Intrasexual Competition and Reproduction in Wild Blue Monkeys

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Submitted in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy
of the Graduate School of Arts and Sciences

COLUMBIA UNIVERSITY

2014

ABSTRACT

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Competition and cooperation with conspecifics affect the costs and benefits of group living and the evolution of social organization and mating systems. Understanding the role of competition – specifically intrasexual competition – in determining reproductive success thus informs models explaining the diverse types of social organization seen across animal species. The research presented in this dissertation combines molecular, demographic, and social behavior data to explore patterns of reproduction in a population of blue monkeys (*Cercopithecus mitis stuhlmanni*) in western Kenya.

Blue monkeys typically live in one-male/multi-female groups and resident males are presumed to have a reproductive advantage over non-resident "bachelors." I used fecal samples from 60 resident and bachelor males and 126 offspring born in 8 study groups over a 10-year period to quantify resident siring success. Residents sired at most 61% of offspring conceived in their groups, a percentage that is less than most other mammals living in one-male groups and may be linked to blue monkeys' unusually dynamic social organization. In the study population, some groups in some years experience influxes of competitor males; these influxes are most likely to occur in years when many females are mating simultaneously. I found a significant and negative effect of female reproductive synchrony and the number of male competitors on resident siring success. These results suggest that it is difficult for a resident male to defend access to multiple sexually receptive females, which may be further complicated by the presence of

many competitors trying to steal matings. Resident male blue monkeys lost a substantial proportion of reproduction (39% of infants sired) to outside males, which challenges the presumed reproductive advantage of residency. Even though rival males are, by definition, less often nearby in one-male groups than in multi-male groups, they pose a competitive threat to resident male blue monkeys.

I used the paternity assignments to identify the factors affecting the siring success of extra-group males, including resident males in adjacent groups and bachelors. When a resident male was unable to monopolize reproduction in his own group, resident males in adjacent groups tended to be more likely to sire offspring than bachelors. Neither bachelor dominance rank nor time spent in a group was a significant predictor of siring success, suggesting that bachelor siring success may reflect a highly opportunistic mating tactic, which succeeds in a visually opaque habitat where estrous females, who mate rarely, are often widely dispersed.

Comparing the success of alternative reproductive tactics provides a more complete understanding of the evolution of mating systems. I used rates of resident and bachelor siring success and home range overlap to compute the number of years the hypothetical average bachelor would have to pursue the bachelor tactic to sire as many offspring as the hypothetical average resident during one or two periods of tenure. In most cases, a bachelor would not live long enough to match resident siring success. If, however, a bachelor was able to reproduce at the average rate in the average number of groups for several years, he may be able to sire as many offspring as a resident male with a short period of residency, especially if that resident was in a small group. These results suggest that the resident male tactic may not always result in the highest reproductive success. The calculation used here is a simple way to estimate and compare the success of alternative reproductive tactics, which is important for understanding the evolution of social organization and mating systems. This study calls for future research that tracks individual males over the course of their lifetimes to determine how often males switch between residency and bachelorhood, to estimate the length of male reproductive lifespans, and thus to assess variance in lifetime reproductive success.

Female blue monkeys face competition with other group members for access to food resources, and such competition may affect fitness. I tested the effect of two indicators of within-group competition – group size and dominance rank – on the probability that a female conceived. The probability of conception was highest for females in medium-sized groups containing about 31 individuals, suggesting the existence of an optimal group size. This optimal size may occur if individuals in small groups do not obtain the full benefits of group living, including decreased predation risk and increased foraging success, and individuals in large groups have lower quality diets or face time constraints that reduce their nutrient intake. Dominance rank had no effect on the probability of conception, which may reflect the use of behavioral tactics like spreading out during feeding and readily switching food resources to minimize within-group contest competition. A relaxed dominance hierarchy may promote group cohesion and increase success in between-group contest competition. These results emphasize the potential disconnect between behavioral proxies and reproduction; specifically, the existence of a dominance hierarchy and the absence of a relationship between group size and travel distance were not good indicators of the effect of rank and of group size on reproduction. When possible, researchers should examine the effects of rank and group size on measures of reproduction directly.

The results of this dissertation emphasize the value of long-term studies of individually-identified subjects when investigating patterns of reproduction in long-lived animals. My findings indicate that intrasexual competition affects reproduction in both sexes and suggests that individuals use behavioral tactics, such as participating in multi-male influxes or using flexible feeding behavior, to maximize their reproductive success in the face of competition.

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ACKNOWLEDGEMENTS

First and foremost, I thank my advisor Marina Cords, who has provided invaluable support and guidance during all phases of my graduate school adventure. Throughout my time at Columbia, she was always willing to read another draft or to put aside her other work to talk about my project. I consider her to be an exceptional mentor and scientist.

I also thank the members of my dissertation committee for their thoughtful comments and suggestions: Anthony Di Fiore, Don Melnick, and Dustin Rubenstein. A special thanks to my committee member, Eleni Nikitopoulos, who, in addition to providing valuable feedback, contributed the maternal genotypes used in the paternity analyses and patiently trained me in the lab protocol.

I am deeply in debt to the members of the Kakamega Monkey Team who collected the field data that made this work possible. Many thanks to: Millie Atamba, Agnes Atieno, Barry Brogan, Cerian Brogan, Kaitlyn Gaynor, Barrett Goodale, Maggie Hirschauer, Patrick Luteshi, Corey Mitchell, Joyce Munayi, Charles Oduor, Ernest Shikanga, Derrick Shilabiga, Erick Widava, and the many others, past, present, and future, who keep the data rolling in. Additional thanks to the data entry team in NYC and Dan Rabinowitz for his advice on data analysis.

This work would not have been possible without the assistance and guidance of Todd Disotell and the members of the Molecular Primatology Laboratory at New York University. Particular gratitude goes to Andy Burrell and Christina Bergey who answered my questions about methods and equipment. I also thank Dorothy Cheney and Robert

Seyfarth who provided me with an academic home in Philadelphia during my writing year.

Genetic resources used in this study were provided by the Government and people of Kenya. I also thank the National Environment Management Authority, the Kenya Wildlife Service, the Kenya Forest Service, and the MUILESHI Community Forest Association for permission to collect and export biological samples.

This work was made possible through the generous financial support of the National Science Foundation (Graduate Research Fellowship and GK-12 Fellowship to S.J.R, and grants BCS05–54747 and BCS10-28471 to Marina Cords), the Leakey Foundation, the E3B Department at Columbia University, and the New York Consortium in Evolutionary Primatology (NSF IGERT DGE 03-33415).

Throughout my years at Columbia, Mary Heskel, Meha Jain, Miriam Marlier, Amir Jina, James Fuller, Maressa Takahashi, and Nicole Thompson were instrumental in providing encouragement, feedback, and friendship. I feel lucky to have been able to share this experience with them.

Dedication

This thesis is dedicated to my parents, Mark and Bee Roberts, and my husband, Tim Kreider, whose encouragement and unwavering support made this work possible.

Statement of Ethical Standards

The research presented in this dissertation adhered to the Animal Behavior Society guidelines for the treatment of animals in behavioral research and teaching. Methods were approved by the Columbia University Institutional Animal Care and Use Committee (# AC-AAAD9003), the National Council for Science and Technology, the Kenya Wildlife Service, and the National Environmental Management Authority. No animals were harmed in the execution of this research.

CHAPTER 1

Introduction

Competition shapes animal behavior. Within a population, competition with conspecifics affects social organization; within a group, competition with group-mates affects patterns of reproduction (Emlen & Oring 1977, Clutton-Brock 1989). Competition for essential resources is expected to be particularly strong among members of the same sex because their reproductive success is limited by the same resource, i.e., in mammals, these are primarily food for females and mates for males (Stockley & Campbell 2013). In group-living species, competitors are often in close proximity to each other, which should strengthen selection pressure for traits that enhance competitive ability in both sexes and in turn affect patterns of reproduction (West-Eberhard 1979, Clutton-Brock & Huchard 2013b). In this dissertation, I explore how intrasexual competition affects reproduction in blue monkeys (*Cercopithecus mitis stuhlmanni*), a frugivorous primate that typically lives in one-male/multi-female groups.

Beginning with Darwin's theory of sexual selection (1871), research on intrasexual competition has focused on male-male competition for mating opportunities (Andersson 1994, Clutton-Brock 2007). If a single male can exclude other males from a group of females, then theory predicts that both selection pressure on male fighting abilities and variance in male reproductive success should be extreme (Clutton-Brock 1989). In species that live in one-male groups (from here, "one-male species"), males fight each other for residency, sometimes risking mortal injury (Lindenfors & Tullberg 2011), and sexual dimorphism in body size and weaponry is often pronounced (Clutton-Brock et al. 1977). Variance in male reproductive success is also high in one-male species (Clutton-Brock 1988, Le Boeuf & Reiter 1988, Struhsaker & Pope 1991). In some cases, resident males monopolize within-group reproduction completely, meaning that lifelong bachelors do not sire any offspring (Pope 1990, Launhardt et al. 2001). In Chapter 2, I review patterns of male reproduction in species living in one-male groups. I draw on research from a variety of mammals to explore the reproductive advantage of being the sole resident male in a group of females compared to being a male in a multi-male/multi-female group or a bachelor. I also synthesize existing research on factors affecting variation in mating or siring success among males following the same reproductive tactic, i.e., residency or bachelorhood. This literature review provides a foundation for further exploration of variation in male reproduction in one-male species.

Blue monkeys are an interesting species in which to study the effect of male-male competition on reproduction because they have an unusually dynamic social organization. Although groups typically include only one male, some groups in some mating seasons experience multi-male influxes, which temporarily transform the one-male group into a multi-male group with changing male membership (Cords 2002c). During both influx and non-influx years, competitors mate with females (Cords et al. 1986, Cords 1988, Pazol 2003) and likely sire offspring (Hatcher 2006), so it appears that residency neither guarantees high siring success nor is it the only successful reproductive tactic. There have been few studies comparing the success of alternative reproductive tactics in long-lived mammals. In Chapter 3, I quantify and compare the siring success of resident males in the study population of blue monkeys, and then I focus on bachelor males in Chapter 4. I use molecular data to determine the number of offspring sired by individual males present in 8 social groups over a 10-year period as well as demographic and behavioral data to identify the factors correlated with high siring success. Using patterns of reproduction and home range overlap, I estimate and compare the number of offspring sired by residents and bachelors. This comparison allows a more complete understanding of the role of intrasexual competition in the evolution of alternative reproductive tactics for males.

Although females are often viewed as showing relatively little reproductive variance, especially in comparison to males, long-term studies have recently begun to document considerable variation in female fecundity and have drawn increased attention to the effect of female-female competition on reproduction (Hager & Jones 2009, Stockley & Bro-Jørgensen 2011, Pusey 2012). In mammals without paternal care, female reproductive success depends primarily on obtaining adequate nutrition (Wade & Schneider 1992) and females are expected to compete with each other to maximize their access to food (Clutton-Brock & Janson 2012). In gregarious species, factors like group size and dominance rank should affect the way a female experiences within-group competition (Silk 2007, Stockley & Bro-Jørgensen 2011, Pusey 2012). Earlier work in the study population showed that blue monkey groups vary considerably in size and that the females have linear dominance hierarchies, but surprisingly group size and rank have few effects on behavior or reproduction (Cords 2000a, Pazol & Cords 2005, Cords 2012, but see Foerster et al. 2011). In Chapter 5, I use a large data set that spans 15 years and includes 10 groups to investigate the effect of group size and rank on the probability that a female conceived in a given month. Conception is a direct measure of fertility and a discrete event, and therefore it can be related to fine-scale variation in demographic and social variables.

Understanding the effect of intrasexual competition on reproduction is a central issue in behavioral ecology. My dissertation addresses how social, demographic, and spatial variables including rank, reproductive synchrony, number of competitors, female group size, and home range size affect male and female reproduction. Regarding males, this project is one of few to assess paternity in a species that lives in one-male groups, specifically one in which the one-male social organization is especially dynamic. Furthermore, earlier work quantifying mating and siring success challenge the presumed reproductive advantage of male residency. Similarly in females, earlier work has challenged the hypothesis that dominance rank and group size affects female reproduction. The following chapters provide a critical analysis of these surprising patterns to elucidate the relationship between intrasexual competition and reproduction in both sexes.

CHAPTER 2

Male Reproduction in One-Male Groups of Mammals, A Literature Review

INTRODUCTION

When females invest more in offspring than males, female reproductive success is limited by access to food resources while male reproductive success is limited by access to mates (Trivers 1972). As such, explanations of the evolution of social organization and mating systems in mammals often focus on how the distribution of risks and resources affects female distribution, which in turn, affects male distribution (reviewed in: Clutton-Brock & Janson 2012, Kappeler 2013, Koenig et al. 2013). When females form groups, defending exclusive access to a group should allow a male to maximize his access to breeding females (Clutton-Brock 1989). Variation in the number of males in a group within and among species, however, suggests that this theoretically optimal male tactic may not be the only factor determining male group size (Kappeler 2000).

The spatio-temporal distribution of breeding females should affect the ability of a single male to effectively repel competitors (Clutton-Brock 1989). Indeed, intra- and interspecific comparative studies of mammals have found that the number of males in a group increases with female group size and degree of female reproductive synchrony, suggesting that female defense is more difficult when many females are present and mating (rodents: Ims 1988b, Maher & Burger 2011, ungulates: Langbein & Thirgood 1989, Brashares & Arcese 2002, carnivores: Iossa et al. 2009, primates: Lindenfors et al. 2004, Nunn 1999, Carnes et al. 2011). Other factors like predation pressure (van Schaik 1983), risk of infanticide (van Schaik & Kappeler 1997), and evolutionary history (Thierry 2013) may be additional or alternative predictors of the number of males in a group. For instance, populations living in habitats with high predation risk often have a within-group sex ratio that is more biased towards males (van Schaik & Hörstermann 1994, Hill & Lee 1998, Nunn & van Schaik 2000).

Social organization should affect patterns of male reproduction because the number of females and males in the group directly affects the number of reproductive opportunities and the proximity of male competitors (Emlen & Oring 1977, Clutton-Brock 1989). Despite the relationship between social organization and reproduction, variation in patterns of mating and reproduction among species and populations with the same social organization indicates that a particular group composition does not necessarily lead to a corresponding mating system (Kappeler & van Schaik 2002, Isvaran & Clutton-Brock 2007). In this review, I synthesize research on male mating and siring success in populations and species of mammals living in one-male groups to understand how a resident male's social monopoly affects the mating and siring success of the resident and competitor males. First, I examine whether residents in one-male groups have a reproductive advantage over males living in multi-male groups and over bachelor males. Then I explore factors that affect an individual male's reproductive output, specifically the effects of female monopolization potential, strength of male-male competition, and female choice for novelty.

I. The Reproductive Advantage of Sole Male Residency

Theoretical models of the evolution of mammalian social organization and mating systems often assume that: (1) it is better to be the sole resident male in a group of females than to share the group with other males and (2) it is better to be a resident male than to live outside a social group as a bachelor (Emlen & Oring 1977, Clutton-Brock 1989). These assumptions are reasonable because having many males in close proximity to females probably decreases the ability of one male to monopolize mating and paternity and resident males spend more time near females than do bachelors and should therefore have more opportunities to mate and reproduce. The relatively recent availability of intra- and interspecific comparative studies – especially those that use molecular data to assess siring success – allows us to test these assumptions.

I.A. Resident Male Reproduction in One-Male versus Multi-Male Groups

Several studies of species living in multi-male groups indicate that the presence of more competitors decreases annual mating and siring success for high-ranking males (alpine marmot: Cohas et al. 2006, Lardy et al. 2012, primates: Alberts 2012, Gogarten & Koenig 2012). One-male species may function similarly, with the presence of more intruding males increasing the probability that a resident male will lose paternity to others. Species that live in both one-male and multi-male groups and one-male species that experience male influxes during some breeding seasons are useful systems in which to quantify the reproductive consequences of having male competitors in or near a one-male group.

The most convincing support for the negative effect of competition on siring success comes from wild horses (*Equus caballus*), in which the annual siring rate (i.e., offspring sired per year) was higher for a single resident male than for a male who shared a harem with another male (Rubenstein & Nunez 2009). A study of toque macaques (*Macaca sinica*), which also live in one-male and multi-male groups, revealed a more complicated relationship. Keane et al. (1997) used exclusion methods to assign or exclude the resident male as the father of 87 offspring conceived in 13 groups over a 12-year period. The total number of males that sired offspring in a group was not correlated with the number of males in the group, suggesting that the presence of more competitors may not greatly reduce the annual reproductive output of successful (usually high-ranking) males. However, whether a male lived in a one-male or a multi-male group did have an effect on a slightly different measure of reproduction, male siring success per reproductive opportunity (measured as whether a male was resident when an offspring was conceived). Specifically, resident males in one-male groups sired a significantly higher proportion of offspring per opportunity than resident males in multi-male groups. The authors suggested that this short-term reproductive advantage could translate into large reproductive benefits for males who can maintain residency in one-male groups for multiple years.

Studies of other species that live in both one-male and multi-male groups did not support the negative relationship between the number of competitors and male reproduction. For example, in 5 groups of red howler monkeys (*Alouatta seniculus*) in which group composition had been stable for at least 2 years, only one male per group sired offspring regardless of the number of males present (Pope 1990). The complete reproductive monopoly by one resident male may occur because males can enter bisexual groups only by forming coalitions and staging a group takeover; males preferentially formed coalitions with close relatives, so joining forces but forgoing reproduction may allow low-ranking males to ensure some inclusive fitness benefits (Pope 1990).

Similarly, in western lowland gorillas (*Gorilla gorilla*), the silverback male in each of 12 study groups (9 one-male and 3 multi-male) could not be excluded as the father of any of the 20 offspring genotyped, suggesting that he had a complete within-group reproductive monopoly even when blackback males were present (Bradley et al. 2004). Not all paternity results were conclusive, however (e.g., ten offspring had between one and ten additional males who were possible fathers), and maximum likelihood rather than exclusion methods would provide additional insight into whether the silverback was actually the most likely sire of each offspring. In a study of 4 multi-male groups of closely-related mountain gorillas (*Gorilla beringei beringei*), Bradley et al. (2005) did use paternity assignment methods, and found that silverbacks lost an average of 15% of offspring to the second-ranking blackback male in the group. Paternity data for one-male groups in this latter study population were not available for comparison, so the effect of additional males in this species remains unclear.

Comparative analyses across primate species have found a positive correlation between the number of males and the number of females in a group (Andelman 1986, Mitani et al. 1996, Nunn 1999, Carnes et al. 2011). Given that relationship, one should consider the number of reproductive opportunities when comparing patterns of paternity across groups. In some cases, the percentage of within-group offspring sired by a resident may be an imperfect proxy for the total number of offspring sired by the resident (the measure of male reproductive success). For example, in 21 gelada (*Theropithecus gelada*) reproductive units, leader males sired 100% of the group offspring born in one-male units and 83% in units that had a follower male; however, multi-male units contained more females and leaders had longer tenures than those in one-male units, resulting in a net reproductive benefit to leaders if they tolerated the presence of a follower (Snyder-Mackler et al. 2012). Similarly in Hanuman langurs (*Semnopithecus* *entellus*), the resident sired 100% of offspring in one-male groups (N=6 group-years) and the most successful resident sired 57% in multi-male groups (N=9 group-years with offspring), but more offspring were born in groups with multiple males and the total number of offspring sired per group-year was the same for males in both group types (Launhardt et al. 2001). The results of both studies indicate that even if the presence of competitors reduces the percentage of within-group offspring sired it does not always decrease a resident's reproductive output.

Several guenons experience influxes of non-resident males during some breeding seasons (Cords 1988, 2000b) and comparisons of mating or siring success between influx and non-influx years can provide additional insight into how the presence of competitors affects resident male reproduction. In patas monkeys (*Erythrocebus patas*), Ohsawa et al (1993) found that single resident males obtained 100% of matings during non-influx years, while the original resident obtained only 31% of matings during influx years. Even if a single male obtained the remaining 69% of matings during the influx, the proportion of mating obtained by the most successful male still decreased when more males were present. In contrast to the mating behavior, the resident male observed in two group-years without influxes sired 2 of the 4 offspring (50%) and three residents observed during three group-years with influxes sired four of the five infants (80%). The apparent increase in resident paternity success in years with more male competitors contradicts the mating results and does not support theoretical predictions. These study, however, was based on very small sample sizes, which reduces the confidence in the conclusions. Additionally, paternity was not assessed for the same cohort that was conceived during the monitored mating season, so paternity and mating data do not correspond and variation in additional factors (e.g. number of conceptive females, number of intruder males) may influence the paternity results.

Another study of patas monkeys found no effect of the number of competitors on copulation rate. Chism and Rogers (1997) studied two groups of patas monkeys in Kenya, comparing the copulations per unit time by the sole resident male in one group with that of five co-resident males in the second group. The authors found no difference in copulation rate and concluded that the sole resident with no competitors did not need to copulate frequently to ensure paternity. Observation time was limited (3.0-10.9 hours per male), however, so these results should be interpreted with caution. Additional studies of patas monkeys, blue monkeys (*Cercopithecus mitis*), and redtail monkeys (*Cercopithecus ascanius*) calculated the mating success of individual males during years with multi-male influxes, finding that copulations were divided among multiple males during influxes and in some cases, the most successful male obtained less than one-third of group copulations (Tsingalia & Rowell 1984, Cords 1984, Cords et al. 1986, Harding & Olson 1986). These studies were limited to influx years, however, so did not explicitly compare the division of mating between influx and non-influx years.

Surprisingly, most intraspecific comparisons found that adding competitor males to a one-male group did not decrease resident mating or siring success and in a few cases (e.g., geladas) actually increased the number of offspring sired by the resident over the course of his tenure. Clutton-Brock and Isvaran (2006) used a meta-analysis of 24 species of mammals to similarly examine whether social organization (which includes the number of males in a group) affected the ability of one male to monopolize within-group paternity. They found that the proportion of group offspring sired by the alpha male did not differ among species that lived in pairs, one-male, or multi-male groups and instead found an effect of association pattern: residents sired proportionally more offspring in species in which males were continuously associated with estrous females (such as meerkats, dik-diks, and red howler monkeys) than in species where males sometimes foraged independently (such as shrews, red deer, and elephant seals). The authors concluded that across species, the intensity of mate guarding is a more important determinant of resident male reproduction than social organization.

