Original Article

Factors affecting low resident male siring success in one-male groups of blue monkeys

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In species that live in one-male/multi-female groups, resident males have more access to females than do bachelor males and should have a within-group reproductive advantage. We used a genetic analysis of 13 microsatellite loci to assign paternity to 111 offspring born over 10 years in 8 groups of wild blue monkeys. Resident males sired a maximum of 61% of the offspring conceived in their groups, indicating that despite their greater access to females, residents lost a substantial number of offspring to outsiders. A resident was less likely to sire an offspring when multiple females were in estrus, suggesting that it is difficult to monitor many fertile females simultaneously. Moreover, multiple estrous females likely attract competitor males, whose presence also decreased the probability that a resident sired an offspring. The negative effect of intruders on resident siring success may occur because females prefer competitors or because an increase in the number of intruders increases the challenge of effective mate guarding by a resident, leading him to miss rare mating opportunities. Tenure length did not affect resident siring success. Identifying the factors affecting patterns of paternity within species will help us to better understand the considerable variation in resident male siring success that occurs in one-male groups.

Key words: alternative mating tactics, male–male competition, paternity, reproductive synchrony, resident tenure.

INTRODUCTION

Understanding the diversity in animal social organization and mating systems has been a focus of evolutionary biology for decades. Despite an obvious connection between social organization (i.e., group composition) and mating system (i.e., who mates with whom), there can be considerable variation in the degree of male reproductive skew among species and populations with the same social organization (Schulke and Ostner 2012; Kappeler et al. 2013). Identifying the extent of variation in reproduction is important for understanding the evolution of grouping patterns and reproductive strategies. Furthermore, identifying populations that deviate from predicted patterns provides opportunities to generate new hypotheses about the factors influencing male reproduction.

In mammals, sex differences in reproductive investment mean that female reproduction is primarily limited by access to food and male reproduction is limited by access to mates (Trivers 1972; Clutton-Brock 1989). Operational sex ratios are thus skewed toward males, who face high competition for reproductive opportunities and high variation in reproductive success (Clutton-Brock and Parker 1992; Kvarnemo and Ahnesjo 1996). Variation among males may be particularly pronounced in species that live in one-male groups, in which 1 resident male is consistently associated with a group of females, whereas nonresident males (i.e., bachelors) live outside heterosexual groups. Increased proximity to females should give resident males a reproductive advantage (Emlen and Oring 1977; Clutton-Brock 2009) although bachelors may have opportunities to mate and sire offspring by sneaking copulations during temporary intrusions (Wolff 2009). Studies of mammals that live in one-male groups (hereafter, one-male species) generally support this prediction, as residents had higher within-group mating and paternity success than bachelors (Hanuman langur: Sommer and Rajpiyohit 1989; red deer: Pemberton et al. 1992; greater sac-winged bat: Heckel and von Heverens 2002; samango monkey: MacLeod et al. 2002; southern elephant seal: Fabiani et al. 2004; hamadryas baboon: Swedell and Saunders 2006; Przewalski’s horse: Feh and Munkhtuya 2008; ring tailed coati: Hirsch and Maldonado 2011). In some cases, residents monopolized paternity completely, suggesting that males who spent their entire reproductive careers as bachelors did not reproduce (yellow-bellied marmot: Schwartz and Armitage 1980;
red howler monkey: Pope 1990; Hanuman langur: Launhardt et al. 2001.

Altman’s (1962) priority-of-access model (POA) was one of the first to identify factors affecting male mating success in mammals that live in multi-male groups. The model predicts that when only 1 female is in estrus at a time, the alpha male will monopolize group reproduction. When multiple females are estrous simultaneously, the alpha male will be unable to mate-guard all of them and subordinate males will have opportunities to mate and reproduce. Several studies of multi-male species (especially primates) have documented a relationship between female reproductive synchrony and the distribution of male mating or paternity success as predicted by POA (domestic cat: Say et al. 2001; reviews of primates: Ostner et al. 2008; Gogarten and Koenig 2012). Although no study has related variation in synchrony to reproduction in one-male species, the same principles should apply when resident males do not completely monopolize mating, with residents and bachelors taking the place of alpha and subordinate males, respectively.

The presence of other males should also limit the ability of 1 male to monopolize paternity by increasing competition for females. Several studies of multi-male groups support this prediction, in that annual mating and paternity concentration for high-ranking males decreased in groups with more males (alpine marmot: Cohas et al. 2006; Lardy et al. 2012; primates: Alberts 2012; Gogarten and Koenig 2012). One-male species may function similarly, with the presence of more intruding males increasing the probability that a resident will lose paternity to others. The effect of the number of competitors has been rarely studied in one-male species, likely because, by definition, competitors are not as consistently present as in multi-male species. The available evidence, however, suggests that having more males present (because of multi-male influxes or colony-living) decreases resident mating or paternity success (e.g., patas monkey: Ohsawa et al. 1993; Chism and Rogers 1997; Carlson and Isbell 2001; greater sac-winged bat: Nagy et al. 2012).

