Original Article

Infanticide risk and male quality influence optimal group composition for *Colobus vellerosus*

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The threat of infanticide by males is suggested to determine upper group size limits for some folivores because large female aggregations attract immigrating males. When groups get large enough to become multimale, infanticide risk should decline because, all other things being equal, more males should deter outside takeovers and the counterstrategies of mothers and sires should lower the consequences of inside takeovers. To determine if this scenario can be generalized to all folivorous primates, we began by examining the influence of female and male group size on 4 increasing levels of infanticide risk in folivorous ursine colobus monkeys (*Colobus vellerosus*) at Boabeng-Fiema, Ghana. Data from 2004 to 2010 on 7 groups analyzed with generalized estimating equation models showed that infanticide risk is heightened in groups with more females and absolutely more males because male immigration is more frequent. However, when controlling for the effect of female group size on male group size, groups with relatively more males have significantly more male immigration and higher infanticide rates. Thus, multimale groups of *C. vellerosus* show higher infanticide risk compared with unimale groups. Resident males in unimale groups may be higher quality than those in multimale groups because they perform more energetically costly displays and win more encounters. However, males in multimale groups may also suffer from collective action problems making them unable to prevent male immigration and infanticide. This study highlights the importance of the quality of male defenders in infanticide risk and demonstrates intersexual and intrasexual conflict in group composition in *C. vellerosus*. *Key words:* black-and-white colobus, group composition, intersexual conflict, intrasexual conflict. *[Behav Ecol]*

INTRODUCTION

The primary reason for group formation in diurnal mammals is suggested to be protection from predation (Hamilton 1971; Alexander 1974; van Schaik 1983, 1989; Shultz et al. 2011). Variation in group size and in group composition can also be influenced by individual strategies that may be sex specific (Trivers 1972; van Schaik and Dunbar 1990), such as access to mates for males (e.g. *Mirounga angustirostris*, Le Boeuf 1974; *Prunella modularis*, Davies 1985; *Equus caballus*, Stevens 1990; *Megaptera novaeangliae*, Craig et al. 2002; delphinids, Möller 2011) and access to food resources (e.g. *Ateles geoffroyi*, Chapman 1990; *Lontra canadensis*, Blundell et al. 2002; delphinids, Baird and Dill 1996; Möller 2011), control of skewed reproduction (e.g. *Helogale parvula*, Rasa 1994; *Lycaon pictus*, Creel et al. 1997; *Mungos mungo*, Cant et al. 2001), or defense against infanticide (e.g. *Panthera leo*, Packer et al. 1990; *Suricata suricatta*, Clutton-Brock et al. 1998; *Alouatta seniculus*, Crockett and Janson 2000) for females. Thus, an ongoing conflict of interest between the sexes over optimal group composition and group size often occurs (Treves 2001; Henzi and Barrett 2003; Ryan et al. 2008; van Belle and Estrada 2008; Kappeler and Schäffler 2008; Fedigan and Jack 2011; Möller 2011). In this article, we examine the link between group size and

composition, and the risk of infanticide by males. More specifically, we argue that the extent to which male and female counterstrategies to infanticide will translate into infant survival may be influenced by group size and composition. As a result, individual males and females may exert control over the size and composition of the groups in which they live (via emigration or resistance to immigration) to achieve maximum protection against infanticide by males (i.e. to protect against inside and outside takeovers).

Infanticide by males is one of the most intense and costly behavioral manifestations of intersexual conflict over reproduction (Pradhan and van Schaik 2008; Palombit 2010). Infanticide occurs in many animal taxa and in a wide range of contexts (Hrdy and Hausfater 1984; Parmigiani and vom Saal 1994), but infanticide by males, or the killing of dependent offspring by males, is primarily seen in primates, sciurognathi rodents, and carnivores (van Schaik 2000a; Blumstein 2000; Packer and Pusey 1984). These are species in which lactation is longer than gestation and females experience lactational amenorrhea, so postpartum mating does not occur (van Schaik 2000a). Males, therefore, benefit from killing a female's offspring if they are not the sire, if they can mate with the female when she returns to estrus, and if they have a chance of siring her next offspring (i.e. the sexual selection hypothesis, Hrdy 1974, 1979). Infanticide by males is costly to the reproductive success of fathers and mothers. The primary male counterstrategy to infanticide is defense of infants (Argell et al. 1998). Natural selection has favored a range of physiological, behavioral, and social counterstrategies in females, such as situation-dependent receptivity (e.g. postconceptive mating), paternity confusion, abrupt cessation

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of investment in the infant (e.g. abortion, early weaning), infant defense, and association with a protector male (reviewed in Argell et al. 1998; Ebensperger 1998; van Schaik 2000b; Roberts et al. 2012).