Clutton-Brock and Isvaran did not include reproductive synchrony in their analysis, but social organization – and specifically the number of males – may have no effect on male reproduction if females are rarely conceptive simultaneously. If only one female is conceptive at a time, the highest-ranking male should be able to monopolize all reproductive opportunities in the group (Altmann 1962). Alternatively or in addition, as suggested for red howler monkeys, high relatedness among males in a group may reduce the strength of competition for reproductive opportunities (Johnstone 2008). Closer examination of demographic, social, and genetic factors may clarify the reason for the lack of effect of number of males in the group on mating and siring success.

I.B. Residency Versus Bachelorhood

Mate-guarding as a resident and sneaking matings as a bachelor may represent alternative reproductive tactics (ARTs) that allow males to maximize reproductive output within the constraints of social, demographic, and ecological conditions (Gross 1996). Resident males are assumed to have a reproductive advantage over bachelors because the costs associated with residency (e.g., fighting with other males, increased energy expenditure) should be balanced by benefits, including reproductive benefits associated with increased access to females (Clutton-Brock 1989). More time spent in proximity to females may ensure that a resident is available to mate when females are conceptive. Also, in many species, females have visual, auditory, olfactory, and/or behavioral signals that provide information about the probability of conception within and between cycles (e.g., Rasmussen & Schulte 1998, Charlton et al. 2010, Higham et al. 2012) and proximity to and familiarity with individual females may allow residents to use those signals most effectively to allocate mating effort (Higham et al. 2011). Although the reproductive advantages of residency are often presumed, few studies have explicitly compared tactics in mammals living in one-male groups, probably because it is difficult to track individual males that move among multiple groups and may switch tactics over the course of their lives.

Studies of 15 populations of mammals living in one-male groups used molecular data to evaluate the siring success of the resident male present at conception, thereby quantifying resident siring success on a small spatial and temporal scale. There was considerable variation in the percentage of offspring sired by the resident male in the group (range: 30%-100%, Table 2 in Chapter 3, though note slight differences in measurements among studies); however, in 13 of the 15 populations, the resident sired more than half of his group's offspring and therefore had higher within-group reproductive output than any other male. In 4 species (yellow-bellied marmot, red howler monkey, Hanuman langur, and gelada), the resident male sired all of the offspring conceived during his tenure, suggesting that lifelong bachelors do not reproduce. In combination, these studies generally support the predicted reproductive advantage of residency.

Most studies evaluate paternity in only one or a small number of adjacent groups, probably for logistical reasons. Theoretically, however, both resident and bachelor males may increase their lifetime reproductive success (LRS) by mating and siring offspring in more than one group in the same year. For example, in a ten-year study of sifakas (a multi-male species), males that divided their reproductive effort over multiple groups produced more offspring over the course of their estimated reproductive lifetimes than those males who sired offspring only within their own groups (Lawler 2007). Additionally, although resident male white-lined bats (*Saccopteryx bilineata*, a one-male species in which harem groups cluster to form colonies) sired only 8 of the 28 (30%) offspring born in their harems, over half of the remaining offspring were sired by residents of adjacent groups, indicating that residents augmented their reproductive output by siring offspring nearby (Heckel et al. 1999). These studies show that it is important to quantify mating and paternity skew on a spatial scale encompassing more than one group, even over a single breeding season, to obtain a more complete picture of paternity distribution in one-male species.

In addition to assessing reproduction across multiple groups, long-term data are necessary to quantify LRS in animals with long reproductive lifespans. These data may be particularly difficult to obtain in species in which males move between groups and between resident and bachelor strategies over the course of their lives. Despite these challenges, three studies of one-male species have amassed enough data on individual males to estimate LRS and quantify variance in male reproduction.

Clutton-Brock et al's (1988) 18-year study of red deer (*Cervus elaphus*) followed 33 stags from birth until likely death. Red deer form harem groups during the breeding season and a female may move freely among harems while she is conceptive. To estimate LRS of individual males, the authors identified an 11-day window in which each offspring was most likely conceived and assigned paternity to a stag based on the proportion of the offspring's 11-day conception window in which the mother was in his harem. Based on this calculation, male LRS varied from 0 to 32 offspring, with a mean of 5.4. Subsequent paternity analysis for 76 infants from the same population confirmed that the probability that a male sired an offspring was positively related to the number of days that a female was in his harem; however, the probability of siring success was not evenly distributed over the 11 days as previously assumed (Pemberton et al. 1992). If a female was in a stag's harem for 1 day during the conception window, his probability of siring her offspring was 0.12; if she was in his harem for at least 6 days, the probability was 1 (Pemberton et al. 1992). Thus, earlier calculations of LRS based on an even distribution of siring success over the 11-day window probably underestimated the number of offspring produced by successful males, suggesting that variation among male red deer is greater than previously estimated.

Le Boeuf & Reiter (1988) tracked the presence of 19 individually-identified male northern elephant seals (*Mirounga angustirostris*) on a rookery for a period of 22 years. They recorded copulations by each male when he arrived at the rookery to breed and estimated annual reproductive output as the percentage of copulations by a male with females in the harem multiplied by the number of harem females who gave birth that year (and thus were conceptive). Le Boeuf & Reiter calculated LRS for each male as the sum of annual reproductive output discounted by the rate of pup mortality and found a range of 0 to 93 with a mean of 3.8. The enormous variance in estimated LRS (exceeding that estimated for red deer) is likely a consequence of variance in harem size. Males actively fight for access to harems and the largest males tend to win (Le Boeuf 1974). Thus, a highly competitive male who can defend access to a large harem in multiple years is likely to have much higher lifetime reproductive success than a less competitive male who guards a small harem. While these estimates incorporated data obtained from close monitoring of the elephant seal population, they also included several assumptions about life history parameters that remain to be tested. For example, death was presumed if a reproductive-aged male who had appeared at the rookery in previous years did not appear during the following breeding season, however, the authors acknowledge that it is possible that the missing male emigrated from the local area (Le Boeuf & Reiter 1988). This truncation may result in an underestimation of LRS for some males.

In the third study, Struhsaker and Pope (1991) used data from 6 groups of redtail monkeys (*Cercopithecus ascanius*) observed over 16 years to estimate male LRS. They assigned an offspring to the resident male present at the estimated time of conception; if conception occurred during an influx year, they divided the share of paternity evenly among all males present. The authors calculated LRS as the sum of the number of offspring sired during a male's known reproductive lifespan and the number of offspring sired during his remaining reproductive lifespan if he continued reproducing at the same rate. Little is known about the actual length of a male's reproductive lifespan and for the purposes of this model, the authors assumed that it was the same as the estimated female reproductive lifespan (7.8 years). After discounting male reproductive success by offspring mortality, the model indicated that the average male LRS was 3.7 offspring with a variance of 18.1. The authors compared these results with similar calculations for red colobus monkeys (*Colobus badius*), which live in multi-male groups, demonstrating that, despite similar reproductive lifespans, the variance in estimated male LRS was much greater for the harem-living redtails. In comparison to the variances in male LRS among red deer and elephant seals, however, the variance for redtails was much lower. This difference may be related to male influxes that characterize redtail groups uniquely, and which give more males the chance to sire offspring; it may also reflect an underestimation of the redtail reproductive lifespan or the challenges of assessing the time of conception in species without external indicators of fertility.

Similar calculations have been used to estimate and compare the reproductive success of resident and bachelor male primates using less extensive data sets (Sommer & Rajpurohit 1989, MacLeod et al. 2002). For example, MacLeod et al. (2002) developed a calculation to determine if, over an entire reproductive lifetime, a bachelor samango monkey (*Cercopithecus mitis labiatus*) could sneak enough matings to make him as successful as a resident male during one period of tenure. In their study population, an average resident obtained 90% of the matings in his group and maintained residency for an average of 1.67 years; the calculation determined that a bachelor would have to sneak matings for 15.07 years to obtain the same number of matings as a resident in one period of residency. The authors judged 15 years as longer than a male's reproductive lifespan, so a lifelong bachelor would never be able to obtain as many matings as a male who has one period of tenure. The comparison makes several assumptions that are unlikely to be true in all populations: (1) the resident male confines his mating activity, and siring, to his group alone, (2) the resident loses matings to only one bachelor male, and (3) the bachelor concentrates all his reproductive effort in only one group. Falsification of the first two assumptions would not change the qualitative conclusion of the comparison as they would increase resident male reproduction relative to bachelors. If the third assumption is false, however, and a bachelor reproduces in multiple groups during one breeding season, the calculation may underestimate bachelor male reproduction. Presumably, if a bachelor male reproduces in enough groups during one breeding season, he may be able to attain similar reproductive output to a resident. It remains unclear if and how often bachelors sire offspring in multiple groups.

In sum, any model of lifetime reproductive success for long-lived male mammals must incorporate mating or paternity data for individuals at sufficiently broad temporal and spatial scales. Reproductive output likely varies over the course of an individual's lifetime as a function of age (e.g., McMillan 1989, Yoccoz et al. 2002, Hollister-Smith et al. 2007) and reproductive tactic (e.g., resident versus bachelor) and a long-term data set is necessary to capture the schedule of that variation. When estimating lifetime reproductive success in a species in which a male has access to multiple groups during one breeding season, reproduction at a large spatial scale must be considered (Heckel et al. 1999, Hoelzel et al. 1999, Lawler 2007). A combination of paternity data from more long-term research projects and behavioral data on male movement throughout entire lifetimes will allow more precise estimates of LRS and comparison of ARTs.

II. Factors Affecting Resident and Bachelor Mating and Siring Success

Although resident males usually have a reproductive advantage over lifelong bachelors, siring success varies among males using the same reproductive tactic (residents: Kaseda & Khalil 1996, Heckel & von Helversen 2002, Fabiani et al. 2004, Hirsch & Maldonado 2011, Roberts et al. 2014, bachelors: Heckel & von Helverson 2002, Ch 4 in this dissertation). Identifying the factors affecting variation in both resident and bachelor reproduction will provide insight into the effectiveness of each tactic. As described earlier, many male mammals can switch among tactics over the course of their lives, so the ability to detect and respond to conditions affecting the success of residency or bachelorhood may allow males to better use environmental cues to make decisions to maximize their lifetime reproductive success. This section specifically addresses how variation in female monopolizability, the strength of male-male competition, and female choice for novelty affects male reproduction.

II.A. Differences Among Populations

Comparing patterns of resident siring success in 15 populations of mammals living in one-male groups (Table 2 in Chapter 3) provides an opportunity to investigate whether the number of females in a group and the presence of competitor males contributed to inter-population variation in resident siring success. For these 15 populations, female group size is likely an important determinant of a resident's ability to monopolize group reproduction: of the 8 populations with resident siring success >80%, most and possibly all live in groups with fewer than 5 females. As found in interspecific comparisons of primates in which a single male was better able to exclude other males from the group when female group size was small (Mitani et al. 1996, Nunn 1999, Carnes et al. 2011), being a resident in a small group may enable not only a social, but also a reproductive monopoly. The multi-species comparison, however, indicates that female group size does not explain all of the variation in resident siring success, because white-lined bats and one population of feral horses also live in small groups but had low resident siring success (30 and 67% respectively).

Species that experience multi-male influxes or live in colonies may have lower resident siring success than those that do not because competitor males are more consistently and conspicuously present, thereby increasing the strength of male-male competition (though see above discussion of resident siring success in one-male versus multi-male groups). The presence of competitors was somewhat, but not completely, predictive of resident siring success: 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), but so do 3 of the 8 populations with high resident siring success (geladas, Hanuman langurs, coatis). Thus, the presence of competitor males does not explain all of the variation among populations.

Although all species considered here live in one-male groups, they differ in many ways other than female group size and the presence of male competitors. This simple comparison suggests that these two factors may explain some of the variation in resident siring success, but the answer is more complex and it may be useful to consider other natural history factors. For example, species in which groups are less cohesive, have larger home ranges, high female reproductive synchrony or live in a habitat with low visibility may have lower resident siring success because it may be more difficult for the resident to monitor multiple conceptive females simultaneously. Further work quantifying these variables in these species will allow a more thorough comparison of resident siring success across species living in one-male groups.

II.B. Differences Among Males

Altmann's (1962) priority-of-access model (POA) was one of the first models to test the drivers of variation in male mating success. Although this model was originally applied to rhesus macaques, a multi-male primate species, the principles are equally relevant in one-male groups where extra-group males may be intruders. The model predicts that when one female is estrous at a time, reproduction should be skewed towards the dominant male (or the resident) in the group. When multiple females are estrous simultaneously, the dominant male should be unable to monopolize access to them and subordinates (or intruders) should have the opportunity to mate, thereby decreasing skew. POA emphasizes the importance of two variables, female reproductive synchrony and dominance rank, in partitioning paternity. Additional variables that may affect the absolute and relative success of residents and bachelors include other measures of female monopolization potential (e.g. female group size), the strength of male-male competition (e.g. individual competitive ability, density of competitors), and female choice.

II.B.1. Female Monopolization Potential

An increase in female group size and reproductive synchrony should decrease the ability of one male to defend access to a group of females (Ims 1988a, Emlen & Oring 1977). On a population level, variation in these factors contributes to differences in social organization. Within a given social organization, variation in female monopolization potential should affect the partitioning of reproduction among males. In one-male groups, there should be a negative relationship between the proportion of group offspring sired by the resident male (i.e., the resident's within-group monopoly) and the number of females and their degree of reproductive overlap. As mentioned earlier, quantifying reproductive output as a proportion of group offspring overlooks the importance of measuring reproductive success as the total number of offspring. Indeed, it is possible (and perhaps likely) that even if a resident male in a larger group has a lower within-group monopoly, he still sires a greater number of offspring.

Data from a population of elephant seals provide some support for the predicted negative relationship between group size and resident's within-group monopoly. Female elephant seals congregate on land in large harems to give birth and breed, with harems varying in size from 2 to 1000 females (Le Boeuf & Laws 1994). Hoelzel et al (1999) calculated the proportion of harem matings and paternities obtained by the resident male in 10 harems of northern elephant seals (*Mirounga angustirostris*). The largest harem included 224 females and the resident sired 5 of 14 (36%) genotyped offspring. The remaining 9 groups ranged in size from 9 to 99 females (average=45 females) and the resident sired an average 51% of the 76 genotyped offspring. While the reproductive monopoly is higher in smaller groups, in only one of these groups did the resident sire more total offspring (8 of 10 genotyped offspring) than the resident in the large group, highlighting the disconnect between measuring reproduction as a proportion of the group offspring or as the total number of offspring. Hoezel et al. (1999) conducted the same analysis in a population of southern elephant seals (*Mirounga leonina*), finding that the resident in the largest group (group size=119 females) sired 50% of the genotyped offspring, which, similarly, was lower than the 60% sired by residents in smaller groups (average group size=55 females, N=5 groups, 44 offspring). Strikingly, however, the resident in the large group sired a total of 3 offspring (out of 6 genotyped offspring) while, the residents in 4 of the 5 smaller groups sired the same number or more in their own groups. The authors did not explicitly test the relationship between harem size and resident reproduction in either elephant seal population, but these comparisons suggest that, consistent with the prediction, a large increase in group size may reduce the percentage of within-group offspring sired by the resident. The relationship between group size and the total number of offspring sired, however, is more complicated. Inconsistent patterns may be linked to having genetic data from relatively few of the total offspring conceived in each group, which may render these results potentially inconclusive.

The effect of female group size on resident siring success is also illustrated by Indian fruit bats (*Cynopterus sphinx*), which live in one-male harems that vary in size throughout the year; in the dry season, harems are 2.3 times larger than they are in the wet season (Storz et al. 2000b). Storz et al. (2001) found that resident males sired 52 out of 54 infants (96%) conceived in their groups in the dry season when harems were large and only 25 out of 64 infants (36%) conceived in the wet season when harems were small. These results contradict the predicted negative relationship between group size and the resident reproductive monopoly, as residents sire proportionally more offspring in larger groups. The authors suggested that the nearly-complete reproductive monopoly in large groups reflects female dispersion; during the dry season many more females are clumped into the same roosting space, facilitating mate guarding by males. The total number of offspring per resident was not reported, so the effect of group size on absolute siring success is unclear. In another species of tropical bat, the sac-winged bat (*Saccopteryx bilineata*), resident males sired only 30% of offspring within their own groups (Heckel & Von Helversen 2003). While lower than other one-male species (Table

2 in Chapter 3), this percentage held across all group sizes, thus the number of infants sired increased when more females were in the group (Heckel & Von Helversen 2003).

Two additional studies of one-male groups of mammals found that resident males in larger groups sire more offspring than males in smaller groups. In yellow-bellied marmots (*Marmota flaviventris*), a species in which the resident male sires all offspring in the group, groups that contained an additional female also contained an additional 2.1 offspring (Armitage 1991). In a 16-year study of feral horses (*Equus caballus*), the number of foals sired per breeding season increased with a stallion's harem size until the group included 6 females, but not above this groups size; thus, there appeared to be a limit on the ability of a stallion to capitalize on reproductive opportunities (Kaseda & Khalil 1996). Consistent with the prediction that resident males should sire proportionally fewer offspring in larger groups, this leveling off of siring success may indicate that stallions with very large harems cannot successfully mate-guard all estrous females.

In contrast, Hirsch and Maldonado (2011) evaluated paternity in one-male groups of ring-tailed coatis (*Nasua nasua*), finding no correlation between female group size and resident reproductive monopoly. The resident sired a consistently high proportion of group offspring (average=82%, N=5 group-years) regardless of female group size and despite very high levels of reproductive synchrony (all females mate within a 1-2 week period) and male influxes during the breeding season. The authors suggested that these surprising results may occur because females chose to mate with the resident male when they were the most likely to conceive. In line with the consistently high proportion of group offspring sired by the resident, residents in larger groups sired more offspring than residents in smaller groups.

According to POA, an increase in the number of simultaneously mating females should decrease the reproductive success of the top-dominant male by reducing his ability to monopolize access to all estrous females at the same time (Altmann 1962). Reproductive synchrony can be quantified using multiple methods. A common method uses length of mating season as a proxy, assuming that female reproduction will overlap more when the mating season is shorter. Length of mating season may be useful to characterize large differences between species (e.g. Ridley 1986), however, it is not a direct measure of the degree to which female cycle overlap and when applied within a species and may overlook the fine-scale variation between groups (Nunn 1999).

Several alternative indices of reproductive synchrony have been used, including: (1) the number of mating or conceptive females per unit time (Say et al. 2001, Isaac 2003, Roberts et al. 2014), (2) the proportion of days during the mating season in which two or more females are mating or conceptive (Nunn 1999, Ostner et al. 2008, Bissonnette et al. 2011), and (3) the square of the pairwise differences in female conception dates (Ims et al. 1988, Wolff et al. 2008). The advantage of these indices is that they provide group-specific measures of synchrony calculated from observations of individual females. Therefore, none of these indices assumes that female conception dates are evenly distributed over time, as is assumed when one uses length of the mating season to measure synchrony.

The calculation of each of these indices poses a significant challenge in wild populations: accurate identification of the period in which each female is able to conceive. The most precise method of assessing fertility is to monitor reproductive hormones to determine when ovulation occurs; however, this process is very laborintensive (Dixson 1998). Because female sexual behavior in most mammals is tightly linked to the conceptive period, observations of mating often provide a good alternative indicator of when a female is able to conceive (Beach 1976). If copulations are rarely observed, knowledge of gestation length and infant birthdates would allow backdating to identify the period in which the infant was conceived (e.g., Clutton-Brock et al. 1988, Ostner et al. 2006, L'Italien et al. 2012, Swedell et al. 2014). Overall, the ability to accurately estimate the conceptive period in wild mammals depends on intensively monitoring populations.

In some catarrhine primates, there is evidence that males can differentiate between conceptive and non-conceptive females because high-ranking males bias their mating behavior towards females that are most likely to conceive (Deschner et al. 2004, Engelhardt et al. 2004, Gesquiere et al. 2007, Higham et al. 2009, Thompson et al. 2011, Lu et al. 2012). This ability may not apply to all species and populations, possibly because there is selection on females to be 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, Hestermann et al. 2001). In these cases, sexual receptivity and even morphological indicators of ovulation (e.g., sexual swellings) are probably decoupled from the conceptive period, making them poor indicators of fertility (Hrdy & Whitten 1987, Pazol 2003).

A male’s ability to differentiate between conceptive and non-conceptive females may have important consequences when one evaluates the effect of female mating synchrony on mating and reproduction. If males can recognize conceptive females, the alpha male should preferentially mate-guard conceptive females. In such cases, the presence of multiple simultaneously mating – as opposed to simultaneously conceptive – females may not affect the distribution of paternity in a group. When studying reproduction in species in which sexual behavior does not coincide with ovulation, more accurate ways of assessing female reproductive state (e.g., measuring hormone levels, backdating from offspring birthdates) should be used.

Studies relating variation in reproductive synchrony to mating or paternity success have been confined to multi-male groups (but see Roberts et al. 2014), generally demonstrating that increased synchrony reduces the alpha male's reproductive monopoly (Altmann 1962, Bulger 1993, Say et al. 2001, Soltis et al. 2001, Isaac 2003, Bissonnette et al. 2011). This effect may be less pronounced in one-male than in multi-male groups as, by definition, male competitors are not as close at hand. One study of captive vervets (*Cercopithecus aethiops*), which live in multi-male groups, found no relationship between female reproductive synchrony and paternity monopolization, although the captive groups were much less synchronous than wild groups, which may have affected the results (Weingrill et al. 2011). No studies found that an increase in synchrony is correlated with an increase in male reproductive skew.

Overall, studies quantifying how the residents' within-group monopoly changes with group size have found that an increase in the number of females in a group is correlated with a decrease, increase, and no change in the proportion of within-group offspring sired by the resident. The total offspring sired by the resident, however, generally increases when the resident is in a larger group, thus for most species, the increased effort of maintaining a larger group pays off in reproduction. The effect of female reproductive synchrony on male reproduction in one-male groups has received comparatively little attention and more studies are necessary to determine if high synchrony reduces a residents' ability to monopolize paternity. Methods for identifying when females are able to conceive are important to quantify reproductive synchrony in species in which estrous behavior is decoupled from ovulation.

II.B.2. Strength of Male-Male Competition

The presence of more male competitors should decrease reproductive skew, as more males are simultaneously vying for the same reproductive opportunities. Male-male competition might be particularly strong in one-male species, as there are relatively few resident positions compared to the number of males in the population. In multi-male species, competitors are considered to be all group-living males (Alberts et al. 2003) but for one-male species, designating competitors is less straightforward. Competitors should probably include all extra-group males that may have even brief access to conceptive females, including residents of adjacent groups and non-residents who are in the vicinity the group. Methods for quantifying the number of competitors in one-male groups should differ by group and by habitat, as group cohesiveness and habitat visibility should affect the ability of the resident male to simultaneously monitor all females (Rowell 1988, Wroblewski et al. 2009). For example, it should be more difficult for a resident male to monitor all females if the group is dispersed over a large area in a habitat with low visibility than if females are clustered in an open habitat. In the former case, extra-group males may approach females with a low chance of being detected by the resident male; in the latter case, an extra-group male may have to stay much farther from the group to avoid the resident male.