There is some evidence that female primates prefer to mate with novel males, which may also affect resident male siring success (Inoue and Takenaka 2008; Weingrill et al. 2011; but see Manson 1995; Charpentier et al. 2005). For animals that live in stable social groups, length of resident male tenure at the time of conception reflects social, and possibly sexual, novelty; if females prefer novel males, they should reproduce more with a new male than one who has been present for multiple years.

We tested the effect of the above factors on resident male paternity success in blue monkeys (Cercopithecus mitis stuhlmanni), an Old World monkey that typically lives in one-male groups. In this and closely related species, resident males do not have a complete social or sexual monopoly over females (Cords 2000). Competitor males are occasionally present in and on the edge of the group during all mating seasons, but competition peaks during multi-male influxes when multiple bachelor males join the group for varying periods, increasing the average number of males present per day (Cords 2002). Such influxes occurred in about 25% of mating seasons at our study site, and more often during seasons in which many females were mating simultaneously, suggesting that a resident male’s ability to exclude competitors breaks down when many of his females are estrous (Cords 2002). During both influx and non-influx years, competitors mate with females and likely sire offspring (Pazol 2003; Hatcher 2006). Although the modal social organization in blue monkeys is the one-male group, variation in the number of reproduction opportunities and the strength of competition could have important effects on male reproductive output.

We tested the hypothesis that a resident’s chance of siring an infant in his group depends on his ability to monopolize conception females and on female choice for novel males. Specifically we predicted that a resident would be less likely to sire an infant when female reproductive synchrony was higher, more competitor males were present, and the resident had been in the group for a longer time.

**METHODS**

**Study site and population**

The Kakamega Forest, Kenya (0°19′N, 34°52′E; Elev. 1580 m), a semideciduous rainforest, supports a dense population of blue monkeys (Fashing et al. 2011). Mitchell et al. (2009) and Cords (2012) provide detailed descriptions of the forest ecosystem and study site, respectively.

Like other guenons (Butynski 1988), Kakamega blue monkeys reproduce seasonally, with 64% of births occurring between January and March (Cords and Chowdhury 2010). We derived demographic data from long-term population monitoring that began in 1979 (Cords 2012). During the 10-year period of this report (2002-2011), the study population expanded via group fission from 3 to 6 groups (Cords 2012). Group members were habituated and distinctive in body and facial features, allowing individual recognition. Near daily monitoring allowed the field team to determine infant birthdates, presence of extra-group males and estrous females, and dates of resident male turnover with high precision.

**Genetic data**

**Fecal sample collection**

We used fecal samples from 126 infants conceived in 8 study groups (Supplementary Table S1) and 60 adult males in the genetic analysis. Samples from 64 mothers (1.80±0.97 offspring per mother, range 1–4, N = 70 mothers including 6 female offspring that conceived during the study period) were collected and genotyped in earlier work (Nikitopoulos et al. unpublished).

Some infants born during the study period were not included in the genetic analysis because they died before we could collect a sample (N = 70) or we failed to obtain a usable sample (N = 10). The rate of infant mortality during our study (34%) is similar to that found in other populations of wild primates (Debyser 1995; Cords and Chowdhury 2010). Infant deaths could seldom be attributed directly to a particular cause, but we considered whether probable sources of infant mortality, inferred from circumstantial evidence, were likely to affect differentially the offspring of different males. Such bias seemed unlikely for most (≥71%) of the infants that died prior to sampling: These included healthy infants that disappeared abruptly from stable groups, most likely victims of predation (N = 30), those for whom predation was either observed or suggested by our finding remains (N = 4), those that disappeared after being seriously wounded in stable groups (perhaps from predation attempts or possibly after within-group aggression; N = 7), those that disappeared with their mother (likely predation or secondary consequences thereof, N = 5), those with obviously careless mothers (N = 3), and one that died after an unusually intense hailstorm. Other causes of death are more plausibly related to sire identity, including infanticide (observed or inferred when a new resident attacked mothers and infants in the days before infant disappearance, 16%), perinatal death (7%), and infant weakness in the 2 weeks after birth (6%). Although we are unable to verify the extent

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of any such bias, the majority of infant deaths were unlikely to be linked to the identity of the sire and so we proceeded under the assumption that the inclusion of these samples would not change our results. Additionally, only surviving infants contribute to reproductive success, so any bias toward or against certain males does not affect our conclusions about overall patterns of male reproduction.

DNA derived from fecal samples is often present in low concentration. When possible, we collected 3 samples per individual to ensure an adequate quantity. We collected samples in sterile tubes, mixing fecal matter with RINAlater™ (Ambion) in a 1:1 ratio to preserve the DNA. Samples remained at ambient temperature in the field, at 4 °C in the laboratory before DNA extraction, and at −20 °C thereafter.

