*), dominant males appear to benefit from (and tolerate) the presence of subordinate males whose defense of the group against potential immigrants reduces the chance of a male takeover, lengthening the dominant's tenure in the group (Port *et al.* 2010; Snyder-Mackler *et al.* 2012). In contrast to these species, blue monkey males that join a single-male group are often present for only a short period (days, weeks, or a few months), and are usually treated as competitors by an established resident male or other intruding males. Furthermore, no aspect of their behavior suggests cooperation against a common enemy. In capuchins (*Sapajus* sp., formerly *Cebus apella*), males may sacrifice mating opportunities in exchange for antipredator activities of other males (van Schaik and van Noordwijk 1989), and relative male group size predicts success in intergroup contests (Scarry 2013). In blue monkeys, however, males are seldom involved in intergroup contests (Cords 2007), and their predator-related loud calls usually *follow* vocalizations and flight responses by other group members, so their role in early warning of groupmates is ambiguous (Cords 1987).

Another possible explanation for males joining or staying in heterosexual groups outside the mating season is that they are simply motivated to be socially integrated with females: after all, they grow up in heterosexual groups but, after natal emigration, spend much of their time away from females and do not form all-male bands. They may take advantage of situations in which a more powerful resident male does not detect them—especially in larger groups—and at times when their presence is less of a reproductive threat to an established resident outside the mating season. Such an explanation has been offered for cases in which a male crowned guenon (*Cercopithecus pogonias*) traveled with black colobus monkeys (*Colobus satanas*: Fleury and Gautier-Hion 1997). Consistent with this hypothesis, all males in blue monkey groups may groom and associate with females, both in mating and nonmating seasons.

Overall, we suspect that male blue monkeys join or remain in female groups for multiple reasons, although access to mates is surely among the most important. Female group size influences the numbers of males per group both because joining groups with many females is advantageous in terms of increasing mating opportunities, but also perhaps because the costs of joining or staying are lower in larger groups.

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