Sexual selection theory proposes that male mammals, which invest relatively little in offspring, should compete for access to breeding females, making individual competitive ability directly linked to reproductive success (Clutton-Brock 1989). Multiple factors may contribute to competitive ability, but body size may be one of the most important in mammals whose males use pushing contests or stereotyped threats to obtain and defend a harem or territory (Clutton-Brock et al. 1988, Le Boeuf & Reiter 1988). In species in which fighting takes another form, such as biting or chasing, male agility may be a better measure of competitive ability (Feh 1990, Lawler et al. 2005).

Across several taxa, larger males are more successful at obtaining and defending territories than smaller males, which likely increases their access to females (pinnipeds: Haley et al. 1994, bats: Dechmann et al. 2005, rodents: Asher et al. 2008, macropods: Miller et al. 2010). For example, in cavies (*Cavia aperea*), only the largest males in the population held territories (Asher et al. 2008). Resident males sired 70% of the offspring born on their territories and residents of adjacent groups sired the remaining 30%, meaning that small satellite males and intermediate-sized roaming males did not sire any offspring (Asher et al. 2008). Additionally, although shelter-making is rare in mammals compared to other taxa (Hansell 1984), resident males of several bat species build roosts in which harem females congregate (Balmford et al. 1992, Dechmann & Kerth 2008, Storz et al. 2000a). Male white-throated round-eared bats (*Lophostoma silvicolum*) excavate active termite nests for roosting, an activity that is costly in both time and energy (Dechmann et al. 2005). Harem-holding males were bigger, in better condition, and sired more offspring than bachelors, suggesting that roost-building is a sexually selected behavior (Dechmann et al. 2005).

An alternative measure of male competitive ability is dominance rank, which reflects the outcome of dyadic agonistic interactions (Drews 1993). In species that live in one-male groups, resident males are presumably dominant to bachelors, an assumption that has been supported in the few one-male primate species in which resident-bachelor aggression has been quantified (Harding & Olson 1986, Cords et al. 1986, Romero & Castellanos 2010). While it is reasonable to assume that resident males outrank non-resident males, the ranks of resident males relative to each other and non-residents relative to each other may affect their access to females. This type of ranking could generate new questions. For example, when a resident male is unable to monopolize access to all conceptive females in his group, does rank among non-residents predict their likelihood of reproducing?

Most of the research on rank-related mating and reproduction has been done in species that live in multi-male groups. As males in multi-male groups live together and have many opportunities to compete for food and females, agonistic encounters may be frequent and dominance rank can be assigned relatively easily. Across mammals, male rank has an inconsistent effect on reproduction (Ellis 1995, Majolo et al. 2012, Alberts 2012). Some have argued that significant correlations may be driven by the inappropriate inclusion of low-ranking, non-reproducing subadult males in the analyses (Bercovitch 1992, 1986, McMillan 1989).

Alberts et al. (2003) aimed to resolve the debate over rank effects on male mating by analyzing 32-group-years of mate-guarding behavior in a population of savanna baboons (*Papio cynocephalus*). When pooling data over all group-years, the proportion of time spent mate-guarding fertile females (which is a good predictor of paternity, Altmann et al. 1996) followed male ranks as predicted by the POA model, but the differences among males were not as pronounced as predicted. Specifically, the highest-ranking male was predicted to obtain 70% of mate-guarding time, but in reality obtained only 20%. Additionally, males lower than rank 5 were predicted to spend no time mate-guarding, but in reality, males as low as rank 13 obtained some (albeit very little) mate-guarding time. When the data were divided into six-month blocks, an interesting pattern emerged: in some blocks, the queue broke down completely, with low-ranking males spending proportionally more time mate-guarding than high-ranking males. The queue was more likely to break down when there were many males in the group, when the age difference between males was large, and when the highest-ranking male had been highest-ranking for only a short time. The authors concluded that the variance in rank-dependent reproduction evident in many short-term studies is true variance reflecting differences in the ability of the highest-ranking male to monopolize mate-guarding.

Other studies of multi-male species have compared the expected success of each male (based on dominance rank and measures of female synchrony) with his observed success, and in many cases, similar to Alberts et al., the highest-ranking male mated or sired offspring less often than predicted (Hayakawa 2008, Wroblewski et al. 2009, Bissonnette et al. 2011, Dubuc et al. 2011, Young et al. 2013). Such deviations are often attributed to a reduced ability of the alpha male to mate-guard females, resulting in the increased success of alternative male reproductive tactics, such as coalitions or sneak matings (Gemmell et al. 2001, Wroblewski et al. 2009, Young et al. 2013). Others have suggested that these deviations occur because of female choice for non-alpha males (Soltis et al. 1997, Dubuc et al. 2011, Young et al. 2013).

In species that live in permanent one-male groups, males in the population interact relatively infrequently, especially outside of the breeding season (Rowell 1988), but even such infrequent interactions can provide insights into dominance relationships. Two studies of one-male species assigned ranks to males in the population. Cords (1984) observed a group of redtail monkeys for 23 months – a period that included a multi-male influx – and constructed a male dominance hierarchy based on dyadic agonistic interactions. After correcting for tenure length, high-ranking males had higher mating success than did low-ranking males in one three-month time block, with inconsistent results during the second three-month time block when few matings occured. Low-ranking males also copulated primarily with non-conceptive females while the highest-ranking male copulated only with females who produced infants later. The ability of the highest-ranking male to monopolize access to the potentially-conceptive females also suggests that male rank contributed to successful reproduction in this population.

Harding and Olson (1986) carried out a similar analysis for a group of patas monkeys during an influx year, demonstrating that male rank had no effect on male mating success. Although not a statistically significant difference when adjusted for observation time, the highest-ranking male completed the fewest copulations while the lowest-ranking male completed the most copulations. If this latter trend is substantiated, it may indicate that low-ranking males can acquire opportunistic matings when higher-ranking males are distracted by other rivals in the group. The relationship between male rank and mating requires further evaluation across species and will benefit by including more species living in one-male groups.

Male competitive ability, as measured by body size, seems to play a large role in determining siring success in species in which males hold territories. The effect of the presence of competitor males and their relative dominance ranks has not been as well studied in one-male species, possibly because competitor males are more difficult to identify than in multi-male species. Moreover, agonism among bachelors or among residents may be relatively infrequent, making it difficult to assign relative ranks to males following the same reproductive tactic. Future studies should consider all males with even temporary access to groups as potential competitors and use all occurrences of agonism among them to quantify the strength of male-male contest competition and assess its effect on male reproduction.

II.B.3. Female preference for novel males

There is some evidence from primates that females prefer to mate with males with whom they have not mated (or reproduced) in the past, i.e., novel males (Manson 1995). Female preference for novel males may reduce father-daughter inbreeding (Huffman 1992). Alternatively or in addition, a preference for novelty may increase genetic diversity among a female's offspring (Small 1993), which can be adaptive in unpredictable environments (Jennions & Petrie 2000). Genetic diversity among a female's offspring may be particularly important when a female produces litters and infant mortality is high, because it allows a female to hedge her bets (Yasui 2001). Finally, there may be selection for mating with novel males if this preference allows females to mate multiply and thereby increase paternity confusion and reduce the probability of infanticide (Hrdy 1981). The risk of infanticide should be higher in one-male groups than multi-male groups if a male's reproduction is restricted to the relatively short period of residency (Borries & Koenig 2000). As infanticide usually occurs during male takeovers (van Schaik & Janson 2000), females may reduce the probability of infanticide by mating with males who have a high probability of becoming a new resident (Wolff & Macdonald 2004).

In one-male groups, length of resident tenure is a good proxy for novelty; if females are choosing to mate with novel males, a reduction in resident paternity success should occur with increased tenure. In patas monkeys, there was no relationship between tenure and number of offspring (Ohsawa et al. 1993), though sample sizes were small (N=9 offspring), which reduces the strength of the conclusion. Additionally, frequent resident turnovers likely weaken the relationship between tenure and reproduction because different residents are present for sequential conceptions by the same female, and therefore each resident represents a novel mate (Manson 1995). Five of the 8 mothers represented only had one offspring in the data set, which may have contributed to the lack of a tenure effect.

Additional studies investigating the effect of tenure on resident reproductive success have been confined to multi-male primate species. Altmann et al. (1996) studied the relationship between a male's total tenure and the number of offspring in yellow baboons (*Papio cynocephalus*). All male baboons with tenure less than a year produced no offspring, while those who remained in the group for at least a year produced 0 to 3.14 offspring annually. The authors concluded that tenure was positively correlated with reproductive output. In this population, however, factors other than tenure length may have affected the fact that males with tenure of less than one year had no offspring. For example, young males may move between groups more often (Pusey 1987) and sire fewer offspring than prime-aged adult males because of low dominance rank (McMillan 1989, Chism & Rogers 1997, Kuester & Paul 1992, Bercovitch 1986) or low fertility (Kuester et al. 1995). Therefore, the age of the short-tenured, non-reproducing males may confound the analysis.

Patterns of reproduction in provisioned Japanese macaques (*Macaca fuscata*) and captive vervet monkeys (*Cercopithecus aethiops*) supported the predicted negative relationship between tenure and male reproduction (Inoue & Takenaka 2008, Weingrill et al. 2011), though in rhesus macaques (*Macaca mulatta*) and mandrills (*Mandrillus sphinx*), there was no consistent relationship between the variables (Manson 1995, Charpentier et al. 2005b). The lack of a relationship may indicate that female preferences are situation-dependent; for example, there may be a threshold effect with females exercising choice for novelty only if the resident has been in the group for a certain number of years. Alternatively, female preferences may be constrained by male-male competition determining the availability of novel mates (Manson 1995). Teasing apart the effects of female choice and male-male competition is difficult in wild populations; studies in captivity (e.g., Nikitopoulos et al. 2005) would allow experimental manipulation of independent variables and would contribute to our understanding of female choice.

CONCLUSION

Studies of mating and paternity have highlighted the differences between social and mating systems, challenging the assumption that increased access to females guarantees male reproductive success (Kappeler & van Schaik 2002). Specifically, studies of one-male groups demonstrate that the resident male does not always have a monopoly over reproduction in his group, although residents do seem to have a reproductive advantage over bachelors. Siring success of both residents and bachelors is probably linked to female group size and reproductive synchrony, although the density of competitor males and female choice for novel mates may also affect patterns of reproduction.

Future research should focus on understanding how short-term reproductive tactics translate into lifetime reproductive success and how often males move between resident and bachelor tactics. Specifically, more studies quantifying bachelor siring success and including multiple groups and multiple years are necessary to assess the relative success of these two tactics. These data would provide insight into whether males pursuing the high-risk high-gain resident strategy have a reduced reproductive lifespan. If so, can a lifelong bachelor sire an equal number of offspring by stealing matings over a longer period? While a few long-term studies of mammalian populations have increased our understanding of lifetime reproductive success, variation among species and populations means that their results may not apply to all mammals. More direct studies of lifetime reproductive success are badly needed.

CHAPTER 3

Factors Affecting Low Resident Siring Success in One-Male Groups of Blue Monkeys

Accepted for publication in *Behavioral Ecology*, March 2014

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ABSTRACT: 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 conceptive 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.

KEYWORDS: paternity, alternative mating tactics, reproductive synchrony, male-male competition, 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 (Schülke & 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 towards males, who face high competition for reproductive opportunities and high variation in reproductive success (Clutton-Brock & Parker 1992, Kvarnemo & Ahnesjo 1996). Variation among males may be particularly pronounced in species that live in one-male groups, in which one resident male is consistently associated with a group of females, while non-resident males (i.e., bachelors) live outside heterosexual groups. Increased proximity to females should give resident males a reproductive advantage (Emlen & Oring 1977, Clutton-Brock 2009), although bachelors may have opportunities to mate and sire offspring by sneaking copulations during temporary intrusions (Wolff 2008). 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 & Rajpurohit 1989, red deer: Pemberton et al. 1992, greater sac-winged bat: Heckel & von Helversen 2002, samango monkey: MacLeod et al. 2002, southern elephant seal: Fabiani et al. 2004, hamadryas baboon: Swedell & Saunders 2006, Przewalski's horse: Feh & Munkhtuya 2008, ring tailed coati: Hirsch & 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 & Armitage 1980, red howler monkey: Pope 1990, Hanuman langur: Launhardt et al. 2001).

Altmann’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 one 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 & Koenig 2012). While 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 one 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 & 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 & Rogers 1997, Carlson & 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 & Takenaka 2008, Weingrill et al. 2011, but see Manson 1995, Charpentier et al. 2005b). 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 2000b). 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 2002c). 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 2002c). 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 conceptive 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. 1,580 m.), a semi-deciduous 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 &

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 three to six 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 (Supplement 1) 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 & 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 two weeks after birth (6%). While we are unable to verify the extent 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 three samples per individual to ensure an adequate quantity. We collected samples in sterile tubes, mixing fecal matter with RNALater™ (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 QIAamp® DNA Stool Mini Kit (Qiagen) following the manufacturer's protocol with modifications at five stages: step 2) overnight in ASL buffer, step 6) centrifuged for 6 minutes, step 8) 35 ul of Proteinase K, step 11) incubated for 30 minutes, and step 18) 75 ul AE buffer and incubated for 15 minutes. We amplified the DNA at 14 human MapPairs® microsatellite markers (Invitrogen) using the Qiagen® Multiplex PCR Kit (Supplement 2). Reaction conditions for all primer pairs were: initial denaturation at 94º C for 15 minutes, 37 cycles of denaturation at 94º C for 30 seconds, annealing at 53º C for 1 minute 30 seconds, and extension at 72º C for 1 minute, then a final extension at 60º C for 30 minutes. 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 seven 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 one 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 one 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 two 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 & 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 (Supplement 3). We ran CERVUS 10 times to test values that spanned the observed range (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 one locus. Similarly, when the resident was assigned as sire (N=68 offspring), he mismatched at zero or one locus only and we concluded that the resident was the sire of these offspring. Most offspring assigned to another male (25 of 36) mismatched the resident at two or more loci and had only zero or one mismatch with their assigned sire. The remaining offspring assigned to another male (11 of 36) had zero or one 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 two or more loci and was therefore excluded as the true sire (N=4). If the resident and offspring mismatched at two or more loci (7 of 22), we concluded that the resident was not the sire. If the pair mismatched at zero or one 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: (a) 2 offspring assigned to the resident mismatched at 2 loci (instead of 0 or 1) and the resident was excluded as the sire, and (b) 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 three 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 offspring was conceived. We first identified a conception window by subtracting the length of one 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±3.0, 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 two 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 proceptive behavior (i.e., lip-puckering, presenting hindquarters, and persistent following) to extend or connect these estrus days if they occurred within two 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 conceptive estrus periods to 86 of the 111 offspring for which we could conclusively assign or exclude the resident as sire. The mean length of the conceptive estrus periods was 4.19±4.49 days (range=1-22, N=86). Estrus 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 date. 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 & 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 three 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 & Schielzeth 2011). We did not use stepwise methods to minimize the probability of erroneously rejecting the null hypothesis (Type I error) (Mundry & 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 2005).

Multicollinearity was low for all predictors (variance inflation factors ranged from 1.02 to 1.21 for all models). To determine if 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 non-conceptive estrus, and males present per day during each mating season (June 1-October 31) for each group.

We used generalized linear mixed models (GLMM) 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 65 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±1.8 loci. The 70 mothers (including 6 female offspring that conceived during the study period) were genotyped at a mean of 12.8±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 eleven 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 58% ± 34% of the offspring conceived in his group during our observations, but there was high variation in siring success among residents (range=0-100%; Fig 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 conceptive 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: χ^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 non-conceptive estrus was not significantly better at predicting the probability of resident siring success than the null model (log-likelihood ratio test: χ^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/odds ratio=2.366, number of competitors: 1/odds ratio=4.092; Table 1A). Each additional female in conceptive estrus decreased the odds that the resident sired an offspring by 58% (Fig 2) and each additional competitor decreased the odds that the resident sired an offspring by 76% (Fig 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 conceptive 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 conceptive estrus only, we found that effects of all three 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 conceptive estrus per day (generalized linear mixed model: $\beta \pm SE=0.011 \pm 0.003$, $z=3.22$, $p=0.001$; Table S4.1 & Fig S4.1) and the average number of females in conceptive or non-conceptive estrus per day (generalized linear mixed model: $\beta \pm SE=0.020 \pm 0.009$, $z=2.19$, $p=0.029$; Table S4.2 & Fig S4.2) 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 (generalized linear mixed model: $\beta \pm SE=0.109 \pm 0.047$, $z=2.30$, $p=0.021$; Table S4.3 & Fig S4.3).

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 towards 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 eight populations with high (>80%) resident siring success, most and possibly all live in small groups (i.e., fewer than five 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 six females, suggesting a decrease in the resident's ability to guard more than five females simultaneously (Kaseda & Khalil 1996). However, two 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 six of the seven 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 & 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 (Cohas et al. 2006, Kutsukake & Nunn 2009, Alberts 2012, Gogarten & Koenig 2012, Lardy et al. 2012) or higher reproductive synchrony (Say et al. 2001, Ostner et al. 2008, Gogarten & 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 stronger evidence that the presence of many estrous females attracts outside males rather than vice-versa (Cords 2002c, Mugatha et al. 2007). While 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/hour; Cords, unpublished data from 86 hours 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 conceptive estrus, the number of females in conceptive or non-conceptive 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 Non-Conceptive 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 & 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-ranking males – such as residents in one-male groups – should face the fewest constraints in selecting mating partners and therefore be best able to mate selectively (Gesquiere 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 conceptive. However, we found that the model that measured female synchrony as the number of females in conceptive or non-conceptive 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 conceptive estrus period, suggesting that resident males may be able to differentiate between conceptive and non-conceptive 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 towards cycles or days when the female is most likely to conceive (Deschner et al. 2004, Engelhardt et al. 2004, Gesquiere 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, Rigaill 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 non-conceptive. Rates of conception failure and miscarriage have been calculated for other primates (e.g., Beehner 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 & 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 (Huffman 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 & 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 & 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 & Fuller 2010), it may be that takeovers by infanticidal males are too unpredictable for females to adjust their attraction to non-residents 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 tenures years also appeared in the dataset 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 population-wide. 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 two 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 conceptive *or* non-conceptive estrus, however, did not affect resident male siring success, suggesting that residents may be able to differentiate between conceptive and non-conceptive 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.

Table 1 Results of logistic regressions that based female reproductive synchrony on conceptive estrus of other females in the group. 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) All Offspring					(B) Without RO's Offspring				
Model Parameters	Coef	SE	Wald z	P	Odds Ratio[a]	Coef	SE	Wald z	P	Odds Ratio[a]
Female Synchrony	-0.861	0.356	-2.417	0.016*	0.423 (2.366)	-0.838	0.328	-2.556	0.011*	0.433 (2.312)
# Competitors	-1.409	0.691	-2.038	0.042*	0.244 (4.092)	-0.801	0.307	-2.608	0.009*	0.449 (2.228)
Tenure	0.122	0.426	0.287	0.774	1.130	0.685	0.433	1.584	0.113	1.984
Intercept	0.507	0.610	0.832	0.406	1.660	1.504	0.371	4.058	<0.001*	4.500

* parameter is significant at $\alpha<0.05$

[a] for odds ratios <1, we present the inverse in parentheses

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. 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 paternity results from one-male groups only.

Species (Population)	**Female Group Size**[a]	**% Offspring Sired by the Resident**	**# of Offspring**	**# of Birth Cohorts**	**# of Residents**	**Refs**[b]
White-lined bat	Small	30%	93	3	18	1, 2
Northern elephant seal	Large	39%	90	1	Not specified	3
Southern elephant seal (Peninsula Valdes, Argentina)	Large	58%	50	1	Not specified	3
Blue monkey	Large	61%	126	10	11	This study
Indian fruit bat	Medium	64%[c]	185	2	Not specified	4, 5
Feral horses (Nevada, USA)	Small	67%	43	4	Not specified	6
Southern elephant seal (Falkland Islands)	Large	69%[d]	183	2	Not specified	7
Red deer	Small	84%[ef]	45	2	67	8, 9

Table 2 continued

Species (Population)	**Female Group Size[a]**	**% Offspring Sired by the Resident**	**# of Offspring**	**# of Birth Cohorts**	**# of Residents**	**Refs[b]**
Ring-tailed coati	Small/Medium	85%	65	2	3	10
Feral horse (Misaki, Japan)	Small	85%	99	16[g]	14	11
Przewalski's horse	Small	97%[e]	59	11[g]	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[g]	14	19, 20

[a]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.

[b]1. Bradbury & Emmons (1974); 2. Heckel & 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 et al (1982); 9. Pemberton et al (1992); 10. Hirsch & Maldodano (2011); 11. Kaseda & Khalil (1996); 12. Feh & Munkhtuya (2008); 13. Downhower & Armitage (1971); 14. Schwartz & Armitage (1980); 15.

Table 2 continued

Pope (1990); 16. Rudran & Fernandez-Duque (2003); 17. Borries (2000); 18. Launhardt et al (2001); 19. Dunbar (1984); 20. Snyder-Mackler et al (2012)

[c]Percentage sired by any resident in the colony (treated as a maximum)

[d]Percentage sired by the resident with the longest tenure during the mating season

[e]Percentage sired by any one of the males that held the female in his harem during her conceptive window

[f]Calculation excludes offspring conceived during the tenure of unsampled residents

[g]Measured in years, number of birth cohorts not specified

Fig 1 Offspring conceived during the observed tenures of 11 resident males, showing those sired by the resident (gray) and those sired by other males (white). These offspring include the 111 for which the resident could be conclusively assigned or excluded. Parentheses indicate the number of mating seasons during which each male was observed as resident.