**DNA extraction and genotyping**

We extracted DNA using the QIamp® DNA Stool Mini Kit (Qiagen) following the manufacturer’s protocol with modifications at 5 stages: step (2) overnight in ASL buffer, step (6) centrifuged for 6 min, step (8) 35 μL of Proteinase K, step (11) incubated for 30 min, and step (18) 75 μL AE buffer and incubated for 15 min. We amplified the DNA at 14 human MapPairs® microsatellite markers (Invitrogen) using the Qiagen® Multiplex PCR Kit (Supplementary Table S2). Reaction conditions for all primer pairs were initial denaturation at 94 °C for 15 min, 37 cycles of denaturation at 94 °C for 30 s, annealing at 53 °C for 1 min 30 s, and extension at 72 °C for 1 min, then a final extension at 60 °C for 30 min. For genotyping, we used the ABI 3730 Automated DNA Analysis system and GeneMapper 3.7 (Applied Biosystems).

To protect against false homozygosity from allelic dropout, we replicated all homozygous loci 7 times according to guidelines for attaining 99% statistical confidence in genotyping (Taberlet et al. 1996). We ran heterozygotes with weak signals at least twice. We checked each offspring genotype against its mother’s genotype to ensure that they shared 1 allele at each locus. Sixteen of the 60 adult males were born in the study groups, and we checked their genotypes against their mothers. We could not check genotypes of the remaining 44 adult males born outside our study groups against known relatives, so when possible, we replicated genotyping using independently collected fecal samples (N = 34 males). Replicate genotypes matched in all cases.

An allele frequency test indicated that 1 locus—17s1290—was not in Hardy–Weinberg equilibrium. Deviation from equilibrium may indicate the presence of marker-specific genotyping errors, so we excluded this locus from further analysis (Chen 2010).

**Paternity assignment**

We conducted likelihood-based paternity analysis with CERVUS 3.0 (Kalinowski et al. 2007). CERVUS assigns paternity by calculating the difference in log-likelihood values for the top 2 candidate fathers, comparing it to a distribution of simulated values (Marshall et al. 1998). If the difference is large enough, the most likely male will be assigned paternity. Per convention, we ran paternity simulations based on 10,000 offspring and set confidence levels at 80% and 95%. CERVUS calculated the rate of mistyping for each locus, which equaled the number of known mother–offspring mismatches divided by the total number of mother–offspring dyads compared at that locus. We set the rate of mistyping at 2%, which was the mean value for the 13 loci.

We included maternal genotypes in the analysis. Candidate fathers (48.3 ± 9.5 per offspring) included all males who had emigrated from their natal groups by the time of offspring conception. Natal males emigrate during adolescence (Ekernas and Cords 2007); those residing in their natal groups have never been observed to copulate, so it is unlikely that they sired offspring before emigration. Emigration dates were known only for males born in study groups, so males born elsewhere were included as candidate fathers for each offspring, regardless of the year conceived.

CERVUS allows users to manipulate the proportion of males in the population that were sampled. We used the number of males observed in the study population to calculate the proportion of males sampled annually. Because there was large variation in this parameter across years, we tested several values to assess the robustness of the paternity results (see Supplementary Document S3). We ran CERVUS 10 times to test values that spanned the observed range (Supplementary Table S3) and found slight variation in the confidence with which CERVUS assigned paternity across the 10 runs. For 86 out of the 108 (80%) offspring with paternity assignments, CERVUS assigned the sire with 95% confidence in all runs. For the remaining offspring, the sire was assigned with 80% confidence in runs in which the proportion of males sampled was low and 95% confidence when the value was high. Despite this slight variation in confidence, the program assigned the same sire to each offspring in all 10 runs and most of the offspring assigned with 80% confidence in some runs mismatched the assigned sire at zero loci, so we considered the assignments to be robust.

We used a combination of CERVUS assignments and exclusion methods to determine if the resident was the sire of each offspring. We examined mismatches between the offspring and resident and the offspring and assigned sire (if different). To protect against false exclusion resulting from allelic dropout, we counted only pair mismatches and only if both individuals were heterozygous at that locus. Our calculation of the number of mismatches was thus extremely conservative to avoid false exclusion of the resident as the father of an offspring.

Known mother–offspring pairs mismatched rarely and never at more than 1 locus. Similarly, when the resident was assigned as sire (N = 60 offspring), he mismatched at 0 or 1 locus only, and we concluded that the resident was the sire of these offspring. Most offspring assigned to another male (23 of 36) mismatched the resident at 2 or more loci and had only 0 or 1 mismatch with their assigned sire. The remaining offspring assigned to another male (11 of 36) had 0 or 1 mismatch with the resident, and all had the same number or fewer mismatches with their assigned sire than with the resident. Given our conservative method of assessing the number of mismatches and the consistent assignments using maximum-likelihood methods, we prioritized the CERVUS assignment and concluded that the resident was not the sire of these 36 offspring.

In some cases, CERVUS did not assign any male as the sire of an offspring (N = 18) or the assigned sire mismatched the offspring at 2 or more loci and was therefore excluded as the true sire (N = 4). If the resident and offspring mismatched at 2 or more loci (7 of 22), we concluded that the resident was not the sire. If the pair mismatched at 0 or 1 locus (15 of 22), we could not conclusively assign or exclude the resident as the sire and so we omitted the offspring from the analysis.