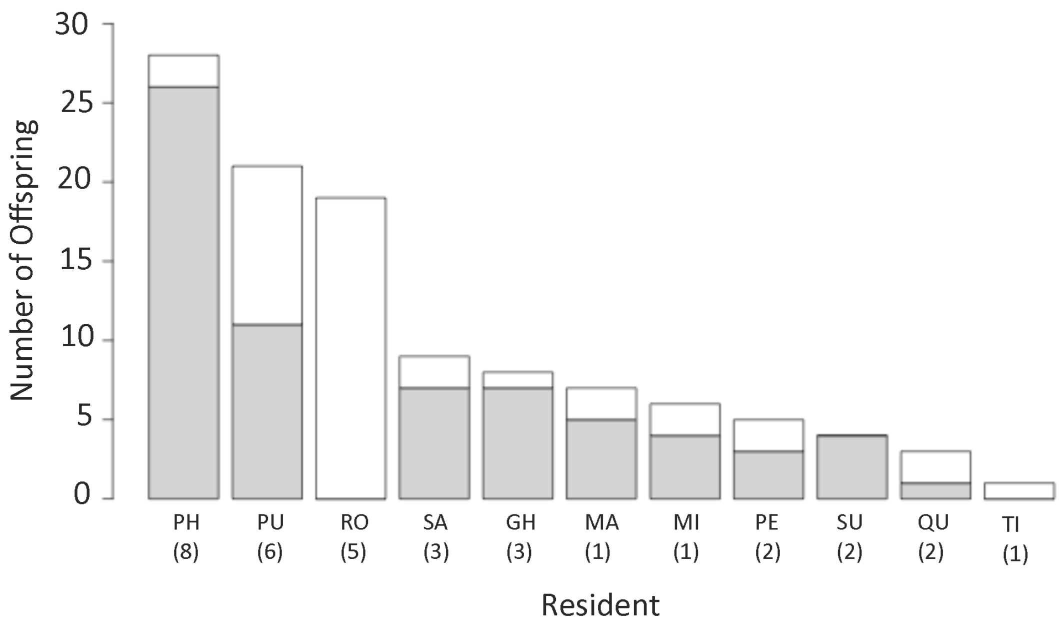


Fig 2 Probability that a resident sired an offspring conceived in his group as a function of the number of females in conceptive estrus as determined by the logistic regression (line) and the actual data (circles). To plot the real data, we separated it into 5 groups by the number of conceptive estrus 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.

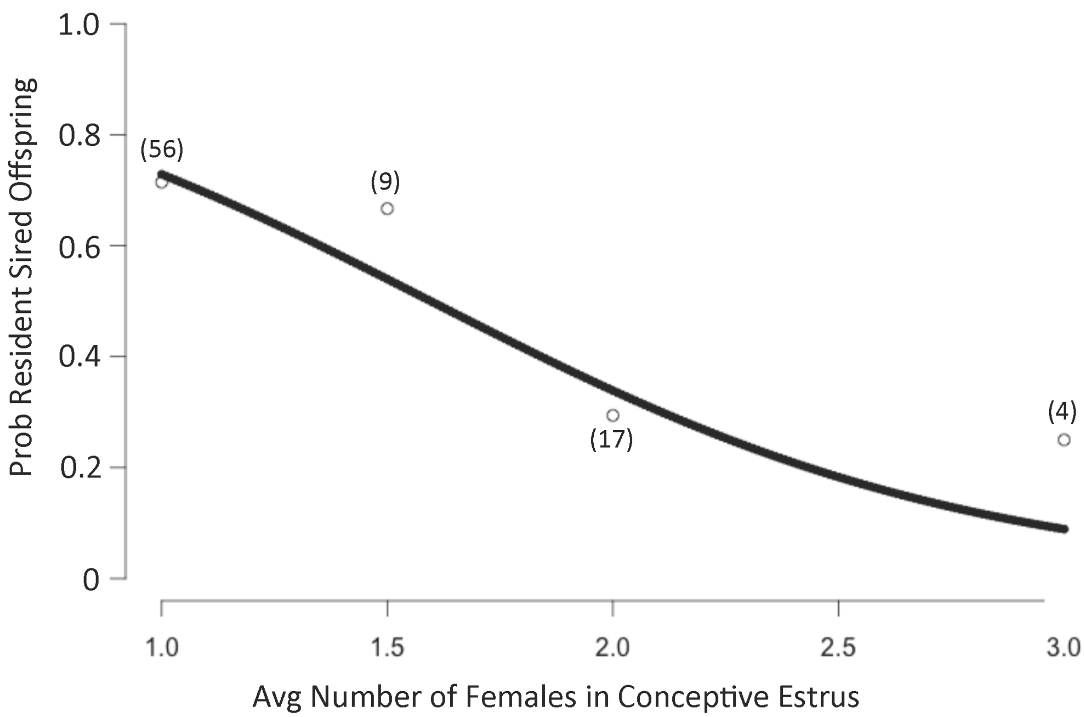
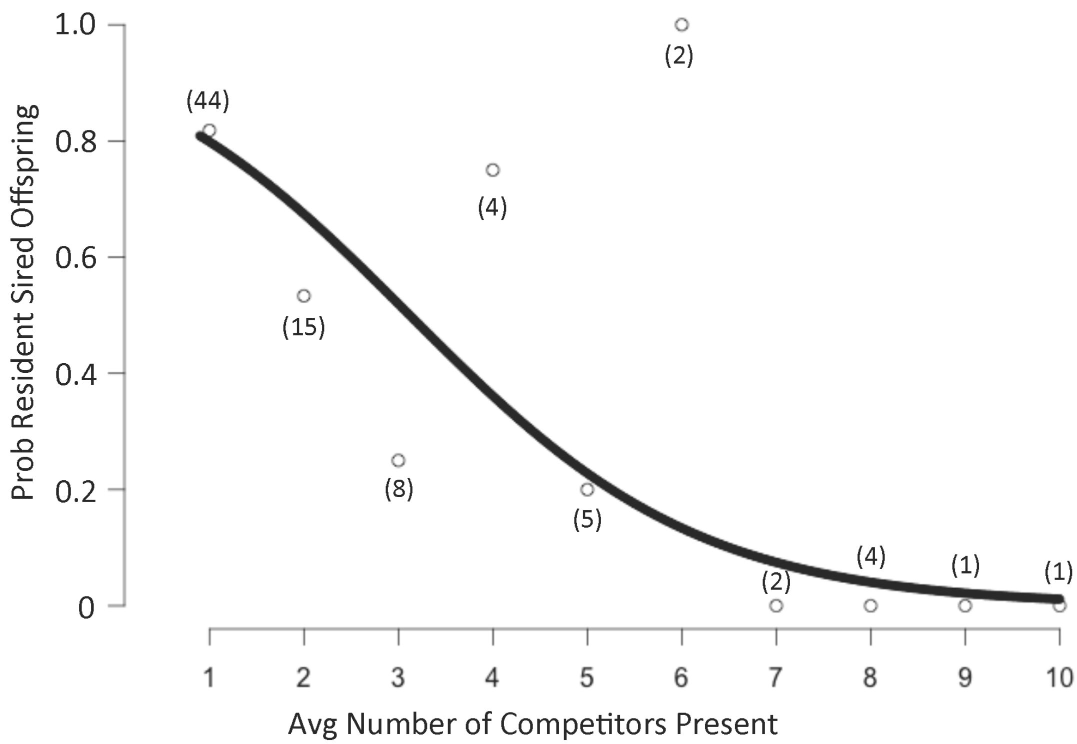


Fig 3 Probability that a resident sired an offspring conceived in his group as a function of the number of competitors present as determined by the logistic regression (line) and the actual data (circles). To plot the real data, we separated it into 10 groups by the number of competitors present (i.e., 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.



S1 The distribution of the 126 genotyped offspring by groups and year of conception. In all cases, the number of mothers per group-year is equal to the number of offspring. The letters in parentheses indicate the identity of the resident male present during the mating season. Gray cells indicate that paternity data were not available, either because we did not have samples from the residents present during those years and therefore could not assess resident siring success or because the group was formed or eliminated via group fission and therefore did not exist during those years.

Year	Tw	Gn	Gs	Twn	Tws	Gsa	Gsaa	Gsc
2002	12 (PU)							
2003	5 (PU)							
2004	2 (PU)	5 (PH)						
2005		5 (PH)	4 (GH)	4 (PU)	10 (RO)			
2006		2 (PH)	4 (GH)	2 (PU)	0 (RO)			
2007		6 (PH)	1 (GH)	1 (PU)	4 (RO)			
2008		5 (PH)	7 (MI)	2 (SU)	9 (RO)			
2009		5 (PH)		3 (SU)	0 (RO)	3 (SA)		
2010		2 (PH)		1 (QU)	1 (TI)		3 (SA)	2 (PE)
2011		0 (PH)		2 (QU)	8 (MA)		3 (SA)	3 (PE)

S2 Allele variation and heterozygosity indices for the 14 blue monkey microsatellite markers as calculated by Cervus 3.0

Locus	Primer Sequence 5' – 3'	Size Range (base pairs)	Number of Alleles	H_O [1]	H_E	HWE [2]	PIC [3]	Null Allele Frequency
D1S207[567]	CACTTCTCCTTGAATCGCTT GCAAGTCCTGTTCCAAGTCT	130-158	9	0.677	0.657	NS	0.626	-0.02
D1S548	GAACTCATTGGCAAAAGGAA GCCTCTTTGTTGCAGTGATT	205-290	10	0.892	0.835	NS	0.813	-0.0354
D2S119	CTTGGGGAACAGAGGTCATT GAGAATCCCTCAATTTCTTTGGA	205-233	10	0.739	0.708	NS	0.672	-0.0235
D3S1238	TGAGACCCTGTCTCTGAAAC TGTATGGGCTCTTGAAATTG	116-136	7	0.65	0.632	NS	0.579	-0.0098
D3S1766[6]	ACCACATGAGCCAATTCTGT ACCCAATTATGGTGTTGTTACC	202-242	11	0.877	0.805	NS	0.778	-0.0457
D5S111	GGCATCATTTTAGAAGGAAAT ACATTTGTTCAGGACCAAAG	151-175	10	0.858	0.8	NS	0.772	-0.0371
D5S117[6]	TGTCTCCTGCTGAGAATAG TAATATCCAAACCACAAAGGT	141-156	6	0.879	0.8	NS	0.769	-0.0505
D6S311[67]	ATGTCCTCATTGGTGTTGTG GATTCAGAGCCCAGGAAGAT	205-253	9	0.799	0.729	NS	0.689	-0.0528
D7S817	TTGGGACCTCTTATTTTCCA GGGTTCTGCAGAGAAACAGA	147-191	9	0.847	0.779	NS	0.742	-0.0428
D8S1106	TTGTTTACCCCTGCATCACT TTCTCAGAATTGCTCATAGTGC	123-165	9	0.794	0.798	NS	0.773	0
D10S611	CATACAGGAAACTGTGTAGTGC CTGTATTTATGTGTGTGGATGG	143-175	8	0.821	0.801	NS	0.771	-0.0132
D11S2002	CATGGCCCTTCTTTTCATAG AATGAGGTCTTACTTTGTTGCC	219-270	15	0.872	0.808	NS	0.789	-0.0446
D17S1290	GCCAACAGAGCAAGACTGTC GGAAACAGTTAAATGGCCAA	163-189	8	0.761	0.674	*	0.635	-0.0713

S2 continued

Locus	Primer Sequence 5' – 3'	Size Range (base pairs)	Number of Alleles	H_O [1]	H_E	HWE [2]	PIC [3]	Null Allele Frequency
D18S72[8]	GCTAGATGACCCAGTTCCC CAAGAGAGCCCTTTGGTTT	171-189	8	0.796	0.771	NS	0.737	-0.0213

[1] H_O = observed heterozygosity; H_E = expected heterozygosity

[2] Hardy Weinberg Equilibrium: NS = not significant; * = $p<0.05$; significant results indicate deviation from HWE after Bonferroni correction (Cervus 3.0).

[4] PIC = polymorphic information content

[5] Identified in *Cercopithecus lhoesti, C. solatus, C. cephus, C neglectus, C. nictantans, C. pogonias* (Clisson et al., 2000)

[6] Identified in *Cercopithecus campbelli* (Petit et al., 2010)

[7] Identified in *Cercopithecus solatus* (Charpentier et al., 2005)

[8] Identified in *Chlorocebus aethiops sabaeus* (Weingrill et al., 2011)

S3. CERVUS input parameters and paternity assignment

CERVUS allows users to manipulate the proportion of males in the population that were sampled. This parameter is specified during the paternity simulation step in CERVUS and are thus the same for all offspring included in each paternity assignment run (Marshall et al. 1998). The proportion of observed males that contributed samples varied greatly over the 10-year study period. Calculating the proportion of males sampled was also complicated by observations of males that were not seen well enough to be identified individually (i.e., “unidentified males”). We therefore calculated the proportion of sampled males in two ways to provide a range of possible values, based on our observations (Table S3). Counting each unidentified male as a unique individual likely underestimated the proportion of candidate males sampled if some of the records of unidentified males referred to the same individual. Excluding observations of unidentified males likely overestimated the proportion of candidate males sampled if some of the unidentified males were individuals that were not present frequently enough to be consistently recognized. These two calculations thus give the lower and upper bounds of this input parameter. Given the large variation in the proportion of males sampled based on the year and calculation method, we ran the paternity assignment analysis using ten different settings that spanned the observed range (0.1 to 1). Comparing the assignments across these runs allowed us to test the robustness of the paternity assignment.

Table S3 Proportion of candidate fathers in the population that were sampled each year, used in the CERVUS paternity simulation. Proportions were calculated in two ways to provide a range of possible values, both including and excluding males who were not individually-recognized by observers.

	Counting each unidentified male as a unique individual		**Excluding unidentified males**	
Year	# Candidate males in population	Proportion sampled	# Candidate males in population	Proportion sampled
1	45	0.11	19	0.26
2	54	0.19	23	0.45
3	73	0.18	33	0.39
4	79	0.20	36	0.44
5	28	0.54	24	0.63
6	66	0.27	29	0.62
7	57	0.40	26	0.88
8	57	0.49	30	0.93
9	116	0.21	28	0.86
10	96	0.36	35	1
Mean	**67.1**	**0.30**	**28.3**	**0.65**
Sd	**25.4**	**0.14**	**5.46**	**0.26**

S4. The Effect of Group Size

Table S4.1 Results of GLMM that based the number of females in conceptive estrus on the average number of females in the group. Group identity was included as a random effect (variance=0).

Model Parameter	Coef	SE	Wald z	P	Odds Ratio
Avg Female Group Size	0.011	0.003	3.220	0.001*	1.011
Intercept	-0.016	0.045	-0.350	0.724	1.016

Fig S4.1 Relationship between female group size and conceptive estrus synchrony. Each point represents one group in one mating season, with symbols corresponding to group identity.

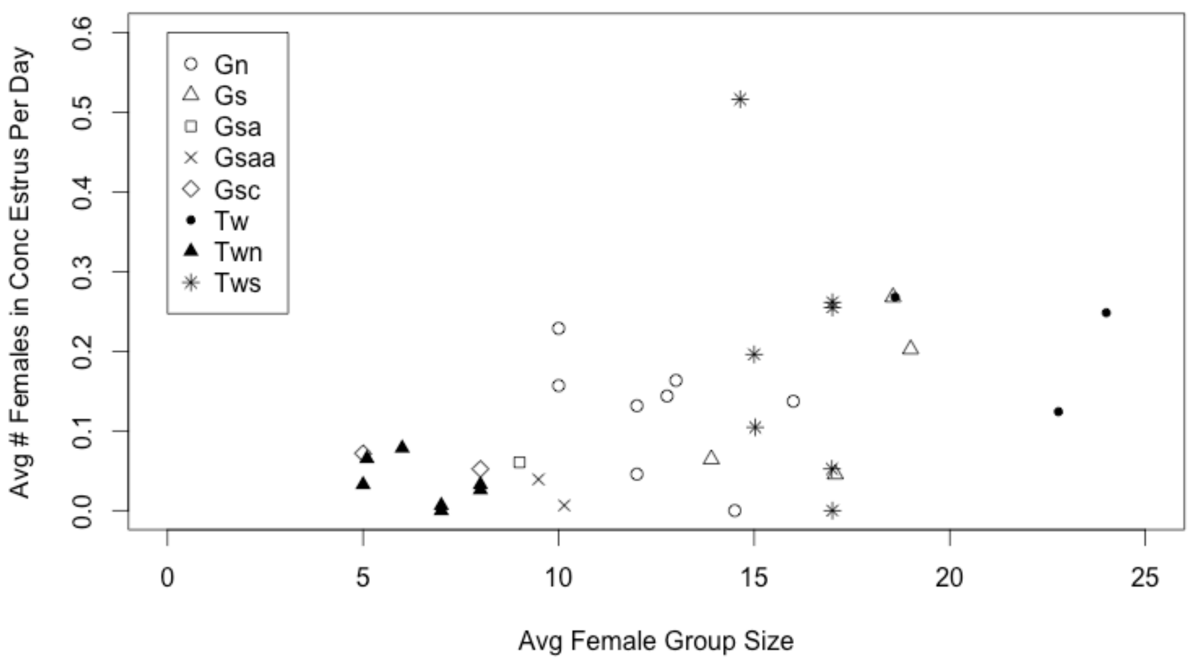


Table S4.2 Results of GLMM that based the number of females in estrus on the average number of females in the group. Group identity was included as a random effect (variance=0.001).

Model Parameter	Coef	SE	Wald z	P	Odds Ratio
Avg Female Group Size	0.020	0.009	2.190	0.029*	1.020
Intercept	0.228	0.126	1.810	0.070	1.256

Fig S4.2 Relationship between the female group size and estrus synchrony (conceptive and non-conceptive estrus). Each point represents one group in one mating season, with symbols corresponding to group identity.

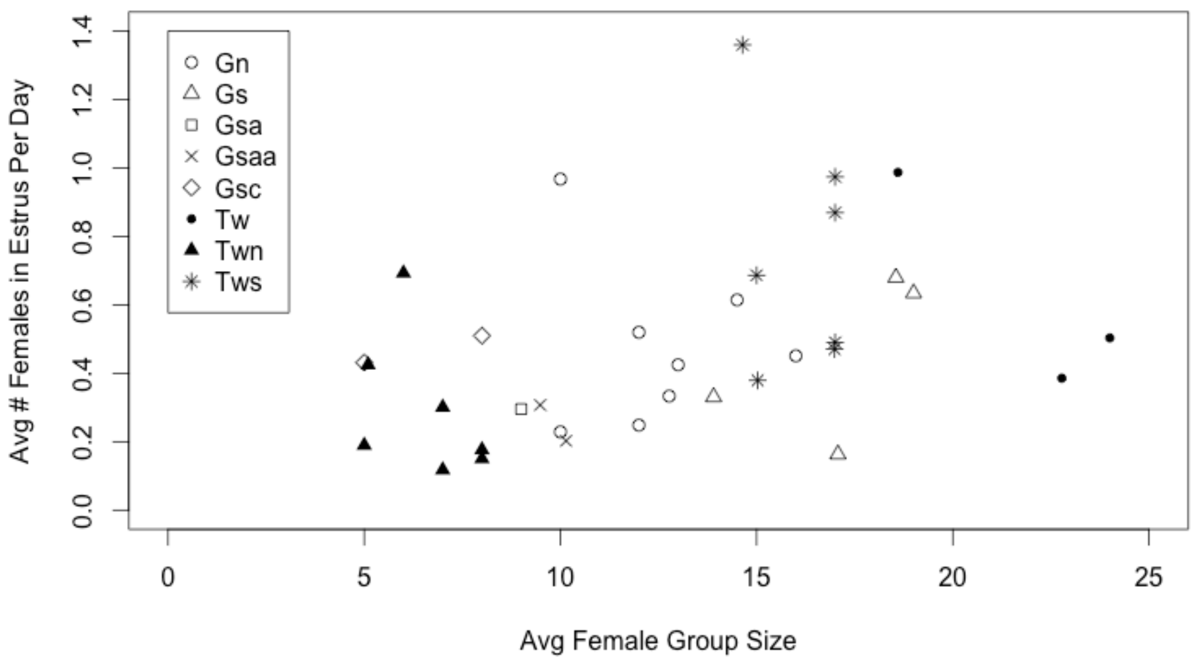
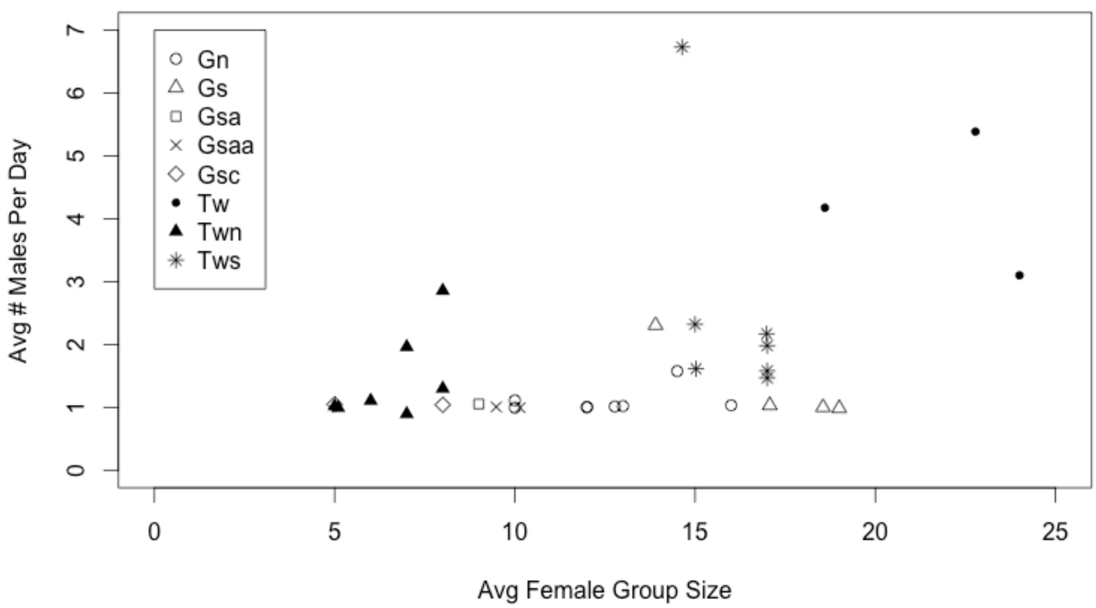


Table S4.3 Results of GLMM that based the number of males on the average number of females in the group. Group identity was included as a random effect (variance=0.211).

Model Parameter	Coef	SE	Wald z	P	Odds Ratio
Avg Female Group Size	0.109	0.047	2.300	0.021*	1.115
Intercept	0.374	0.662	0.570	0.572	1.454

Fig S4.3 Relationship between the female group size and the number of competitor males. Each point represents one group in one mating season, with symbols corresponding to group identity.



CHAPTER 4

Life as a Bachelor: Quantifying the Success of an Alternative Reproductive Tactic in Male Blue Monkeys

ABSTRACT

In species that live in one-male groups, resident males monopolize access to a group of females and are assumed to have higher reproductive success than bachelors. We tested this assumption using genetic, demographic, and behavioral data from 8 groups of wild blue monkeys observed over 10 years to quantify reproduction by residents and bachelors and compare the success of the two strategies. We used maximum-likelihood methods to assign sires to 104 offspring born in the study groups, 36 of which were sired by extra-group males, i.e., residents of adjacent groups and bachelors. A Cox proportional hazards test indicated that when a resident male did not monopolize reproduction in his group, residents of adjacent groups were more likely to sire offspring than bachelor males. When bachelors competed for reproductive opportunities with other bachelors, neither rank nor time spent in group affected the probability that a bachelor sired an offspring, suggesting that opportunistic mating with females in conceptive estrous plays some role in bachelor reproduction. We used long-term data to estimate resident and bachelor reproductive success to determine if there are any circumstances under which a typical bachelor may sire as many offspring as a typical resident during one or two periods of residency. Our findings generally support the assumption of a resident reproductive advantage because in most circumstances, a lifelong bachelor would be unable to sire as many offspring as a resident. However, a bachelor who performs at the average rate in the average number of groups for several years may have similar lifetime reproductive success as a male whose reproduction is limited to one short period of residency, especially in a small group. Our findings suggest that one should not assume a resident reproductive advantage for all males in all circumstances.

KEYWORDS: siring success, one-male groups, male-male competition, comparing alternative reproductive tactics, male reproductive lifespan

INTRODUCTION

In species with strong male-male competition for females, individual males often adopt various behaviors or alternative reproductive tactics (ARTs) to maximize reproductive output within the constraints of current social, demographic, and ecological conditions (Dominey 1984, Gross 1996, Neff & Svensson 2013). In male mammals, ARTs usually have unequal fitness payoffs; the most competitive males use the tactic with the highest payoff, while less competitive males use surreptitious behaviors to gain access to females, resulting in lower reproductive success (Setchell 2008, Wolff 2008, Taborsky & Brockmann 2010). Individuals may, however, switch tactics over the course of a lifetime or even during a single breeding season, so even tactics that produce few offspring can be evolutionarily stable if males use an evolved decision rule to identify the tactic that will have the biggest payoff under current conditions (Repka & Gross 1995, Gross 1996, Brockmann 2001). The tactic used at any given time likely depends on several factors, including relative competitive ability, the number of other males pursuing each tactic, and the costs and benefits of each tactic (Repka & Gross 1995, Taborsky & Brockmann 2010).

Many mammals live in one-male/multi-female groups, a type of social organization in which one resident male is consistently associated with a group of females while bachelor males live alone or form bachelor groups. Males compete for the resident position (e.g., Le Boeuf 1974, Clutton-Brock 1982, Tsingalia & Rowell 1984), suggesting that the resident tactic of defending access to a group of females results in higher fitness than the bachelor tactic of stealing matings. Paternity studies from several one-male species strongly support this prediction, in that residents sired all offspring born in their groups (marmot: Schwartz & Armitage 1980, red howler monkey: Pope 1990, Hanuman langur: Launhardt et al. 2001), which suggests that lifelong bachelors do not sire any offspring. In studies of other one-male species, however, residents lost paternity of some offspring to outsiders, including bachelors and residents of adjacent groups (feral horse: Bowling & Touchberry 1990, Asa 1999, Gray 2009, red deer: Pemberton et al. 1992, elephant seal: Hoelzel et al. 1999, Fabiani et al. 2004, Indian fruit bat: Storz et al. 2001, white-lined bat: Heckel & Von Helversen 2003, Przewalski's horse: Feh & Munkhtuya 2008, ring-tailed coati: Hirsch & Maldonado 2011, blue monkey: Roberts et al. 2014). The possibility that bachelors sire some offspring suggests that an ART exists in these species, though the absolute success of individual bachelors and their success relative to residents has rarely been quantified.

Factors Affecting Bachelor Siring Success

Just as maintaining residency is presumed to ensure a male's access to conceptive females (Emlen & Oring 1977, Clutton-Brock 1989), bachelors that spend more time near a group should increase their chances of encountering conceptive females. The consistent presence of intruders may also increase the time that a resident must spend chasing away rivals and defending access to his females, which may give intruders more opportunities to steal matings (Roberts et al. 2014).

Dominance rank may also influence bachelor success. Rank probably indicates a male's relative competitive ability, though the importance of rank in determining siring success is variable across populations (Ellis 1995, Majolo et al. 2012, Alberts 2012). Males compete to be resident in one-male groups, and thus it is likely (and often very clear) that resident males outrank bachelors. The relative ranks of bachelors, however, may influence how they partition paternity among themselves when the resident does not monopolize paternity in his group. Several studies of guenons have ranked bachelor males that joined a group during a temporary breeding-season influx of multiple males, and found both a positive and no effect of male rank on mating success, depending on the days and males included in the analysis (Cords 1984, Tsingalia & Rowell 1984, Cords et al. 1986, Harding & Olson 1986). No studies have ranked bachelors in years in which the one-male social organization is maintained, nor have any studies ranked bachelors in one-male species that do not experience influxes. In both cases, bachelors may have opportunities to steal matings (Wolff 2008).

Comparing Alternative Reproductive Tactics

Comparing the success of ARTs in invertebrates, reptiles, fish, and birds has been a focus of investigation for many years (e.g., bluegill sunfish: Gross 1982, salmon: Gross 1985, swordtail: Ryan & Causey 1989, marine isopod: Shuster & Wade 1991, side blotched lizard: Sinervo & Lively 1996, ruff: Widemo 1998). The relatively short lifespans of these species allow even short studies to capture a large proportion of a male’s reproductive career, increasing confidence that the observed patterns of reproduction are good indicators of lifetime reproductive success. Moreover, the existence of some genetically determined male morphs results in reproductive tactics that are fixed for life (e.g., horned versus unhorned beetles: Eberhard 1982), thereby avoiding the complications of following males that switch tactics during their reproductive careers.

Although research in other taxa has increased our understanding of the costs and benefits of ARTs, there are few studies that compare the success of tactics used by long-lived mammals in which males may adopt multiple tactics over a lifetime. The paucity of research on these species likely reflects the demands of tracking individual males over many years. Moreover, when groups live in close proximity, both residents and bachelors may augment their reproductive output by siring offspring in multiple groups in the same year (Heckel et al. 1999, Hoelzel et al. 1999, Lawler 2007). Thus, studies quantifying reproduction across a large spatial scale are necessary to obtain a complete picture of the success of each reproductive tactic.

A few studies of mammals living in one-male groups have used long-term observations of individual males to estimate male lifetime reproductive success (LRS) (red deer: Clutton-Brock et al. 1988, elephant seal: Le Boeuf & Reiter 1988, red tail monkey: Struhsaker & Pope 1991, greater sac winged bat: Nagy et al. 2012). Studies of red deer and elephant seals quantified variance in male LRS by tracking individuals over parts of their lifetimes (including periods of residency and bachelorhood) and estimating the number of females inseminated each year. In red deer, the most important predictor of LRS was the number of days a male held a harem; in elephant seals, female group size mattered most. Both results suggest that increased access to females translates into higher LRS, but neither study explicitly compared the success of resident versus bachelor males.

Other studies drawing on shorter-term data sets have estimated the LRS of resident and bachelor male primates to allow comparison (e.g., Sommer & Rajpurohit 1989, MacLeod et al. 2002). MacLeod et al developed a model to determine if, over an entire reproductive lifetime, a bachelor samango monkey could steal enough matings to make him as successful as a resident male. Using data on the average duration of resident tenure (1.67 years) and the proportion of matings obtained by the resident male (0.9) in their 3 study groups, they determined that a bachelor would have to pursue the steal strategy for 15.07 years to obtain the same number of matings as a resident in one average period of residency. They judged 15 years as likely to exceed the length of the male reproductive lifespan and concluded that a resident male with only one period of tenure still obtains more matings than a bachelor. Importantly, however, this model was based on short-term data and made several assumptions that are unlikely to hold for all species (e.g., residents and bachelors reproduce in a single group only). New models incorporating paternity data from more groups over many years will allow a more precise comparison of resident and bachelor LRS.

Study Species

We studied male reproductive tactics in blue monkeys, very close relatives of samangos, that also live typically in one-male groups and in which males actively compete for the resident position (Tsingalia & Rowell 1984). Bachelors and resident males of adjacent groups spend time in or on the edge of groups during all mating seasons, suggesting that a resident faces competition for access to his females even after attaining residency (Cords 2000b). In our study population, about 25% of mating seasons are characterized by particularly strong male-male competition when bachelors join the group for various periods, leaving when the mating season ends (Cords 2002c). These multi-male influxes are especially likely when multiple females are simultaneously estrous (Cords 2002c, Mugatha et al. 2007). Females do mate with bachelors (Cords et al. 1986, Cords 1988), and the presence of many females in conceptive estrus and many competitor males significantly reduces the probability that a resident male sires an offspring conceived in his group (Roberts et al. 2014). These findings suggest that stealing matings may be a profitable bachelor tactic.

Individual bachelors in the study population typically sired fewer offspring than residents within a single group-year (Roberts et al. 2014), but little is known about how following the resident or bachelor tactic translates into lifetime reproductive success. Comparing resident and bachelor reproductive success would help to determine if the high costs associated with residency allow bachelors to make up some of the difference in reproduction by pursuing the lower-cost, lower-gain tactic for an extended period (Widemo 1998, MacLeod et al. 2002). In other words, is a bachelor male is simply "making the best of a bad job" or does bachelorhood represent an alternative reproductive tactic that may result in similar reproductive success as residency?

We used molecular, demographic, and behavioral data collected from 8 social groups of wild blue monkeys over 10 years to assess the absolute and relative success of the bachelor tactic. First, we identified the factors predicting the siring success of extra-group males (i.e., bachelors and residents of adjacent groups). Second, we used rates of resident and bachelor siring success calculated across multiple groups and years to determine how long it would take the hypothetical "average bachelor" to sire as many offspring as the hypothetical "average resident" in a small or large group. Quantifying the success of alternative tactics and identifying the conditions under which each does best allows us to better understand the role of male-male competition in determining the evolution of social organization.

METHODS

Study Site and Population

The study population of blue monkeys is located in the Kakamega Forest, Kenya (Mitchell et al. 2009) and has been monitored since 1979 (Cords 2012). This study focuses on the period between 2002 and 2011. Three group fissions increased the number of study groups from three in 2002 to six in 2011; this study used data from 8 unique groups (Gn, Gs, Gsa, Gsaa, Gsc, Tw, Twn, Tws) present for varying length of time during the study period (range: 1-10 years). Authors and field assistants observed the groups on a near daily basis to record demographic information including infant birthdates, the presence of extra-group males and estrous females, and dates of resident male turnover. They also recorded all observed agonistic interactions among males, noting the identity of participants and the outcome.

Genetic Data

We used fecal samples from 126 infants, 64 mothers, and 60 adult males, including 11 resident males in our study groups, for genetic analysis. We collected samples shortly after defecation, storing them in sterile tubes mixed with RNALater™ (Ambion) in a ≥1:1 ratio to preserve the DNA.

Extraction and genotyping methods are described in Roberts et al. (2014). Briefly, we extracted DNA from fecal samples using the QIAamp® DNA Stool Mini Kit (Qiagen) and amplified it at 14 human MapPairs® microsatellite markers (Invitrogen). We used the ABI 3730 Automated DNA Analysis system and *GeneMapper 3.7* (Applied Biosystems) for genotyping. We replicated homozygous loci seven times to protect against false homozygosity from allelic dropout (Taberlet et al. 1996) and ran heterozygotes with weak signals at least twice. The program CERVUS indicated that locus

17s1290 was not in Hardy-Weinberg equilibrium, so we did not use this locus for paternity assignment.

We conducted likelihood-based paternity analysis with CERVUS *3.0* (Kalinowski et al. 2007), as described in Roberts et al. (2014). We ran paternity simulations based on 10,000 offspring and set confidence levels at 80% and 95% and the rate of mistyping at 2% (the mean value for the 13 loci). We included maternal genotypes and all males who had emigrated from their natal groups by the time of offspring conception were candidate fathers. The proportion of males in the population that were sampled varied across years, so we tested 10 values for this parameter and compared paternity results across CERVUS runs (for details see Roberts et al. 2014). CERVUS assigned a male as the sire of 108 of the 126 offspring. For 86 (80%) of these offspring, CERVUS assigned the sire with 95% confidence in all runs. For the remaining 22 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, so we considered the assignments to be robust.

We further verified assignments by examining the number of mismatches between the offspring and assigned sire. We counted mismatches for which both individuals were heterozygous, excluding homozygous mismatches because they may have resulted from allelic dropout. Mother-offspring pairs mismatched rarely and never at more than one locus. Similarly, 104 of the 108 offspring-assigned sire pairs mismatched at zero or one locus and we considered these assignments to be robust. The remaining four offspring mismatched their assigned sire at two loci, so we omitted them, leaving 104 offspring in the final analysis, 68 assigned to resident males and 36 to extra-group males.

Behavioral Data

We used demographic data from long-term population monitoring to identify social and demographic factors affecting the siring success of extra-group males. We were interested in how extra-group males compete among themselves for reproductive opportunities that a resident male fails to monopolize and therefore restricted this data set to the 36 offspring sired by bachelors and residents of adjacent groups. Specifically, we tested the effect of male status (i.e., bachelor or a resident of an adjacent group), the time spent in a group, and the dominance rank of bachelors on the probability that a male sired each offspring.

We identified a 29-day conception window for each offspring by subtracting the length of one gestation (176±14 days, the 95% confidence interval, Pazol et al. 2002) from offspring birthdates. Twenty-five of the 36 offspring (69%) had birthdates known to the day. The remaining 11 offspring had birthdates known to 2 or 3 days, and we assigned the birthdate to the first date (if 2 days) or middle date (if 3 days), unless observations of the offspring when first seen suggested otherwise (e.g., infant with umbilicus attached, or still wet).

We then used observations of sexual behavior to identify a shorter conceptive estrus period within the 29-day window, following Pazol's (2003) guidelines and further described by Roberts et al. (2014). Briefly, we considered a female as estrous on a given day if she copulated or had semen on her genitals. We allowed gaps of one or two days to count as part of the estrus period, as long as she copulated or had semen on genitals immediately before and after the gap. We used days with only proceptive behavior to extend or connect estrus days if these behaviors occurred within two days of a copulation or semen on genitals. We identified multiple estrus periods within the 29-day conception window for the mothers of 9 of the 36 offspring and in these cases, we selected the period closest to the middle of the window. We identified conceptive estrus periods for the mothers of 28 of the 36 offspring; the mean length of these periods was 5.43±5.07 days (range=1-22 days, N=28). Estrus behavior was not observed for mothers of the remaining 8 offspring and we excluded them from analyses that used conceptive estrus periods.

We summarized our data as offspring-male pairs, each corresponding to one male observed in or near the group during the conceptive estrus period for the mother of each offspring. We included offspring-male pairs only if the male was individually-identified and genotyped because we were unable to predict siring success for males who we could not readily identify or for whom we lacked genetic data. Individually-identified and genotyped males comprised most of the males observed in the groups during conceptive estrus periods (mean±sd = 83±18%, range=44-100%, N=28 offspring). We removed offspring-male pairs that included the resident of the group in which the offspring was conceived because we were focused on competition among extra-group males. This practice led to the elimination of 7 offspring for which the resident was the only male observed, leaving 21 offspring in the analysis.

Predictors

For our first predictor, male status, we noted whether the male in each offspring-male pair was a bachelor or a resident of a neighboring group. Our second predictor, time spent in the group, equaled the proportion of days during each conceptive estrus period during which each male was observed in or near the group. Frequent and intensive monitoring of the study groups meant that there was a high probability of observing extra-group males that were in or near the groups.

Male blue monkeys interact agonistically, thus establishing dominance relationships that may order them into a queue for reproduction (Alberts et al. 2003). We assessed dominance rank among bachelors only, as residents invariable dominated bachelors and residents' high rank was therefore captured by the male status variable. We used records of bachelor-bachelor dyadic agonistic behavior (chase, attack, lunge, bite, hit, avoid, flee, nasal scream) in which there was a clear winner and loser. We compiled agonism data for one-year periods (March 1 to February 28/29 of the following year) centered on the June-October mating season, which allowed us to capture changes in rank across mating seasons. We analyzed interactions for each group-year separately, as bachelors present in the same group were competing for access to the same females and more likely to interact.

We assessed bachelor rank relative to the other bachelors that were present in the group during the conceptive estrus period corresponding to each offspring. Our rank measure equaled the number of other bachelors that won against each bachelor in most of their interactions and therefore had first access to females in conceptive estrus. If two bachelors were tied (e.g., Bachelor 1 beat Bachelor 2 twice and Bachelor 2 beat Bachelor 1 twice in the same period), we counted neither as winner. Our rank measure allowed multiple bachelors to have the same rank, with the highest-ranking bachelor(s) assigned a rank of 0. We removed records of all bachelors that were not observed to interact agonistically with any other bachelors in that group-year, as we were unable to rank them. Removing these bachelors led us to omit one offspring for which unranked bachelors were the only extra-group males observed.

Statistical Analysis

To test whether the probability that a male sired an offspring related to the time he spent in the group during the offspring's conceptive estrus period, we used the SAS procedure PHREG to conduct a Cox proportional hazards regression. Each data point corresponded to one male observed during the conceptive estrus period of one offspring. We stratified the analysis on offspring because some individual males were represented during the conception of more than one offspring. The dependent variable was whether that male sired the offspring and we included male status, time spent in the group, and bachelor rank as predictors. To assess how our predictors affected the relative success of bachelor males, we generated a secondary data set that included only offspring sired by bachelors. For this latter analysis, we removed offspring-male dyads in which the male was the resident of neighboring group.

Comparing Resident and Bachelor Tactics

Comparing the long-term success of resident and bachelor tactics required estimating reproduction across multiple groups and years. While our paternity data set spanned multiple groups and years, some parameters were not directly measured and were inferred based on known patterns of reproduction in study groups. As such, our calculations were exploratory and served to (1) determine if there are any conditions under which bachelorhood and residency may be comparably successful reproductive tactics and (2) if so, to evaluate the likelihood of those conditions.

Our calculations were based on MacLeod et al. (2002) who aimed to determine if, over an entire reproductive lifetime, a bachelor samango monkey could steal enough matings to be as successful as a resident male siring offspring at the average rate for one period of residency of average length. MacLeod et al. made several assumptions: (1) the resident male confines his mating activity to his group alone, (2) the resident male loses matings to only one bachelor male, and (3) the bachelor concentrates all his mating effort in one group. Our paternity results indicated that our study population violated all three assumptions. During a single mating season, two bachelors sired offspring in two adjacent groups and four residents sired offspring in their own group and an adjacent group. Also, resident males may lose paternity to multiple bachelors. Therefore we developed a new method for comparing bachelor and resident siring success, following a similar approach to that of MacLeod et al. Specifically, we identified factors contributing to bachelor and resident reproductive output and used summary statistics to determine how long a hypothetical average bachelor would have to pursue the bachelor tactic to sire as many offspring as a hypothetical average resident sires in one period of tenure lasting from 1 to 8 years (i.e., the range of tenure length in our study population).

As acknowledged earlier, blue monkey males may switch among tactics during their lives, so some males may sire offspring as bachelors before or after attaining residency and some may be resident in two groups sequentially. In our population, 1 of the 10 males observed as both bachelor and resident (in study groups or in adjacent non-study groups) sired offspring in our study groups before attaining residency and none sired offspring in our study groups after losing residency. Thus, a resident's siring success appears to be concentrated during his period of residency. Four of the 11 resident males in our study groups were known to have two periods of residency. We therefore chose to compute a resident's siring success based on one or two periods of residency.

Resident Parameters

The number of offspring sired by a resident during one period of residency can be expressed as follows (Equation 1):

$$R = \sum_{t=1}^{T} (R_i + R_o N_r)_t$$

R_i is the annual siring rate (number of offspring) in the resident's own group, R_o is his annual siring rate per outside group, N_r is the number of outside groups, and T is tenure length, measured as the number of mating seasons (one per year in blue monkeys). In the equation, the product of R_o and N_r equals "outside-group" siring success and thus, the value in parentheses is equal to the resident's total annual siring success, which is summed over his entire tenure.

We estimated within-group siring success (R_i) by summing the number of offspring sired in a resident's group during his entire tenure and dividing by the number of years he was resident. One resident, Ro, did not sire any of the 19 offspring conceived in his group despite mating during most conceptive windows, which suggests that he was infertile. We therefore calculated summary statistics for within-group and outside-group siring success excluding Ro.

There are likely more reproductive opportunities in larger groups, so we calculated R_i for small and large groups separately. A resident was considered to be in a small group if the average number of females over age 5 (the age at which females begin to exhibit proceptive behavior) during his residency was ≤15 (N=6 periods of residency) and in a large group if the average number of females over age 5 was >15 (N=6 periods of residency). Two group fissions during the study period resulted in two study group residents (Sa and Pu) being represented twice, once as resident of the parent group and once as resident of one of the daughter groups. Sa was a resident in a small group before the fission (GSA) and resident in a small daughter group after the fission (GSAA). Pu was a resident in a large group before the fission (TW) and resident in a small daughter group after the fission (TWN).

We calculated average tenure length (T) as the number of mating seasons that a resident male was in his group, using observations of 18 study group residents and 5 residents of adjacent non-study groups (including 2 who later became residents in study groups) for which we observed complete periods of tenure from 1994. From 1994 through mid-1997, observations were generally limited to a 4-6 month period during the mating season; however, the same single male was present during consecutive observation periods and we assumed that his tenure was uninterrupted. From mid-1997 on, observations occurred on a near-daily basis, allowing us to determine dates of resident turnovers. We knew the tenure length of adjacent resident males, as these groups were often seen during intergroup encounters at territory boundaries. Most conceptions occur during the 5-month mating season from June-October (Cords & Chowdhury 2010) and we considered a resident male to be present for a mating season if he was in the group for more than half of this 5-month period.

We estimated the number of outside groups in which a resident may sire offspring (N_r) as the number of adjacent groups, because a resident has never been observed more than one home range away from his group (pers. obs.). Group members collaborate to defend territories against adjacent groups (Cords 2007) and we used observations of intergroup encounters from 2002-2012 to assess the number of adjacent groups for each study group. Demographic changes (e.g., group fissions) and home range shifts may cause the number of adjacent groups to change over time, so we assessed the number of adjacent groups annually. In a few cases, the identity of the adjacent group was ambiguous because it was a non-study group without readily identifiable individuals in an area where multiple group home ranges overlapped. In those group-years, we calculated the minimum and maximum number of adjacent groups and used the average of those values. Minimum values reflected the number of identified adjacent groups and maximum values included the unidentified adjacent groups, which may have been a known group that was unrecognized at the time.