Our method of assessing the number of mismatches increased the chance that we would be unable to conclusively exclude the resident as sire. To investigate the impact of these conservative criteria, we computed the number of mismatches between an offspring and resident and offspring and sire in an alternative way, including mismatches that occurred when either individual was homozygous. These more relaxed criteria increased the likelihood
of finding mismatches and affected our classification of some offspring. Specifically 1) 2 offspring assigned to the resident mismatched at 2 loci (instead of 0 or 1) and the resident was excluded as the sire, and 2) 10 offspring that were not assigned to any male mismatched the resident at 2 or more loci (instead of 0 or 1) and the resident was excluded as the sire.

Demographic data

We used data from long-term population monitoring to measure the 3 variables that were the focus of our analysis of resident male paternity: Female reproductive synchrony, number of competitor males, and resident’s tenure length when an offspring was conceived. We used gestation length and observations of estrous behavior to identify a “conceptive estrus period” during which each estrus was conceived. We first identified a conception window by subtracting the length of 1 gestation (mean ± 95% CI = 176 ± 14 days; Pazol et al. 2002) from offspring birthdates, thus specifying a 29-day window in which conception almost certainly occurred. Of the 111 offspring for which we could assign or exclude the resident as the sire, 75% had birthdates known to the day, while for the remaining 25% of offspring, birthdates were assigned as the midpoint of a known range (mean ± SD = 3.1 ± 5.0, range = 2–17 days).

We then used behavioral data to identify an estrus period within the 29-day conception window. Following Pazol (2003), we scored a female as estrous on a given day if she copulated (including non-ejaculatory mounts with thrusting) or had semen on her genitals (i.e., indirect evidence of copulating). Given the difficulty of observing infrequent copulations in a forested habitat, we allowed up to 2 days without such behavior to count as part of the estrus period, as long as a copulation or semen on genitals occurred immediately before and after the gap. We also allowed days with only copulatory behavior (i.e., lip-puckering, presenting hindquarters, and persistent following) to extend or connect these estrus days if they occurred within 2 days of a copulation or semen on genitals. If there were multiple estrus periods within the 29-day conception window (N = 34), we selected the period closest to the middle of the window. We assigned conception to a resident period to 86 of the 111 offspring for which we could conclusively assign or exclude the resident as the sire. The mean length of the conceptive estrus periods was 4.19 ± 4.49 days (range = 1–22, N = 86). Estrous behavior was not observed for mothers of the remaining 25 offspring, and they were excluded from the analysis.

We calculated all predictor variables using the conceptive estrus period as the time base. During observations of study groups, field assistants recorded the presence and identity of extra-group males. The number of competitors equaled the average number of males (including the resident) seen in the group per day during a female’s conceptive estrus period (mean ± SD = 2.34 ± 2.17, range = 0.91–9.29, N = 86). Length of resident tenure at offspring conception was the number of mating seasons a resident had been present in his group (mean ± SD = 2.55 ± 1.66, range = 1–7 mating seasons, N = 86).

We overlaid conceptive estrus periods for females in each group to determine the number of females in conceptive estrus present on any day. We included all conceptive estrus periods that resulted in birth (live or stillbirth), even if we did not have genetic data from offspring conceived. We could not reliably identify conceptions that ended in miscarriage so were limited to conceptions that resulted in birth. Overlaying the conceptive estrus periods allowed us to express female reproductive synchrony as the average number of females in conceptive estrus that were present per day during a given female’s conceptive estrus period (mean ± SD = 1.29 ± 0.52 females per day, range = 1–3, N = 86).

Blue monkeys lack visual indicators of ovulation and are known to mate when they are unable to conceive (Pazol 2003), so we also calculated female reproductive synchrony during a given female’s conceptive estrus period as the average number of estrous females per day; regardless of whether other females’ estrus was conceptive (mean ± SD = 1.75 ± 0.76 females per day, range = 1–4, N = 86). If males use mating as an indicator of female fertility (i.e., ovulation), an increase in the number of estrous females should decrease resident siring success, whether estrus is conceptive or not.

Statistical analysis

To test whether the probability that a resident sired an offspring conceived in his group related to various predictor variables, we used R Project Software version 2.15.0 (R-Development-Core-Team 2012) to conduct a mixed-effects logistic regression (lme4 package, Bates and Maechler 2009). We used maximum-likelihood estimation, a binomial error structure, and the logit link function. Each offspring was a single data point and the dependent variable was whether the resident sired that offspring. We included female synchrony, number of competitors, and resident tenure length as fixed effects. Each resident and female appeared with different frequencies in the data set, so we included both as random effects. Female identity did not contribute to variance in the dependent variable, and we removed it from the final model.

Before fitting the models, we standardized all 3 fixed effects to improve model convergence and to allow us to compare the relative importance of the predictors (Gelman 2008). We present parameter estimates and standard errors from the full models because they 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 (Type I error) (Mundry and Nunn 2009). We tested interactions between each pair of fixed effects, but none were significant (P > 0.05), so we removed them to allow interpretation of main effects (Engqvist 2003).

Multicollinearity was low for all predictors (variance inflation factors ranged from 1.02 to 1.21 for all models). To determine whether the whole set of variables influenced resident male siring success, we conducted a log-likelihood ratio test to compare the full models to the models containing the random effect only.

We carried out follow-up analyses to see how the variables that influenced resident paternity were related to group size. We calculated the average number of females, females in conceptive estrus, females in conceptive or nonconceptive estrus, and males present per day during each mating season (June 1–October 31) for each group. We used generalized linear mixed models (GLMMs) with maximum-likelihood estimation to relate the average number of adult (parous) females in the group in a given mating season to the average number of estrous females and to the average number of males. We included group identity as a random effect.

RESULTS

Paternity assignment and exclusion

Altogether, we genotyped 126 offspring at a mean of 12.1 ± 1.6 loci. The 63 adult males (including 5 male offspring that emigrated during the study period and returned later as adults) were genotyped
at a mean of $11.9 \pm 1.8$ loci. The 70 mothers (including 6 female offspring that conceived during the study period) were genotyped at a mean of $12.8 \pm 0.45$ loci.

Of 126 genotyped offspring, 68 were assigned to the resident male in their group and 36 were assigned to another male. Seven offspring were unassigned, but the resident was excluded as the sire. In sum, we were able conclusively to assign or exclude the resident as the father of 111 offspring, 61% sired by the resident and 39% not sired by the resident. Our conservative exclusion methods make it very unlikely that we would falsely exclude the resident as the sire of an offspring, so we view 61% as a maximum percentage sired by the resident and 39% as the minimum sired by outside males. We used this set of paternity assignments/exclusions for analyses quantifying variation in resident siring success and identifying factors affecting resident siring success.

Counting heterozygous and homozygous mismatches made it more likely that the resident would be excluded as the sire of an offspring. Of the 126 genotyped offspring, 68 were assigned to the resident, but 2 were excluded as the offspring of the resident because the pair mismatched at 2 loci. Thirty-six offspring were assigned to another male, and 17 were unassigned but the resident was excluded as the sire. Using these more liberal exclusion criteria, we assigned or excluded the resident as the sire of 121 offspring, 55% sired by the resident and 45% sired by outside males.

Variation in resident male siring success

There were 11 resident males in the study groups over the 10-year study period, with some periods of residency continuing after our study ended. On average, a resident sired 38% ± 34% of the offspring conceived in his group during our observations, but there was high variation in siring success among residents (range = 0–100%; Figure 1).

Factors affecting resident male siring success

The models using the different measures of female synchrony generated different results. The full logistic regression model including number of females in concepive estrus, number of competitors, and resident tenure as fixed effects, and resident identity as a random effect, differed significantly from the null model including only the random effect (log-likelihood ratio test: $\chi^2 = 10.772$, df = 3, $P = 0.013$). In contrast, the full model that measured female synchrony as the number of females in conceptive or nonconceptive estrus was not significantly better at predicting the probability of resident siring success than the null model (log-likelihood ratio test: $\chi^2 = 6.245$, df = 3, $P = 0.1001$).

When we measured female synchrony as the number of females in conceptive estrus, both synchrony and the number of competitors had a significant negative effect on the probability that a resident sired an offspring with the number of competitors having a slightly stronger effect (female synchrony: $1/\text{odds ratio} = 2.366$, number of competitors: $1/\text{odds ratio} = 4.092$; Table 1A). Each additional female in concepive estrus decreased the odds that the resident sired an offspring by 54% (Figure 2), and each additional competitor decreased the odds that the resident sired an offspring by 76% (Figure 3). Tenure length did not have a significant effect on the likelihood that the resident sired the offspring.

One resident, RO, sired none of the 19 offspring conceived in his group (of which 18 were included in the model) despite mating during most concepive windows. We removed the offspring sired during this outlier male’s residency and reran the analysis to test the robustness of our results. In the reduced model that included female synchrony based on concepive estrus only, we found that effects of all 3 predictors were qualitatively similar to the original model (Table 1B).

The effect of group size

Female group size was a significant positive predictor of the average number of females in concepive estrus per day (GLMM: $\beta \pm \text{SE} = 0.011 \pm 0.003$, $z = 3.22$, $P = 0.001$; Supplementary Table S4 and Supplementary Figure S4) and the average number of females in concepive or nonconceptive estrus per day (GLMM: $\beta \pm \text{SE} = 0.020 \pm 0.009$, $z = 2.19$, $P = 0.029$; Supplementary Table S5 and Supplementary Figure S5) across 34 group mating seasons. Female group size was also a significant positive predictor of the average number of males present during a mating season (GLMM: $\beta \pm \text{SE} = 0.109 \pm 0.047$, $z = 2.30$, $P = 0.021$; Supplementary Table S6 and Supplementary Figure S6).