We estimated outside-group siring success (R_o) from resident paternity success in other *study* groups. We calculated this parameter for 20 residents with a total of 22 periods of residency (8 study group residents, 10 residents in adjacent non-study groups, and 2 residents that had 2 periods of tenure each, one in a study group and one in an adjacent non-study group). For each residency period, we divided the total number of offspring sired in adjacent study groups by the number of adjacent study groups and by tenure length.

Bachelor Parameters

Bachelor siring success can be expressed as follows (Equation 2):

$$B = \sum_{l=1}^{L} (R_b N_b)_l$$

R_b is the annual siring rate per group, N_b is the number of groups encountered, and L is a bachelor's reproductive lifespan. The value in parentheses equals the number of offspring a bachelor produces annually, which is summed over his entire lifetime.

We genotyped 47 males who were bachelors for part or all of the time they were observed in the study population and used long-term records to identify the years of bachelorhood and study groups each male visited. To calculate the annual siring rate per study group (R_b), we divided the total number of offspring a bachelor sired in the study groups by the total number of study groups in which he was observed and the total number of years that he was observed.

We later omitted some of these males from the calculations to ensure that the summary statistics are good estimates of true bachelor parameters. First, we omitted 19 bachelors observed for only one year, as most were subadults who had recently emigrated from their natal groups but had not yet dispersed from the local population or males who were just passing through (i.e., male seen only few times that could not be consistently identified). We also omitted an additional 3 bachelors who were observed in the study area but not in any of the study groups because we were unable to assess their siring success. These 22 bachelors were particularly unlikely to sire offspring in the study groups (only one sired one offspring) and removing them increased bachelor siring rate. Of the remaining 25 bachelors, 10 eventually became residents in the study groups or adjacent non-study groups. To control for differences between "committed" bachelors and bachelors who later became residents, we limited our calculations to the 15 bachelors who were bachelors for the entire time we knew them, although we acknowledge that they may have been residents before or after they were present in our study population.

We estimated the total number of groups a bachelor encountered as the number of group home ranges that his home range overlapped. From June-September 2011, SJR walked transects following pre-existing linear footpaths spanning the study group home ranges. When encountering a bachelor, she followed him and recorded his location every 30 minutes with a handheld GPS unit until she lost him. We have location data for 11 bachelor males, but used data from only 5 of those tracked for at least 15 hours each (mean±sd=24.3±9.4, range=16-38 hours over 5-11 days).

During the same period, we collected location data to map the home ranges of the 6 study groups. The field team contacted each study group every day and recorded the location of the group center every 60 minutes with a handheld GPS unit. If the center of the group could not be located, no GPS point was recorded for that time interval. We recorded 414±167 (mean±sd) hours of location data per study group (range=139-579) distributed over 81-123 days. SJR and one field assistant also tracked the location of 4 adjacent non-study groups, recording the location of the group center every 30 minutes for a mean of 74±30 hours of location data per group (range=37-110) distributed over 14-19 days. We plotted all points on a 50x50m grid. When a point fell within a grid cell, that cell was considered to be part of the group home range (Fig 1).

We overlaid the bachelor points on top of the group home ranges and counted the number of group home ranges in which each bachelor was observed. We considered this value to be the minimum number of groups a bachelor encountered. Four of the five bachelors were observed in areas outside of the mapped group home ranges. Based on the home range sizes of known groups and opportunistic observation of unidentified groups of monkeys, we estimated the number of additional group home ranges that bachelors may have overlapped, considering this value to the maximum number of groups encountered. We used the midpoint of the minimum and maximum values for each bachelor as the total number of groups encountered.

Comparing Tactics

We used mean values for each parameter to calculate the number of years a bachelor siring offspring at the average rate in the average number of groups (i.e., the hypothetical average bachelor) would have to pursue the bachelor tactic to sire as many offspring as a resident siring at the average rate in his own group and at the average rate in the average number of outside groups (i.e., the hypothetical average resident) for one period of tenure. The way in which we calculated all variables accounted for variation across years, so setting the resident and bachelor equations equal to each other and solving for the length of a bachelor's reproductive lifespan (L) yields Equation 3:

$$L = \frac{T(R_i + R_o N_r)}{R_b N_b}$$

The length of male reproductive lifespans varies widely among cercopithecines (4.3 years in Japanese macaques to 12.7 years in mandrills, Clutton-Brock & Isvaran 2007). We do not know the length of male reproductive lifespans in blue monkeys, so we used estimates of female lifespan to identify plausible values. The oldest female in the study population was 33.5 years old (Cords & Chowdhury 2010). Males attain full body size around 9 years old and we estimate the maximum male reproductive lifespan to be the difference between these two values, or 24.5 years. We considered it to be impossible for a bachelor to sire as many offspring as a resident if Equation 3 yielded an estimate of L that exceeded 24.5 years.

Given the large range in tenure length in our population (1-8 years) and the importance of tenure in the above equation, we repeated the calculations using the same parameters but replacing average tenure length with minimum or maximum tenure length. We also doubled all values of L to compare the average bachelor to the average resident with two periods of tenure. These repetitions allowed us to compare bachelor and resident success in a total of 12 unique circumstances.

RESULTS

Paternity Assignment

We genotyped the 126 offspring at 12.1±1.6 loci, the 65 adult males at 11.9±1.8 loci, and the 74 mothers at 12.8±0.4 loci. Of the 104 offspring with verified paternity assignments, 68 were assigned to residents. The remaining 36 were assigned to extra-group males, 12 to residents of adjacent groups and 24 to bachelors.

Factors Determining Siring Success of Extra-Group Males

The full model that tested the effect of male status, time in group, and bachelor rank on the siring success of extra-group males was significantly better at predicting whether a male sired an offspring than the null model (log-likelihood ratio test: χ^2=14.413, df=3, p=0.002, Table 1). Residents of adjacent groups tended to be more likely to sire an offspring than bachelor males, but the effect of male status did not reach significance at α=0.05 (χ^2=3.465, df=2, p=0.063, Table 1). Neither bachelor rank nor the time a male spent in the group affected siring success. When restricting the analysis to offspring sired by bachelor males only, the model was not significantly better at predicting siring success than the null model (log-likelihood ratio test: χ^2=1.624, df=2, p=0.444).

Comparing Bachelor and Resident Tactics

Resident Parameters

The mean value for resident's annual siring success in his own group was 1.4±0.9 offspring per year in small groups (N=5 residents in 4 study groups) and 2.9±1.7 offspring per year in large groups (N=6 residents in 4 study groups; Table 2). Four residents in our data set sired offspring in adjacent groups; three residents sired one offspring each and one resident sired nine over his 8-year tenure. Despite high outside-group siring success by some males, the average rate across residents was low (mean±sd=0.1±0.3 offspring per adjacent group per year, N=20 residents during 22 periods of residency; Table 2). The number of adjacent groups varied across group-years, but given low rates of outside-group siring success, reproduction in adjacent groups contributed much less to the total number of offspring sired during resident tenure than did the rate of within-group siring success.

Tenure length varied greatly across residents (mean±sd=2.8±2.1, range=1-8 mating seasons, N=21 residents during 23 periods of residency; Table 2), with observed values skewed towards shorter tenure lengths. Three males maintained residency for 6 years each, but only one was resident for the maximum 8 years.

Plugging mean values for resident within-group and outside-group siring success and the number of outside groups into our equation indicates that the average resident in a small group produces 1.4 offspring in his own group and 0.4 offspring in adjacent groups each year, for a total of 1.8 offspring annually. Maintaining this rate would yield

5.0 offspring during a period of tenure of average length and 14.7 offspring during a period of tenure of maximum length (Fig 2). In contrast, the average resident in a large group produces 3.3 offspring annually, 9.2 offspring during a period of tenure of average length, and 26.8 offspring during a period of tenure of maximum length (Fig 2).

Many of the 10 residents in our study (excluding Ro, who seemed to be infertile) matched the siring profile of the hypothetical “average resident,” siring approximately as many offspring during their periods of tenure as predicted by the calculations (Fig 2). One resident male, Pu, spent 3 years as resident in a large group and 3 years as resident in a small group (after the large group fissioned) and his siring success closely matches the predicted siring success of a resident in a small group.

Bachelor Parameters

An average bachelor sired 0.1 offspring per study group per year (Table 3). The 5 bachelors we tracked spent most of their time in the interstices and little time in the centers of group home ranges and we found little variation in the number of group home ranges that a bachelor used (mean±sd=3.2±0.4, range=2.5-3.5 groups, Table 3). Using mean values for R_b and N_b, the average bachelor would sire 0.3 offspring per year.

Bachelorhood versus Residency

Our calculations indicate that the average bachelor may eventually sire as many offspring as the average resident who is present for one period of tenure of minimum length in either a small or large group (Table 4). It will always take less time for the average bachelor to match the siring success of a resident in a small group than a resident in a large group. As such, there are more plausible circumstances that allow the average bachelor to sire as many offspring as a resident in a small group. For example, the average bachelor may catch up to the average resident who is present for one period of tenure of average length if that resident is in a small group, but not if he is in a large group. The average bachelor would never be able to sire as many offspring as a resident if that resident remains in his group for the maximum tenure length, regardless of group size.

Doubling all values of L indicate that there are fewer circumstances in which the average bachelor can catch up with the average resident with two periods of residency. Specifically, a bachelor may be as successful as a resident with two periods of residency if tenure length in both cases is short (i.e., minimum tenure length, Table 4). Additionally, if the average resident has one period of tenure in a small group that lasts the minimum tenure length and a second period of tenure in another small group that lasts that mean length, a bachelor may match the resident's siring success in 21.9 years, which is less than our estimate of the maximum male reproductive lifespan.

DISCUSSION

Factors Affecting Extra-Group Male Siring Success

The model including offspring sired by all extra-group males suggested that residents of adjacent groups may be more likely to sire offspring than bachelor males, but this trend did not reach significance. If substantiated, this pattern would suggest that when a resident does not monopolize all reproduction in a group, residents of adjacent groups have priority of access to females in conceptive estrus, followed by bachelors.

The relationship between rank and male mating and siring success has been a topic of investigation for decades (e.g., Cowlishaw & Dunbar 1991, Ellis 1995, Majolo et al. 2012). Studies have focused on species living in multi-male groups where males interact regularly and competitors are in close proximity. To our knowledge, our study is the first to rank bachelor males and use those ranks to predict siring success. Bachelor rank was not a significant predictor of siring success, which suggests that bachelors do not engage in contests with other bachelors for access to reproductive opportunities. Bachelor blue monkeys probably use an opportunistic tactic to reproduce, mating when they encounter an estrous female rather than queuing for reproduction (Alberts et al. 2003). Opportunistic matings may be more likely to occur in forest-dwelling guenons than in species living in open habitats, because limited visibility decreases the chance that a higher-ranking competitor would directly or indirectly interfere with mating (Rowell 1988). We have seen bachelors copulate with females in our study population near to but on the other side of vine tangles from a resident, suggesting that limited visibility may allow bachelors to steal some copulations. The dense forest habitat may similarly negate any effect of dominance rank on siring success among bachelors, allowing low-ranking bachelors to mate and reproduce opportunistically, despite the presence of higher-ranking bachelors in the vicinity of the group.

The time a male spent in the group during a mother's conceptive estrus was not a significant predictor of siring success. This result indicates that extra-group males that are consistently present in a group are not more likely to sire an offspring than males that are present infrequently. This lack of effect may occur if males present in the group are unable to effectively monitor females in conceptive estrus. Large group spread (mean±sd=81±46m, range=15-282m, N=198 measurements of 6 groups ranging in size from 8 to 49 individuals, SJR unpublished data) in a visually opaque environment may make it difficult to track the location of individual females, thereby reducing the predictive effect of time in group. Furthermore, females mate infrequently (copulations and mounts during conceptive estrus periods occurred at a rate of 0.21 events/hour; Cords, unpublished data from 86 hours of focal samples of 48 adult females in conceptive estrus) and even males who are present and vigilant for reproductive opportunities may miss these rare mating events.

Comparing Male Reproductive Tactics

If bachelor male blue monkeys are pursuing an alternative reproductive tactic instead of simply making the best of a bad job, we expect the LRS of a lifelong bachelor to be similar to that of a male who incorporated a period of residency into his reproductive lifespan. Although resident males have a verified reproductive advantage in the short term (i.e., within one year) and on a small scale (i.e., within one group, Roberts et al, 2014), a bachelor male may be able to make up for this reproductive disadvantage by reproducing for a longer period of time or in more groups (MacLeod et al. 2002). Our calculations, however, indicate that it will usually take many years for a bachelor to sire as many offspring as sired by a resident during one period of tenure and in most circumstances, the resident tactic probably results in higher LRS than the bachelor tactic.

Although residency usually confers a reproductive advantage, we identified some circumstances in which the average bachelor would attain similar reproductive success as the average resident with one or two periods of tenure. Specifically, the average bachelor would take 5.8 years to match the siring success of the average resident in a small group with a period of tenure of minimum length. This estimate increases to 10.4 years when comparing the average bachelor to the average resident in a large group with a period of tenure of minimum length and to 16.1 years when comparing to the average resident in a small group with period of tenure of average length. There were fewer circumstances in which the average bachelor could sire as many offspring as the average resident with two periods of tenure, but it was not impossible.

When calculating resident and bachelor parameters, we made several decisions that affected the comparison. First, we chose to limit resident siring success to the period of tenure because we know little about siring success before attaining or after losing residency. Data from our population indicate that the siring success of males with at least one period of residency was concentrated during their residency, but it remains possible that this restriction caused us to underestimate the LRS of a male who is resident for some period.

When calculating annual siring success for bachelors, we eliminated young bachelors who had recently emigrated from their natal groups and temporary visitors that were seen few times in the study population and were unable to be recognized. These bachelors had very low siring success, so omitting them from our calculation increased the average bachelor siring success and gave the average bachelor a better chance of catching up with a resident. If we included these males, the rate of bachelor siring success was half of the estimated values (0.05 offspring per group per year instead of 0.1 offspring per group per year), which would double the number of years required for the average bachelor to sire as many offspring as a resident. The average bachelor would be unable to catch up with the average resident with one period of tenure unless the resident had a very short tenure. The average bachelor would be able to catch up with the resident with two periods of tenure only if the resident had two very short periods of tenure in a small group.

We judged the estimates of bachelor reproductive lifespan to be plausible if they were less than 24.5 years, based on the difference between maximum female lifespan and the age at which males attain full adult body size and become likely competitors for reproductive opportunities. This male reproductive lifespan represents a maximum, as it is unlikely that male blue monkeys live as long as females. In long-lived species that live in one-male or multi-male groups, males typically show higher annual mortality rates and a more rapid decline in survival with age (Clutton-Brock & Isvaran 2007). Unfortunately, we do not have a reliable estimate of male reproductive lifespan because male-biased dispersal and periods without any group affiliation makes it challenging to track individual males throughout their lives. If male blue monkeys have a reproductive lifespan less than 24.5 years, there will be fewer circumstances under which a bachelor male could sire as many offspring as a resident during one period of tenure.

Overall, adjusting our calculations to account for siring success outside of the period of residency, lower annual bachelor siring success, or a reproductive lifespan shorter than 24.5 years make it less likely that the average bachelor would be able to sire as many offspring as the average resident. However, our findings still lead us to question the presumed advantage of residency under all circumstances. Specifically, a bachelor who is able to sustain a high siring rate in multiple groups for several years may have similar LRS as a male whose reproduction is limited to one period of residency of average length. Following males over the course of their lives would allow us to judge whether 24.5 years is a reasonable estimate for the length of a male's reproductive lifespan. Additionally, our comparative analysis suggests that a large determinant of lifetime reproductive success is the amount of time that a male spends as a resident or as a bachelor. Long-term tracking data would allow us to determine how often males switch among tactics and thereby expand our calculation to include reproduction during sequential periods of bachelorhood and residency.

Conclusion

Although resident male blue monkeys sire the majority of offspring born in their groups, they lose about 40% of paternity to outside males (Roberts et al, 2014). When a resident male did not monopolize reproduction in his group, residents of adjacent groups likely had first access to females in conceptive estrus, followed by bachelors. Neither bachelor rank nor time spent in group affected extra-group male siring success, suggesting that bachelors do not engage in contests with other bachelors for reproductive opportunities and opportunistic matings may play an important role in bachelor siring success.

Bachelor males sire offspring at a much lower rate than do residents, but a bachelor may be able to make up for this reproductive disadvantage by reproducing for a longer period of time or in multiple groups. Our comparison of bachelor and resident siring success indicated that in most circumstances, a lifelong bachelor would be unlikely to sire as many offspring during his lifetime as a resident during one or two periods of residency. However, our calculations suggest that a bachelor who sires offspring at the average rate in multiple groups for several years may have similar lifetime reproductive success as a male whose reproduction is limited to one average period of residency, especially in a small group. Future research that tracks individual males and generates precise estimates of male reproductive lifespans would add to our understanding of the relative success of resident and bachelor tactics.

TABLES AND FIGURES

Table 1 Results of the Cox proportional hazards models testing the effect of rank and time spent in group on extra-group male siring success (log-likelihood ratio test: χ^2=14.413, df=3, p=0.002).

	Coef	SE	χ^2	**df**	**P**
Bachelor Status	-4.750	2.552	3.465	2	0.063
Time Spent in Group	3.635	3.133	1.345	1	0.246
Bachelor Rank	-0.647	0.652	0.984	1	0.321

Table 2 Resident parameters

Statistic	**Annual within-group siring rate in small groups (R_i)**	**Annual within-group siring rate in large groups (R_i)**	**Annual siring rate per neighboring group (R_o)**	**Number of neighboring groups (N_r)**	**Tenure length in years (T)**
Mean ± sd	1.4 ± 0.9	2.9 ± 1.7	0.1 ± 0.3	4.4±1.5	2.8± 2.1
Median	1.3	3.1	0	4	2
Range	0.5-3	0-5	0-1	1-7	1-8
N	5 residents in 4 study groups	6 residents in 4 study groups	20 residents in the study pop, 22 periods of residency	45 group-years	21 residents in the study pop, 23 periods of residency

Table 3 Bachelor parameters

Statistic	Annual siring rate per group (R_b)	Number of groups (N_b)
Mean ± sd	0.1±0.1	3.2 ±0.4
Median	0	3.5
Range	0-0.3	2.5-3.5
N	29 bachelors	5 bachelors

Table 4 The number of years the average bachelor would have to pursue the bachelor tactic to sire as many offspring as the average resident with one or two periods of tenure lasting the minimum, mean, or maximum length. Gray cells correspond to values that exceed a male's reproductive lifespan (24.5 years, see text) and therefore circumstances in which a bachelor would be unable to sire as many offspring in his lifetime as a resident sires during his tenure.

	Average Resident with One Period of Tenure					
	Min Tenure (1 year)		Mean Tenure (2.8 years)		Max Tenure (8 years)	
	Small Group	Large Group	Small Group	Large Group	Small Group	Large Group
L for the Average Bachelor	5.8	10.4	16.1	29.3	46.0	83.5
	Average Resident with Two Periods of Tenure					
	Min Tenure (1 year)		Mean Tenure (2.8 years)		Max Tenure (8 years)	
	Small Group	Large Group	Small Group	Large Group	Small Group	Large Group
L for the Average Bachelor	11.6	20.8	32.2	58.6	92.0	167.0

Fig 1 Home ranges of the study groups (solid) and four adjacent non-study groups (hatched) tracked from June-September 2011.

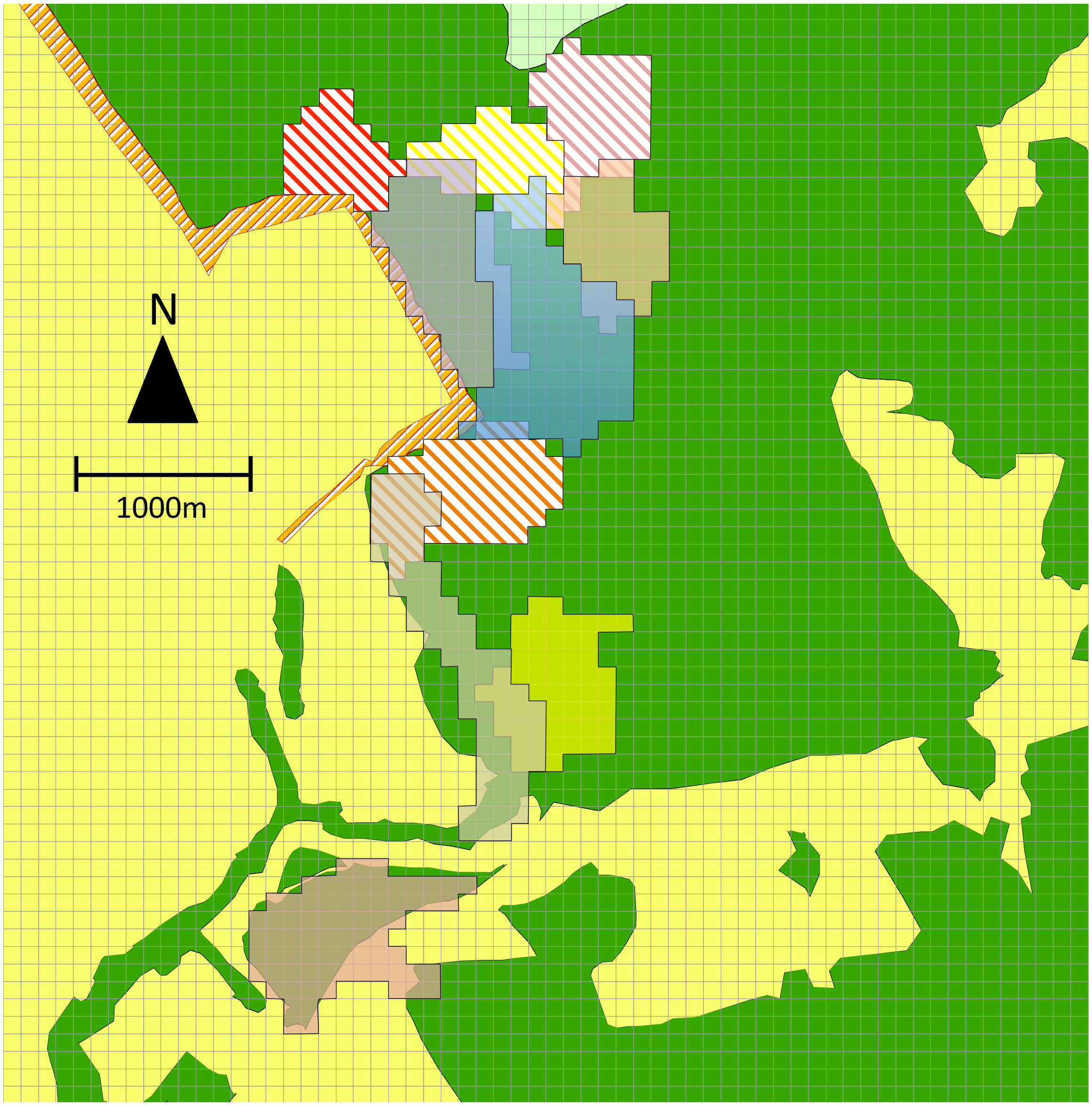


Fig 2 Predicted siring success of hypothetical average residents in large and small groups as calculated by substituting mean values for R_i, R_o, and N_r into Equation 1. Points correspond to 10 real residents in our study population and indicate the total number of offspring sired in the study groups during one period of tenure.