DISCUSSION

Resident siring success in one-male groups of mammals

There are relatively few studies of one-male mammals that evaluated whether the resident male present at conception was the father of the offspring, probably because these studies require monitoring during both the mating season (to identify residents) and the following birth season (to collect samples from offspring). We identified studies of 15 populations of mammals that measured resident siring success in this way and found considerable variation across studies in the percentage of offspring sired by the resident male in the group (range: 30–100%, Table 2, though note slight differences in measurements). In our study, the resident sired a maximum of 61% of offspring and when we used more liberal exclusion criteria, we found that the resident sired a smaller percentage (55%) of the offspring conceived in his group. Either way, blue monkeys fell toward the low end of the range for one-male species.

Drivers of this variation are difficult to identify, but we examined the effect of group size. Notably, of the 8 populations with high (>80%) resident siring success, most and possibly all live in small groups (i.e., fewer than 5 females; Table 2), which may have
enabled residents to monopolize reproductive opportunities more easily. Further emphasizing the importance of group size to resident paternity success, in the Misaki feral horse population, the number of offspring sired by the resident male leveled off when harem size reached 6 females, suggesting a decrease in the resident's ability to guard more than 5 females simultaneously (Kaseda and Khalil 1996). However, 2 populations (white-lined bats, feral horses) with low resident siring success (<80%) also live in small groups, so female group size is not sufficient to explain variation among populations.

Contact with extra-group males may also explain some of the variation. In species that experience multi-male influxes or in which one-male groups join to form colonies or larger troops, residents may be more likely to lose paternity to outsiders because of the proximity of competitor males. While 6 of the 7 populations with low resident siring success experience influxes or live in colonies (white-lined bats, Indian fruit bats, blue monkeys, elephant seals; Table 2), so do several populations with high resident siring success (geladas, Hanuman langurs, coatis). As with female group size, contact with extra-group males does not explain all of the variation among populations.

Identifying one or a few traits that explain variation in the percentage of offspring sired by the resident among populations is challenging given the considerable natural history differences among one-male species. Our simple comparison suggests that female group size and exposure to extra-group males may explain some of the variation, but the answer is more complex. Studies identifying the drivers of resident siring success within populations may contribute to our understanding of variance among them.

### Resident siring success in blue monkeys

#### Number of competitors and female reproductive synchrony

We found that a resident’s ability to monopolize access to his females decreased when more competitor males were present and when more females were in conceptive estrus simultaneously. These results resemble those found in studies of multi-male species in which the siring success of the alpha male was lower in groups with more males (Cobas et al. 2006; Kutsukake and Nunn 2009; Alberts 2012; Gogarten and Koenig 2012; Lardy et al. 2012) or higher reproductive synchrony (Say et al. 2001; Ostner et al. 2008; Gogarten and Koenig 2012).

Previous work on the study population identified a relationship between the number of simultaneously estrous females and the number of males in a group, and a stronger evidence that the presence

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#### Table 1

**Results of logistic regressions that based female reproductive synchrony on conceptive estrus of other females in the group**

| Model parameters | Coefficient  | SE   | Wald $\chi^2$ | $P$   | Odds ratio$^a$ |
|------------------|--------------|------|---------------|-------|---------------|
| Female synchrony | −0.861       | 0.356| −2.417        | 0.016 | 0.423 (2.366) |
| # Competitors    | −1.409       | 0.691| −2.038        | 0.042 | 0.244 (4.092) |
| Tenure           | 0.122        | 0.426| 0.287         | 0.774 | 1.130         |
| Intercept        | 0.507        | 0.610| 0.832         | 0.406 | 1.660         |

Results in part (A) include all offspring for which the resident could be conclusively assigned or excluded as the sire ($N = 86$ offspring). Results in part (B) eliminated offspring conceived during the tenure of outlier resident RO (leaving 68 offspring in the analysis).

$^a$For odds ratios < 1, we present the inverse in parentheses.

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#### Figure 2

Probability that a resident sired an offspring conceived in his group as a function of the number of females in conceptive estrus as determined by logistic regression (line) and the actual data (circles). To plot the real data, we separated it into 5 groups by the number of conceptive estrus females present (i.e., 1.00, 1.01–1.50, 1.51–2.00, etc.). The number of offspring used to determine the probability of resident siring success for each value of $x$ is in parentheses near the data point. Note that no offspring were conceived when 2.01–2.50 females were in conceptive estrus.

#### Figure 3

Probability that a resident sired an offspring conceived in his group as a function of the number of competitors present as determined by logistic regression (line) and the actual data (circles). To plot the real data, we separated it into 10 groups by the number of competitors present (i.e., 0–1.00, 1.01–2.00, 2.01–3.00, etc.). The number of offspring used to determine the probability of resident siring success for each value of $x$ is in parentheses near the data point.
Table 2
Comparison of 15 populations of mammals that live in one-male groups, ordered by the percentage of offspring sired by the resident in the group

| Species (population)               | Female group size | % Offspring sired by the resident | # of offspring | # of birth cohorts | # of residents | References |
|-----------------------------------|-------------------|-----------------------------------|----------------|-------------------|----------------|------------|
| White-lined bat                   | Small             | 30%                               | 93             | 3                 | 18             | 1, 2       |
| Northern elephant seal            | Large             | 39%                               | 90             | 1                 | Not specified  | 3          |
| Southern elephant seal            | Large             | 58%                               | 50             | 1                 | Not specified  | 3          |
| (Peninsula Valdes, Argentina)     |                   |                                   |                |                   |                |            |
| Blue monkey                       | Large             | 61%                               | 126            | 10                | 11             | This study  |
| Indian fruit bat                  | Medium            | 64%                               | 185            | 2                 | Not specified  | 4, 5       |
| Feral horses (Nevada, USA)        | Small             | 67%                               | 43             | 4                 | Not specified  | 6          |
| Southern elephant seal            | Large             | 69%                               | 183            | 2                 | Not specified  | 7          |
| (Falkland Islands)                |                   |                                   |                |                   |                |            |
| Red deer                          | Small             | 84%                               | 45             | 2                 | 67             | 8, 9       |
| Ring-tailed coati                 | Small/Medium      | 85%                               | 65             | 2                 | 3              | 10         |
| Feral horse (Misaki, Japan)       | Small             | 85%                               | 99             | 16‡              | 14             | 11         |
| Przewalski’s horse                | Small             | 97%                               | 59             | 11§              | 9              | 12         |
| Yellow-bellied marmot             | Small/Medium      | 100%                              | 66             | Not specified     | Not specified  | 13, 14     |
| Red howler monkey                 | Small             | 100%                              | 15             | Not specified     | 5              | 15, 16     |
| Hanuman langur                    | Small             | 100%                              | 13             | 3                 | 3              | 17, 18     |
| Gelada                            | Small             | 100%                              | 47             | 5§                | 14             | 19, 20     |

Studies were included only if they assessed the siring success of identified resident males that were present at the time of offspring conception. When species live in both one-male and multi-male groups, figures reflect parity results from one-male groups only.

*Small: <5, Medium: 5–10, Large: >10 females; Classification based on mean female group size if provided, else based on range. If range spanned multiple categories, all are included.

1. Bradbury & Emmons (1974); 2. Heckel and von Helversen (2003); 3. Hoelzel et al. (1999); 4. Storz et al. (2000); 5. Storz et al. (2001); 6. Gray (2009); 7. Fabiani et al. (2004); 8. Clutton-Brock (1982); 9. Pemberton et al. (1992); 10. Hirsch and Maldonado (2011); 11. Kaseda and Khalil (1996); 12. Fein and Munkhtuya (2008); 13. Downhower and Armitage (1971); 14. Schwartz and Armitage (1980); 15. Pope (1990); 16. Rudran and Fernandez-Duque (2003); 17. Boeke (2000); 18. Lunnhardt et al. (2001); 19. Dunbar (1984); 20. Snyder-Mackler et al. (2012).

†Percentage sired by any resident in the colony (treated as a maximum).

‡Percentage sired by the resident with the longest tenure during the mating season.

§Percentage sired by one of the males that held the female in his harem during her conceptive window.

| Calculation excludes offspring conceived during the tenure of unsampled residents.

| Measured in years, number of birth cohorts not specified.

of many estrous females attracts outside males rather than vice versa (Cords 2002; Mugatha et al. 2007). Although both predictors were significant, the number of males had a slightly stronger effect than reproductive synchrony on the probability that a resident sired an offspring. When many males are present, a resident blue monkey has to spend more time defending his position as resident and limiting other males’ sexual access to his females, which means greater vigilance and aggression toward intruders, potentially reducing his opportunities to mate and increasing the chance that an intruder sneaks matings with unguarded females. Furthermore, females mate infrequently (copulations and mounts during conceptive estrus periods occurred at a rate of 0.21 events/h; Cords, unpublished data from 86 h of focal samples of 48 adult females in conceptive estrus) and a resident who is vigilant for and repelling intruders may be especially likely to miss these rare mating opportunities. Examining 26 mammal species living in both one-male and multi-male groups, Isvaran and Clutton-Brock (2007) showed that the number of females in a breeding group is positively correlated with the percentage of offspring sired by outside males, suggesting that as group size increases, resident males are less able to mate-guard individual females successfully. GLMMs suggested that group size may affect resident siring success by blue monkey males in a similar way. We found that female group size was a significant and positive predictor of the number of females in concepitive estrus, the number of females in concepitive or nonconceptive estrus, and the number of males in the group. Our results thus support the use of group size as a proxy for female monopolizability when individual reproductive data are not available (but see Nunn 1999).