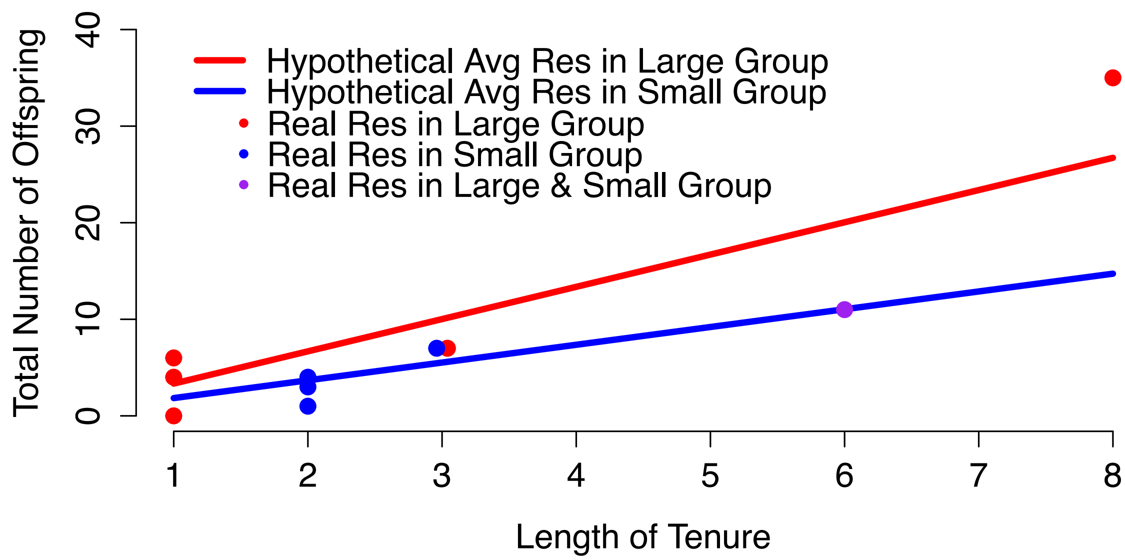
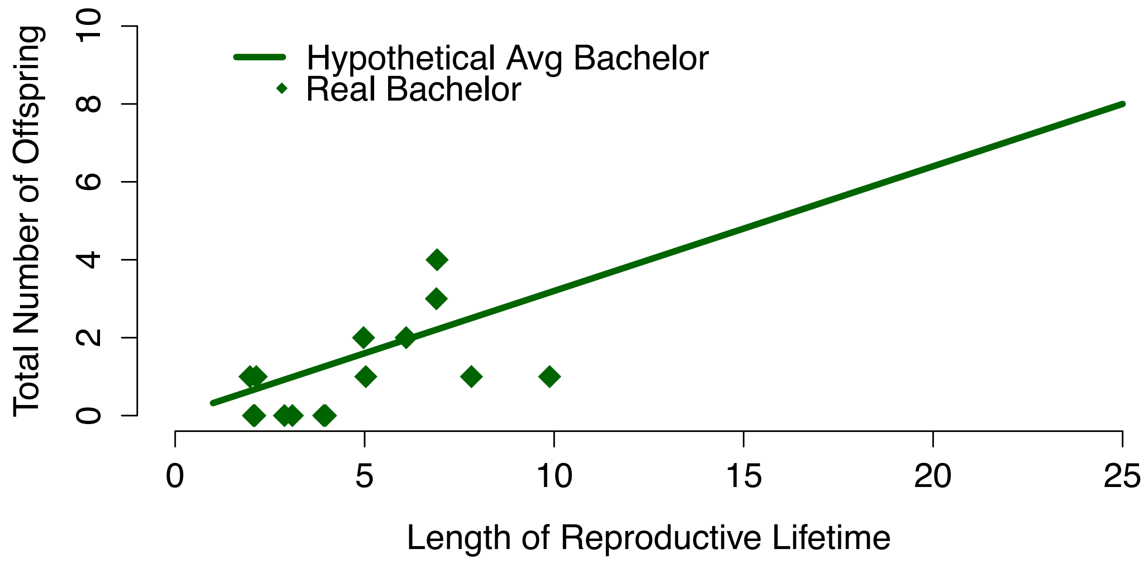


Fig 3 Predicted siring success of a hypothetical average bachelor as calculated by substituting mean values for R_b and N_b into Equation 2. Points correspond to 15 real bachelors and indicate the total number of offspring sired in the study groups during the years the bachelor was observed in our study population.



CHAPTER 5

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

Published in *Behavioral Ecology and Sociobiology* (2013) 67: 1995-2009

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ABSTRACT

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

KEYWORDS: within-group competition, female reproduction, breeding success, flexible feeding behavior

INTRODUCTION

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

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

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

In the absence of rank effects and controlled for variation in habitat quality, negative correlations between group size and behavioral or reproductive proxies of fitness suggest the occurrence of indirect within-group competition (i.e., scramble competition). For instance, because larger groups deplete local feeding areas more quickly, each individual must travel farther to sustain itself (Chapman & Chapman 2000). Because travel imposes energetic costs, larger group size (beyond a theoretical minimum) may correspond with reduced reproductive success for all group members (Janson &

Goldsmith 1995). Majolo et al's (2008) meta-analysis of primate studies indicated that larger groups generally did travel farther and their individual members spent more time feeding. As with rank, however, evidence for a relationship between group size and direct measures of female reproduction is more complex. In the same meta-analysis, the relationship between group size and female fecundity was significant and negative when the data set included studies of two social groups (i.e., one large and one small), but the relationship was not significant when the data set included studies of four or more social groups. Conversely, Ebensperger et al's (2012) meta-analysis of 51 mammal species showed that the number of adults and the number of non-breeders in a group had modest, but significant, *positive* effects on fitness, which included group fecundity and survivorship measures; however, the effect was not significant for other measures of group size (e.g., total group size, number of males, number of females), nor when female fecundity constituted the fitness measure.

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

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

Aggression among female blue monkeys occurs mostly and disproportionately in the context of feeding, and especially disproportionately when females feed on fruits (Cords 2000a, Pazol & Cords 2005, Foerster et al. 2011). Linear dominance hierarchies are detectable (Klass & Cords 2011), with high-ranking individuals directing and low-ranking individuals receiving agonism at the highest rates (Foerster et al. 2011, Cords 2000a). Prior studies, however, have generally failed to identify rank-related differences in feeding behavior or reproduction, including time spent feeding and proportion of feeding time devoted to different food types (Pazol & Cords 2005; but see Foerster et al. 2011, Cords 2000a), fruit intake rate, and rate of producing offspring that survived to one year (Cords 2002b).

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

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

METHODS

Study Site and Population

The study population of blue monkeys (*Cercopithecus mitis stuhlmanni*) inhabits the Isecheno area of the Kakamega Forest, a rainforest in western Kenya (0° 19' N, 34° 52' E; Elev. 1,580 m; mean annual rainfall, 1997-2011, 1942 mm). Rainfall is variable across years (range: 1,343 – 2,334 mm, 1997-2011), and falls seasonally, with the wettest period typically in April and May and a smaller peak from August through October (Mitchell et al. 2009). The study site supports a dense population of blue monkeys, with 192 individuals per km^2 in areas of natural forest (Fashing et al. 2011). Like other guenons (Butynski 1988), the Kakamega blue monkeys reproduce seasonally, with 64% of births occurring from January to March (Cords & Chowdhury 2010), a period that includes or immediately follows the two months (January-February) of peak ripe fruit availability (Foerster et al. 2012; M. Cords, unpublished data).

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

Demographic Data

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

Birthdates

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

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

Deaths and disappearances

We rarely found carcasses that allowed us to confirm that an individual died; thus we usually inferred deaths from permanent disappearances. Female blue monkeys are strictly philopatric, so we presumed that all females that disappeared from the group were dead. Natal males emigrate around seven years old (Ekernas & Cords 2007) and we no longer considered them to be group members after they permanently left the group.

Female Reproductive Parameters

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

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

We were unable to control for these factors, providing additional justification for excluding these months.

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

Predictor Variables

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

Group size

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

The number of adult males in a blue monkey group is more variable than the number of females, especially during the breeding season when multi-male influxes may occur (Cords 2002c). We calculated male group size directly from daily observations, making no presumptions that males were present if they were not observed. Three periods in 1997 and early 1998 were exceptions to this practice. During these periods, groups were not observed for 1.5 to 5.5 months, making it impossible to assign a monthly male group size based on observations alone. Each observation gap occurred outside the mating season at times of year when male influxes are generally rare, and the same resident male was alone in the group before and after each gap. We therefore presumed that there was only one male in the group during the gaps. We added the average female/juvenile group size (mean±sd = 36.4±14.1; range = 7-64.6) to the average male group size (1.46±1.09; range = 0.1-8.48) for each month to obtain the total group size (43.8±12.8; range = 7.9-69.2).

We also tested an alternative measure of group size – the number of females over age five (17.9±5.5; range = 4-29) – to determine if individuals in the same age/sex class were particularly important competitors. Five is the age at which females approach adult size, and begin to behave like adults (e.g., participate in inter-group encounters, exhibit sexual behavior, engage in prolonged grooming) and are likely to become important participants in within-group competition.

Dominance rank

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

We compiled data on agonism for one-year periods to compute dominance hierarchies using Matman 3.2 (Noldus Information Technology). We chose one-year periods because they capture rank changes while minimizing the number of unknown relationships in the data matrix, which can cause unstable rank output (Klass & Cords 2011). Blue monkeys show agonism at low rates, necessitating data collation over one year periods to detect linear hierarchies (Klass & Cords 2011, Cords 2000a). Females that interacted agonistically with fewer than three partners during the year were excluded from the data set because they could not be placed reliably in the hierarchy. For each hierarchy, Matman calculates a directional consistency index (DCI), which is a measure of dyadic outcome predictability. The DCI equals the total number of dyadic encounters with an outcome in the main direction for that dyad minus the number of encounters with outcomes in the opposite direction, divided by the total number of interactions; thus, 0 indicates that the outcome of an encounter is unpredictable based on earlier encounters and 1 indicates that all encounters have the same directionality (van Hooff & Wensing

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

Matman implements the I&SI method of ranking, minimizing the number and strength of inconsistencies within an ordinal hierarchy (de Vries 1998). For eight of the 54 hierarchies, we extended the period of data collation one to six months before and after the calendar year in question to increase sample size and achieve a stable hierarchy. In these cases, some agonism data were used to construct more than one hierarchy. Fifty-two of the hierarchies (96%) were significantly linear. Thirty-seven (69%) produced stable rankings over 10 Matman runs; the remaining 17 included blocks of 2-7 females that were variously placed relative to one another in repeated Matman runs. In these cases, we assigned the median rank to all females in a block.

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

Maternal traits

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

Seasonality

Two variables – rainfall and time of year – provided information about seasonality. We used **rainfall** matching each month of our study (mean±sd = 170±88mm; range: 0-399) to indicate environmental change. **Time of year** also tracked environmental change, as fruit availability is known to vary across months. We identified four three-month categories from changes in the availability of major foods eaten by blue monkeys (Foerster et al. 2012; M. Cords, unpublished data), grouping together December –

February, March – May, June – August, and September – November. Generally, fruit is most available in December – February and June – August, and least available in March – May.

Data Analysis

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

We tested 11 two-way interactions by including them in the model as fixed effects (Table 1). These included interactions between time since last conception and (1) lactation stage, (2) age, (3) rank, and (4) group size because we predicted that females might require extended recuperation time between conceptions if they were nursing an infant, very young or very old, low-ranking, or living in a large group. We included interactions between lactation stage and (5) rank and (6) group size because we predicted that females that were nursing an infant might benefit most from reduced within-group competition associated with high rank or small group size. We included interactions between age and (7) rank and (8) group size because we predicted that young females simultaneously investing in growth and reproduction might benefit most from the reduced within-group competition associated with high rank and small group size (Pusey 2012). We included the interaction between (9) rank and group size because we predicted that conception by low-ranking females might be more strongly affected by group size than conception by high-ranking females (Takahata et al. 2008). We included the interaction between (10) time of year and rank because we predicted that priority of access associated with high rank might be particularly advantageous during certain times of year, specifically periods of low fruit availability (Foerster et al. 2011). Finally, we included the interaction between (11) time of year and rainfall because we predicted that conception might be more likely only in conception seasons with particular rainfall characteristics.

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

Standardizing both age and group size before transformation reduced the correlation between the linear term and its quadratic so both could be included in the model (Schielzeth 2010).

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

We present the parameter estimates and standard errors from the full models because the full models minimize bias to effect size estimates and p-values, and provide a balanced representation of all hypotheses tested (Forstmeier & Schielzeth 2011). We did not use stepwise methods to minimize the probability of erroneously rejecting the null hypothesis of no effect (Type I error) (Mundry & Nunn 2009, Whittingham et al. 2006). We did, however, remove non-significant ($p>0.05$) interaction terms to allow for the interpretation of the estimates, standard errors, and p-values of the main effects (Engqvist 2005). This process eliminated ten interactions, leaving only the interaction between time since last conception and lactation stage. Thus, the full model of the probability of conception included ten fixed effects (rank, group size, group size^2, age, age^2, time since last conception, lactation stage, the interaction of time since last conception and lactation stage, rainfall, and time of year) and two random effects (female identity and year). To confirm the overall significance of the one categorical variable (i.e., time of year), we used a log-likelihood ratio test to compare the full model to the model without this variable.

Multicollinearity was low for most predictor variables (variance inflation factors ranged from 1.02 to 1.63 for the model with total group size and standardized rank; VIFs were similar for other models). VIFs were somewhat higher for time since last conception and the one significant interaction retained in our final models (7.41 for both), but values below 10 suggest that multicollinearity was not a problem (Chatterjee & Price 1991, Zuur et al. 2009). We plotted normalized residuals against each predictor variable and confirmed that there was no systematic pattern in residual spread. To determine if the whole set of predictor variables influenced conception, we conducted a log-likelihood ratio test using the ANOVA function in R to compare the full models to the null model (including only random effects). We also conducted a log-likelihood ratio test to compare the full models to a model that contained all control variables (all except rank, group size, and group size^2) to assess the joint significance of the variables of interest. We used odds ratios to assess the relative importance of the fixed effects.

RESULTS

With the probability of conception as the dependent variable, log-likelihood ratio tests indicated that full models including total group size and one measure of rank differed significantly from the null model including only random effects (log-likelihood ratio tests: standardized rank: χ^2=456.26, df=12, p<0.001; ordinal rank: χ^2=457.55, df=12, p<0.001) and from models including only control variables (log-likelihood ratio tests: standardized rank: χ^2=9.75, df=3, p=0.021; ordinal rank: χ^2=11.04, df=3, p=0.012). Results were similar for both models, so for simplicity, we present the results of the model with standardized rank only (Fig 1; results of model with ordinal rank is S1). Regardless of the index used, rank was never a significant predictor of conception. However, there was a significant quadratic relationship between group size and the probability of conception. The probability of conception peaked at a group size of 30.5 members in the model with standardized rank (Fig 2) and 31.5 members for the model with ordinal rank.

When we substituted female group size for total group size, results were again similar for the models with standardized and ordinal rank and again we present only the model with standardized rank (Fig 3; results of model with ordinal rank is S2). With female group size as a predictor, the quadratic transformation of the number of adult females was not significant. Removing the quadratic term did not significantly change model fit (log-likelihood ratio test: standardized rank: χ^2=2.30, df=1, p=0.129; ordinal rank: χ^2=2.15, df=1, p=0.142), so we reran the models without this term to test for a linear effect of number of females. In the final models, the number of females was not a significant predictor of the probability of conception (Fig 3, S2). The models also indicated that dominance rank was not a significant predictor of conception. The models including female group size were significantly different from models including only random effects (log-likelihood ratio tests: standardized rank: χ^2=450.66, df=11, p<0.001; ordinal rank: χ^2=452.23, df=11, p<0.001). However they were not significantly different from the model including only control variables (log-likelihood ratio test: standardized rank: χ^2=4.15, df=2, p=0.123; ordinal rank: χ^2=5.72, df=2, p=0.057), indicating that removing the non-significant group size and rank terms did not reduce model fit.

In all models, five of the six control variables were important predictors of conception. Specifically, the three maternal traits, the interaction, and time of year were significant predictors, but rainfall was not (Figs 1, 3). There was a quadratic relationship between age and the probability of conception with the probability of conception peaking at 13 years in all models (see S3 for probability curve for model with total group size and standardized rank). Predictably, the probability of conception increased if more time had passed since a female's last conception and if she did not have a dependent infant. The significant interaction indicated that the probability of conception for non-lactating females was much higher than the probability of conception for lactating females, however, the difference between these groups decreased with time. Time of year was a significant predictor of conception, as expected, with females most likely to conceive between June and November.

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

DISCUSSION

Rank and the probability of conception

Blue monkeys prefer and consume contestable foods like fruit, compete aggressively and disproportionately for this food category, and exhibit linear dominance hierarchies based on highly asymmetric agonistic relationships in which high-ranking females have priority of access to feeding sites (Pazol & Cords 2005, Foerster et al. 2011, Cords 2000a). This suite of behaviors suggests that they experience high within-group contest competition and high-ranking animals should have a reproductive advantage

(Isbell 1991, Snaith & Chapman 2007). We found, however, that rank did not affect the probability that a female conceived. While surprising from a theoretical perspective, our results support previous research on the study population, which documented limited, inconsistent, or no rank effects on feeding behavior (Foerster et al. 2011, Pazol & Cords 2005, Cords 2000a), energetic stress (Foerster et al. 2011), or the rate of producing offspring that survived to one year (Cords 2002b). Together, these findings suggest that individuals actually experience low within-group contest competition.

Flexible feeding behavior may offer a proximate explanation for the discordance between theoretical predictions and our results. For example, feeding individuals may avoid contests by maintaining large inter-individual distances, thereby mitigating rank effects on behavioral and reproductive proxies of fitness (Vogel & Janson 2007). In ring-tailed coatis, another mammal with linear dominance hierarchies, individuals increase the distance to neighbors when feeding on contestable fruit relative to uniformly-distributed insects (Hirsch 2007). While similar resource-related adjustment of inter-individual spacing does not seem to occur in blue monkeys (Cords 2002a), group members do spread out over large distances (mean group spread=65.6m, range=6-321m, N=3162 measurements of six groups, Plumptre 2000, mean group spread=109m, range=60-190m, N=35 measurements of one group with 45 members, Cords 1987) and individuals often feed alone in a tree crown (39% overall, 13-40% of fruit-feeding time while in trees large enough to hold several monkeys) or feed in trees that could accommodate others (76% of feeding time; Cords 2002a). Given the potential costs of spreading out, such as increased predation risk (Cheney et al. 2004) and inefficient transfer of information (Di Bitetti &

Janson 2001), individuals that adopt such behavior should obtain substantial benefits, and the reduction of within-group contest competition is likely to be one of them.

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

In species with low within-group contest competition, high rank may not confer an energetic advantage. Foerster et al. (2011) tested this hypothesis in the same population by measuring fecal glucocorticoids (fGCs), an indicator of energetic stress (Sapolsky et al. 2000). Controlling for other factors that could influence fGC levels, they found a significant relationship between rank and fGCs in one of two groups studied. Many of the females in this group were lactating during a period of low fruit availability, suggesting that rank effects may appear only during periods when energetic demand is high and particularly when it is difficult to meet this demand. Indeed, among lactating females, fGC levels were always lower for higher-ranked vs. lower-ranked individuals. Based on these earlier findings, we tested the interactions between rank and lactation stage (a proxy for energetic demand) and rank and time of year (a proxy for fruit availability) predicting that high rank would be particularly important during periods of energetic stress. These interactions, however, were not significant predictors of the probability of conception. Our results build on those from Foerster et al., suggesting that subtle rank-related differences in energetic stress do not translate into differences in the probability of conception. However, this conclusion should be confirmed by evaluating the relationship between direct measures of food availability and the probability of conception.

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

If increased social tolerance results in a relatively relaxed dominance hierarchy within the group, we may expect few or no rank effects on feeding behavior or reproduction, as we observed. Blue monkey group-mates jointly defend feeding territories (Cords 2002b, Cords 2007), suggesting that group-wide cooperation is important to secure access to resources. The need to cooperate may provide an ultimate explanation for the lack of a rank effect on reproduction. However, the social consequences of strong between-group competition generally remain poorly understood

(Schülke & Ostner 2012) and evidence for a link between success in between-group contests and social tolerance, facilitated by low levels of within-group contest competition, is required to substantiate this hypothesis.

Our results are consistent with an earlier report from our study population that rank did not affect the rate of producing offspring that survived to one year (Cords 2002b). Rank, however, may affect other measures of reproduction, such as age at first reproduction, reproductive lifespan, or infant survival. Indeed, across primate species and populations, rank effects on different components of reproductive success appear to vary in strength and prevalence, and recent reviews of rank and female reproduction do not agree on which components show the most consistent rank effects (Pusey 2012, Majolo et al. 2012). To some extent, this variation likely reflects which studies were included and the way in which comparisons were made. For example, in a recent meta-analysis, controlling for phylogeny affected the relationship between dominance rank and fecundity; a significant positive effect on rank on fecundity was evident only in the analysis in which phylogeny was not controlled (Majolo et al. 2012). These complex results highlight the value of additional high-quality data.

Group size and the probability of conception

We found that total group size had a significant quadratic relationship with the probability of conception, which peaked at a medium group size. Individuals in intermediate-sized groups are expected to have the highest fitness if they experience the maximal difference between the benefits of group living, such as predator avoidance and success in between-group contests, and its costs, such as within-group competition (Wrangham 1980, van Schaik 1983, Sterck et al. 1997) and the "social time" commitment required to maintain a cohesive unit (Lehmann et al. 2008). In addition, when group size is regulated via group fission, as in all cercopithecine monkeys, it is likely that both the smallest and the largest groups in a population will exhibit sub-optimal breeding success (Sterck et al. 1997). This pattern occurs because groups that have exceeded the optimal size may have to grow even larger to reach a point at which fission would produce new groups of a viable minimum size. These new groups – minimal but also not optimal in size -- could then grow toward the optimum size. Thus, in a population at any one time, intermediate-sized groups should exhibit greater breeding success than those at the extremes of the size range.