Conceptive versus nonconceptive estrus
Many female mammals have visual, auditory, olfactory, and/or behavioral signals that provide information about the probability of conception within and among cycles (e.g., elephants: Rasmussen and Schulte 1998; pandas: Charlton et al. 2010; macaques: Higham et al. 2012). A male’s ability to interpret these signals should allow him to bias his mating effort to the cycles and days within those cycles that offer the highest probability of fertilization. High-rank-male—such as residents in one-male groups—should face the fewest constraints in selecting mating partners and therefore be best able to mate selectively (Gasquiere et al. 2007). In some cases, however, females may benefit from being able to conceal or manipulate ovulation signals if it allows them to exercise mate choice, confuse paternity, or avoid harassment (Ostner et al. 2006; Thompson et al. 2011).

Blue monkeys lack the conspicuous sexual swellings, changes in coloration, and copulation calls of some other cercopithecines (Maestripieri 2004; Higham et al. 2008; Higham et al. 2011), so sexual signaling is more likely to involve other cues, including sexual behavior. Female blue monkeys mate even when they are unlikely or unable to conceive, suggesting that sexual behavior may function to confuse paternity (Pazol 2003). If residents use female sexual behavior as the only signal of fertility, the probability that a resident sired an offspring should decrease with an increase in the number of simultaneously estrous females, even if some or all of the other estrous females were not concepitive. However, we found that the model that measured female synchrony as the number of females in concepitive or nonconceptive estrus did not show a
significant effect of synchrony. The presence of an additional mating female reduced the resident’s chance of siring an offspring with a given female only if the additional female was also experiencing a conception estrus period, suggesting that resident males may be able to differentiate between conception and nonconception estrus. Other studies of primates have similarly found that males—particularly high-ranking males—can identify periods with the highest probability of conception and bias their consortships or mating behavior toward cycles or days when the female is most likely to conceive (Deschner et al. 2004; Engellhardt et al. 2004; Gesquière et al. 2007; Higham et al. 2009; Thompson et al. 2011; Lu et al. 2012). Our finding suggests that residents use cues other than the presence or absence of sexual behavior to allocate mating effort. Olfactory signals or rates of sexual behavior may function as cues (Petrulis 2013; Rigal et al. 2013); however, their importance in blue monkeys remains unknown.

Our result must be treated with caution because in the absence of external signs of fertility or hormone data, we determined if a female was able to conceive only if she later gave birth. Estrous females that did not conceive or that later miscarried were therefore classified as nonconception. Rates of conception failure and miscarriage have been calculated for other primates (Bechner et al. 2006), but we do not know how often these events occur in our study population.

Tenure length

Reports of mating behavior suggest that female blue monkeys often prefer bachelor males to residents (Tsingalia and Rowell 1984; Cords et al. 1986), perhaps because of the benefits of reproduction with novel partners. Our analysis directly tested the novelty hypothesis and we found that tenure at the time of conception did not affect resident siring success.

Females might choose novel males to avoid inbreeding (Huffin 1992). This function is unlikely to be important for blue monkeys, however, because all males emigrate from their natal groups before reproducing (so females are unlikely to mate with brothers) and the time it takes for a female to reach reproductive maturity usually exceeds resident tenure length (so females are unlikely to mate with fathers). Female choice for novelty could be a way to ensure multiple sires, thus allowing females to increase genetic diversity among offspring to reduce offspring competition or allow bet-hedging in unpredictable environments (Jennions and Petrie 2000). However, theory focuses on species that produce clutches or litters because offspring of the same age are likely to experience the environment similarly. We do not know if females who give birth to single offspring spaced years apart will obtain the same benefits.

Most studies of primates view female choice for novel mates as a strategy that reduces the probability of infanticide (Palombit 2012). Blue monkey males entering a group may kill infants (Cords and Fuller 2010), so females in groups with long-term residents may be particularly motivated to mate with other males who are probably imminent challengers to the current resident. We did not, however, find support for this prediction. Given considerable variation in infanticidal behavior among male blue monkeys (Cords and Fuller 2010), it may be that takeovers by infanticidal males are too unpredictable for females to adjust their attraction to nonresidents so precisely. Alternatively, our data set included relatively few offspring conceived when residents were in the group for many years, as all residents with long tenure years also appeared in the data set as males with short tenures. Thus, it is possible that too few offspring were conceived during the residency of long-tenured males to detect an effect.

CONCLUSION

Paternity results from blue monkeys illustrate a mismatch between social and mating systems; even in one-male groups, the resident male may not sire a large fraction of the infants, which has implications for the degree of reproductive skew populationwide. In blue monkeys, this failure related to the number of competitor males visiting the group and the degree of female estrus synchrony. Each of these 2 factors has an independent effect on resident male paternity although they are each related to group size. Residents may lose paternity because monopolizing access to females is more difficult when more competitors are present and residents challenge intruders. The number of females in conception or nonconception estrus, however, did not affect resident male siring success, suggesting that residents may be able to differentiate between conception and nonconception periods and allocate their mating effort accordingly. Our results add to the growing evidence of considerable variation in resident male siring success among mammals living in one-male groups. Identifying the factors affecting patterns of paternity within species will help us to better understand both interspecific variation and the evolution of social organization.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/.

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