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

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

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

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

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

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

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

As with rank, group size might affect other measures of reproduction differently. A comparison of birth rate and infant survival before and after a group fission in our study population revealed no group size effect on either reproductive parameter (Cords

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

Effects of Control Variables

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

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

Conclusion

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

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

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

Table 1 Variables included in the analysis

Variable	Type	Description
Dependent		
Conception*	Categorical (yes/no)	Did the female conceive?
Independent		
Fixed Effects		
Group Size*^		
Total Group Size	Continuous	Average number of individuals in the group in a month
Female Group Size	Continuous	Average number of females over age five in the group in a month
Group Size^2#	Continuous	Group size squared
Dominance Rank*^		
Standardized Rank	Continuous (0-1)	The proportion of group females who outrank a given female (highest-ranking female in the group is 0, lowest-ranking is 1)
Ordinal Rank	Ordinal (1-N)	The value for the highest-ranking female is 1; the value for the lowest-ranking female is the number of adult females in the group (N).
Age*	Continuous	Female's age calculated to the nearest month
Age^2*	Continuous	Female's age squared
Time Since Last Conception*	Continuous	Number of months since the month of the female's last conception
Lactation Stage*	Ordinal (Very High, High, Mid, Low, None)	Reflects whether the female's last offspring is present and suckling; very high to low lactation as offspring ages; if last offspring was dead or older than 32 months, the female was classified as "no lactation"
Rainfall*	Continuous	Measured in millimeters
Time of Year*	Categorical (4 groups)	Three-month groups defined based on the availability of major blue monkey foods; groups: December-February, March-May, June-August, and September-November

Table 1 continued

Variable	Type	Description
	Time Since Last Conception x Lactation Stage*, Time Since Last Conception x Age, Time Since Last Conception x Rank, Time Since Last Conception x Group Size, Lactation Stage x Rank, Lactation Stage x Group Size, Age x Rank, Age x Group Size, Rank x Group Size, Time of Year x Rank	
Random Effects		
Female identity*, Year*, Group		

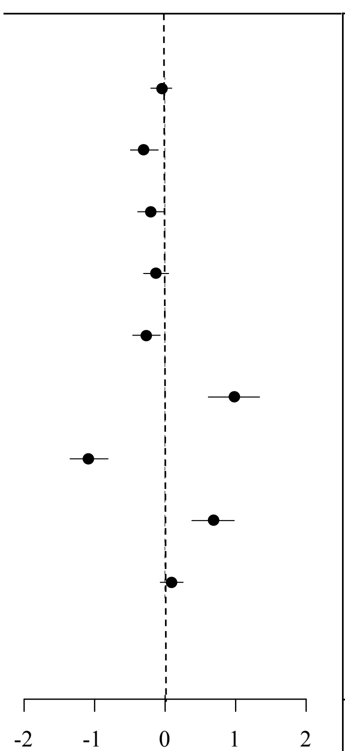
* variables included in the final model

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

^ only one alternative measure was included in each model

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

Estimate & 95% CI



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

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

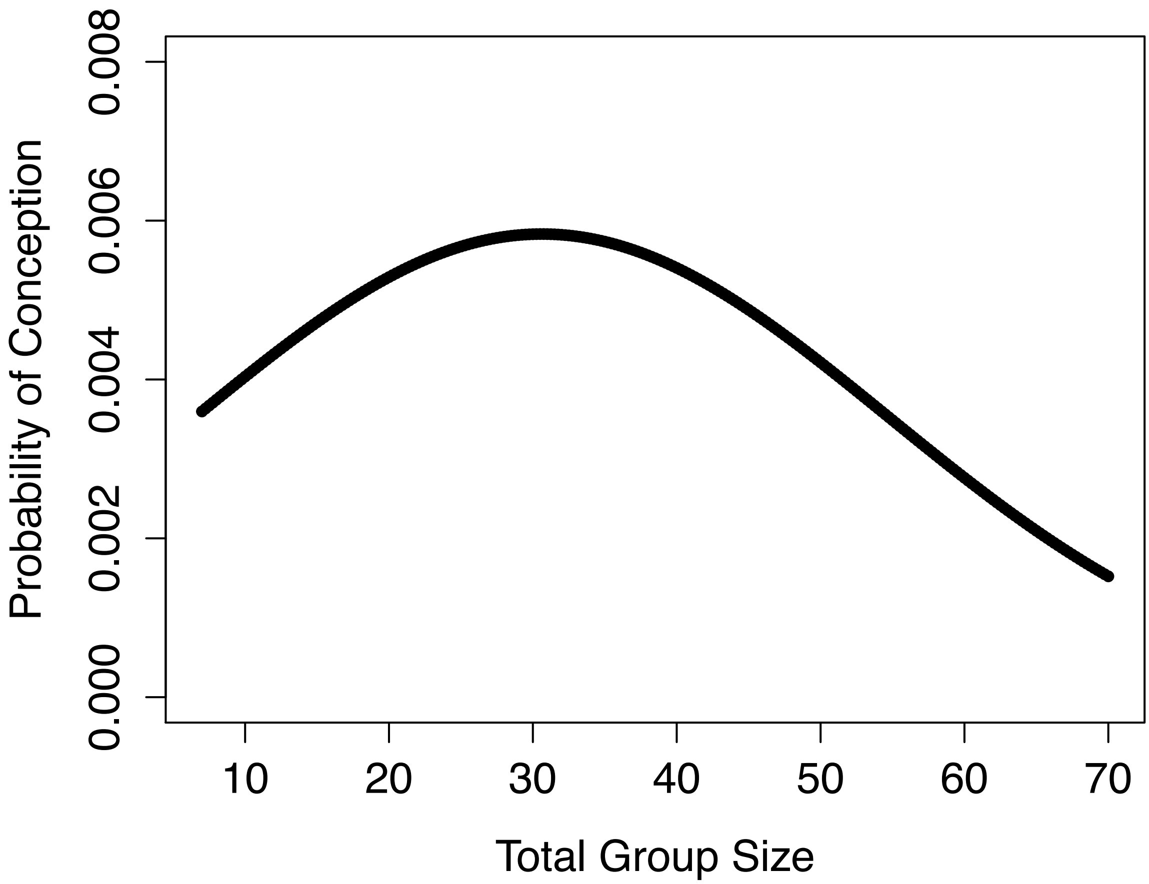
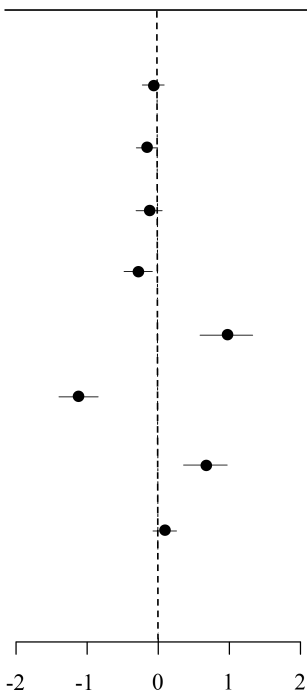


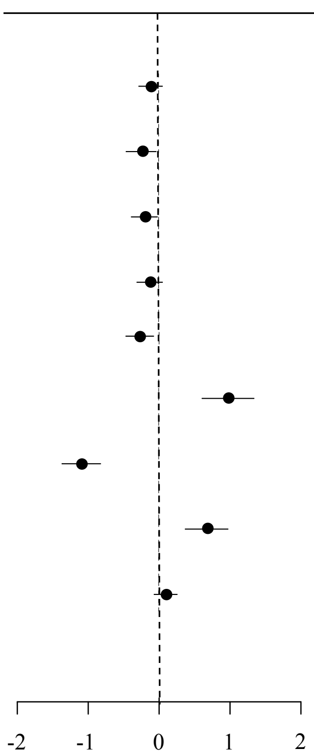
Fig 3 Results of the logistic regression in which *female group size* and *standardized rank* were entered as fixed effects and female identity (variance = 0.144) and year (variance = 0.301) as random effects. The figure on the left is a plot of the coefficient and 95% CI for each fixed effect; variables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



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

S1 Results of the logistic regression in which *total group size* and *ordinal rank* were entered as fixed effects and female identity (variance = 0.126) and year (variance = 0.272) as random effects. The figure on the left is a plot of the coefficient and 95% CI for each fixed effect; variables with CIs that do not cross 0 are significant predictors of conception. The corresponding table includes the estimate, standard error (SE), Wald score, degrees of freedom (df), significance (P), and odds ratio (e^estimate) for each fixed effect. If the odds ratio was less than one, we presented the inverse in parentheses to ease comparisons among fixed effects.

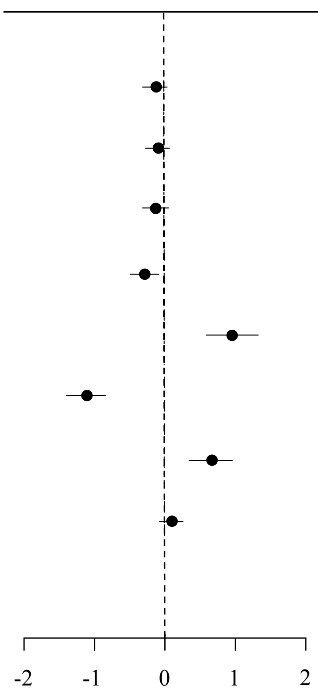
Estimate & 95% CI



	Estimate	SE	Wald z	df	P	Odds Ratio
Fixed Effects						
Ordinal Rank	-0.113	0.086	-1.319	1	0.187	0.893 (1.120)
Total Group Size	-0.247	0.109	-2.262	1	0.024*	0.781 (1.280)
Total Group Size^2	-0.201	0.095	-2.105	1	0.035*	0.818 (1.223)
Age	-0.126	0.093	-1.355	1	0.176	0.882 (1.134)
Age^2	-0.273	0.101	-2.694	1	0.007*	0.761 (1.314)
Time Since Last Conception	0.978	0.188	5.208	1	< 0.001**	2.659
Lactation Stage	-1.092	0.140	-7.815	1	< 0.001**	0.336 (2.980)
Time Since Last Conception x Lactation Stage	0.676	0.155	4.354	1	< 0.001**	1.966
Rainfall	0.098	0.084	1.169	1	0.243	1.103
Time of Year			168.830	3	< 0.001**	
Intercept	-5.445	0.321	-16.950	1	< 0.001**	0.004 (231.560)

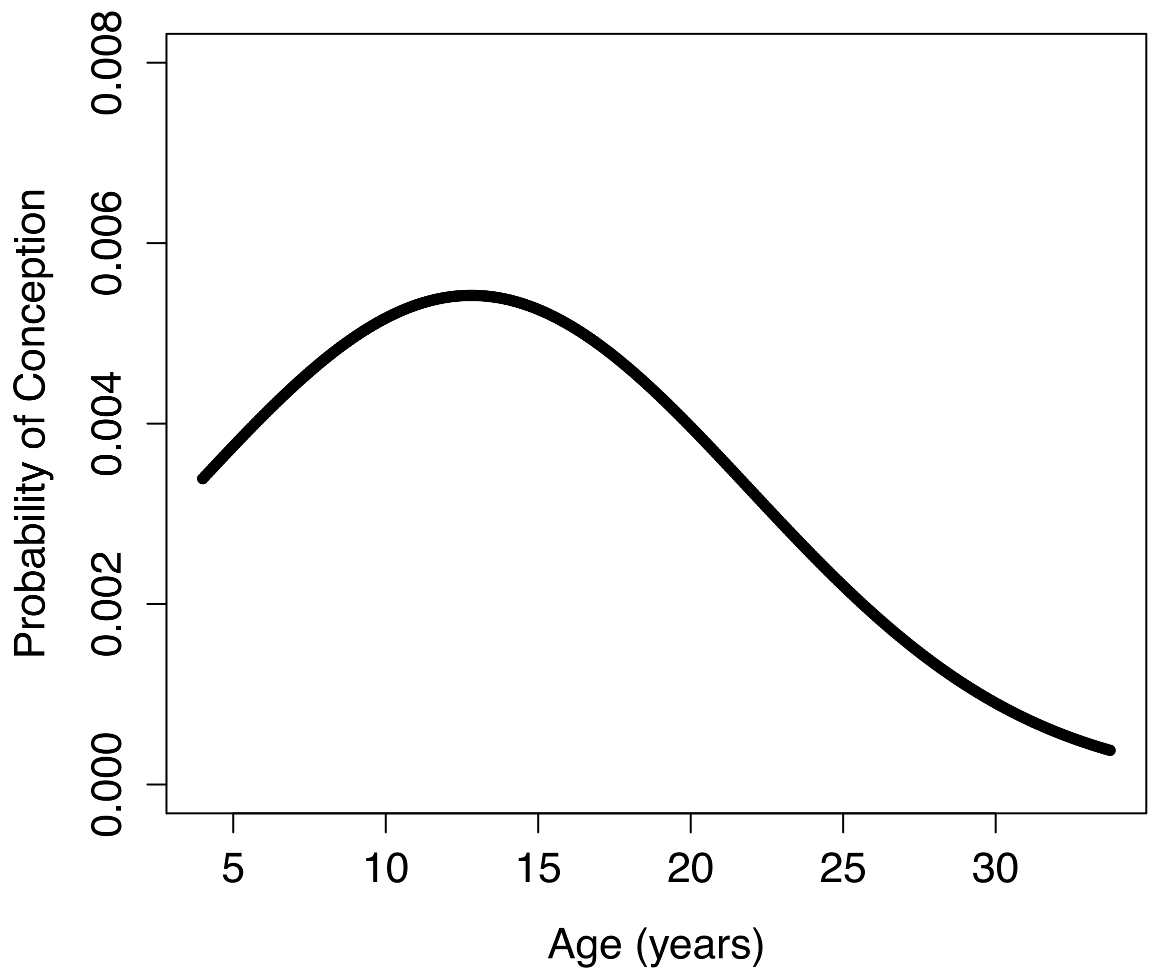
S2 Results of the logistic regression in which *female group size* and *ordinal rank* were entered as fixed effects and female identity (variance = 0.147) and year (variance = 0.292) as random effects. The figure on the left is a plot of the coefficient and 95% CI for each fixed effect; variables with CIs that do not cross 0 are significant predictors of conception. The corresponding table includes the estimate, standard error (SE), Wald score, degrees of freedom (df), significance (P), and odds ratio (e^estimate) for each fixed effect. If the odds ratio was less than one, we presented the inverse in parentheses to ease comparisons among fixed effects.

Estimate & 95% CI



	Estimate	SE	Wald z	df	P	Odds Ratio
Fixed Effects						
Ordinal Rank	-0.127	0.088	-1.444	1	0.149	0.881 (1.135)
Female Group Size	-0.090	0.085	-1.054	1	0.292	0.913 (1.094)
Age	-0.118	0.094	-1.261	1	0.207	0.889 (1.125)
Age^2	-0.279	0.102	-2.730	1	0.006*	0.757 (1.322)
Time Since Last Conception	0.965	0.188	5.119	1	< 0.001**	2.625
Lactation Stage	-1.115	0.141	-7.929	1	< 0.001**	0.328 (3.050)
Time Since Last Conception x Lactation Stage	0.659	0.156	4.232	1	< 0.001**	1.933
Rainfall	0.098	0.084	1.163	1	0.245	1.103
Time of Year			168.690	3	< 0.001**	
Intercept	-5.444	0.324	-16.818	1	< 0.001**	0.004 (231.365)

S3 Probability of conception as a function of age as determined by the predicted values from the logistic regression including total group size and standardized rank.



CHAPTER 6

Summary and Conclusions

The preceding chapters present new information on the effect of intrasexual competition on reproduction in a forest-dwelling primate with an unusually dynamic social organization. The studies included in this dissertation highlight the importance of long-term individual-based studies of multiple social groups in understanding factors affecting reproduction in both sexes. This final chapter will review my main findings and propose directions for future research.

Although many mammals live in one-male/multi-female groups, there have been relatively few studies that quantify resident siring success in species with this social organization and fewer still that use demographic and social data to identify drivers of variation in among residents or among bachelors (Chapter 2). This study population of blue monkeys provided a unique opportunity to test predictions about how the strength of male-male competition for a limited number of reproductive opportunities affects siring success. The large paternity data set, which included genetic data from 126 offspring conceived over 10 years in 8 study groups, combined with high-resolution data on mating behavior and male presence and interactions allowed a robust analysis of the factors affecting patterns of male reproduction.

In Chapter 3, I used genetic data to assign or exclude the 11 resident males as the sire of each offspring conceived in his group. I found that residents sired at most 61% of the offspring born in their groups, which is a lower percentage than most other species living in one-male groups. I extracted demographic data on female reproductive synchrony, the number of competitor males, and resident tenure length to identify factors affecting the probability that a resident sired an offspring conceived in his group. Mating is concentrated from June-October (Cords & Chowdhury 2010), but long interbirth intervals and large variation in the size of the study groups contributes to high variation in the number of female that are simultaneously in conceptive estrus across group-years. Additionally, some groups in some years experience multi-male influxes, during which the close proximity of competitors likely increases the strength of male-male competition for access to conceptive females. Finally, there was high variation in resident tenure length, which ranged from 1 to 8 years.

A resident was less likely to sire an offspring when multiple females were in conceptive estrus simultaneously and multiple competitor males were present. These results suggest that it is more difficult for a resident to monitor many conceptive and mating females at the same time. Additionally, the negative effect of intruders on resident siring success may occur because females prefer outside males or because an increase in the number of intruders increases the difficulty of defending access to females. Tenure length did not affect resident siring success.

In Chapter 4, I conducted a similar analysis to identify the factors affecting the siring success of extra-group males, including residents of adjacent groups and bachelors. Resident males of adjacent groups tended to be more likely to sire offspring than bachelors, but this pattern only neared significance. Neither bachelor dominance rank nor time spent in group predicted were significant predictors of siring success. These surprising results indicate that even when a bachelor is high-ranking (relative to other bachelors) and remains near the group, he may miss reproductive opportunities. Bachelor reproduction may be primarily driven by opportunistic encounters with females in conceptive estrous rather than by contests with other bachelors.

Quantifying resident and bachelor siring success in a small scale (within the study groups during the 10-year study period) allowed me to conduct a simple calculation to estimate and compare the lifetime reproductive success of residents and bachelors. This comparison was exploratory, with the goal of determining if there were any conditions under which a lifelong bachelor could sire as many offspring as a resident during one period of residency. The components of resident reproductive success were: annual siring rate in his own group, annual siring rate in adjacent groups, the number of adjacent groups, and resident tenure. Bachelor reproductive success depended on annual siring rate in groups and the number of groups contacted. I computed mean values for each resident and bachelor parameter using paternity data and long-term observational data from the study population. I used mean values to determine the number of years it would take for the hypothetical average bachelor to sire as many offspring as the hypothetical average resident.

I found that in most circumstances, a lifelong bachelor would not live long enough to sire as many offspring as a resident. However, the average bachelor who can perform for several years may have similar lifetime reproductive success as a male whose reproduction is limited to a short period of residency, especially if he is the resident male of a small group. This finding therefore draws into question the assumed resident reproductive advantage for all males in all circumstances. This study also highlights the importance of future work to determine how often males switch between residency and bachelorhood and generate more precise estimates of the length of male reproductive lifespans.

Chapter 5 focused female reproduction, specifically investigating the relationship between within-group competition for food, as measured by group size and dominance rank, on the probability that a female conceived. Blue monkey groups vary greatly in size, but previous work has found no effect of group size on travel distance, birthrate, or offspring survival (Cords 2012). Additionally, females compete aggressively for access to fruit resources, but previous studies have found weak or no effect of dominance rank on access to food or birthrate (Cords 2002b, Pazol & Cords 2005, Cords 2012). We used large data set spanning 15 years, 10 social groups, and 92 reproductive females to measure the effect of group size and dominance rank on the probability of conception, a direct measure of fertility.

After controlling for additional factors that might affect the probability of conception (i.e., age, time since last conception, presence of a dependent infant, rainfall, and time of year) and their interactions, results indicated that group size had a significant quadratic effect on the probability of conception and rank had no effect. The probability of conception peaked for medium-sized groups containing around 31 individuals, suggesting the existence of an optimal group size. More surprising is that rank continued to have no effect on reproductive parameters, despite aggressive competition for preferred food resources and the existence of significant linear dominance hierarchies. The lack of a rank effect may occur if females use flexible feeding behavior (e.g., spreading out, feeding on diverse food items, using cheek pouches) to reduce the strength of within-group competition for resources. It is also possible that these proximate mechanisms for reducing within-group competition promote group cohesion, thereby increasing success in between-group contests. Overall, behavioral measures of within-group competition, including the existence of a dominance hierarchy or the lack of a group size effect on travel distance, may not have the expected effects on reproduction. When possible, researchers should measure the effect or rank and group size on direct measures of reproduction, like the probability of conception.

Intrasexual competition plays an important role in shaping animal societies. Regarding males, future work to quantify factors affecting resident siring success, like female reproductive synchrony, would promote interspecific comparisons and explain the considerable variation in resident siring success across species living in one-male groups. Additionally, tracking individual males will provide a better understanding of how males adjust their behavior in response to the environmental changes and how these behaviors affect reproduction. Our results suggest that a main factor determining male reproductive success may be the amount of time that a male spends as a resident and as a bachelor. While it is a daunting task, research that tracks males throughout entire lives will allow us to determine how often males switch among tactics and provide enormous insight into age- and tactic-related reproductive output and more precise estimates of the length of a male's reproductive lifespan.

Regarding females, this research on the effects of within-group competition on reproduction calls for a better understanding of the interaction between within-group and between-group competition. For example, does low within-group competition promote social tolerance and increase success in between-group contests? Additionally, do group size and rank affect other measures of fitness? Finally, current research is beginning to highlight the importance of female-female competition for resources other than food (Clutton-Brock 2009, Huchard & Cowlishaw 2011, Rubenstein 2012, Stockley & Campbell 2013), which calls for a broader consideration of the role of intrasexual competition in females.

In conclusion, the literature review and three empirical studies presented here expand our understanding of the reproductive effects of intrasexual competition for limited resources. They emphasize the value of using longitudinal data on individually-identified animals to investigate patterns of reproduction as well as the importance of measuring reproduction directly instead of using behavioral proxies. I hope that the research included in this dissertation can inform models describing the evolution of social organization and mating systems.

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