Group size and composition are probably both a cause and a consequence of the presence of infanticide and of the effectiveness of counterstrategies (Borries and Koenig 2000; Crockett and Janson 2000; Clarke et al. 2009). For instance, in several species, larger female groups are more of a target for immigrating males, increasing infanticide threat by making male defense against new males more difficult, thus increasing infanticide rates (e.g. *P. leo*, Packer et al. 1988; *Semnopithecus entellus*, Borries 1997; *Theropithecus gelada*, Dunbar 1984; *A. seniculus*, Crockett and Janson 2000). Female counterstrategies may include attempting to maintain smaller group sizes by dispersing from large to small groups, evicting other females, resisting the immigration of new females, or fissioning groups (e.g. Crockett and Janson 2000; Teichroeb et al. 2009), as under these conditions, the intensity of infanticide threat is reduced. If female group size increases, groups may become too large for 1 male to monopolize access to the females (Nunn 1999). Once several males reside in the group, infanticide rates may decrease because of new sets of female counterstrategies. Indeed, some studies report that within-species infanticide may occur less in multimale groups than in unimale groups (e.g. *Gorilla beringei beringei*, Robbins 1995; *Procolobus rufomitratus*, Leland et al. 1984; *Papio ursinus*, Palombit et al. 2000; *S. entellus*, Newton 1986; but see Borries 1997; Borries and Koenig 2000). The presence of several resident males allows females to mate polyandrously, probably confusing paternity, which decreases the risk of infanticide by within-group males (Janson and van Schaik 2000; Clarke et al. 2009) and may lead to male defense of infants in the case of threat by immigrant or outside males (e.g. Borries et al. 1999; Teichroeb and Sicotte 2008a; Nguyen et al. 2009; Huchard et al. 2010).

Infanticide may be an important selective pressure on the social organization of ursine colobus (*Colobus vellerosus*) at our study site, the Boabeng-Fiema Monkey Sanctuary (BFMS) in central Ghana. All males disperse from their natal group and are attracted to groups with a larger ratio of females to males than their previous group (Teichroeb et al. 2011). Male competition for residence in groups is intense and aggressive and has lead to the death of several males by injuries sustained in male–male contests (Sicotte et al. 2007; Teichroeb and Sicotte 2010; Teichroeb et al. 2011). Infanticide by males occurs when new males immigrate and become high ranking, though resident males may defend infants (Saj and Sicotte 2005; Teichroeb and Sicotte 2008a). Female dispersal occurs facultatively (i.e. some females remain in their natal group whereas some emigrate), and females tend to move from larger to smaller groups. Females may emigrate voluntarily when the male composition of their group is unstable or, alternatively, they may emigrate involuntarily when adult, parous females force the emigration of new adult, nulliparous females. Females also resist new female immigration (Teichroeb et al. 2009). We interpreted these dispersal patterns as female avoidance of infanticide because larger female groups appear to be a target for new male immigration (Teichroeb et al. 2009, 2011). When females live in multimale groups, they mate polyandrously (Teichroeb and Sicotte 2010). Extragroup copulations have been observed in both unimale and multimale groups (Teichroeb et al. 2005; Teichroeb JA, Wikberg EC, Bădescu I, unpublished data).

Male quality also appears to play a role in influencing group composition for *C. vellerosus*. Males that display frequently are able to exclude other males from their group and thus appear to have good fighting ability (Teichroeb and

Sicotte 2010), and females attempt to transfer into groups where the male(s) win encounters against the male(s) in their own group (Teichroeb et al. 2009). By preventing male immigration altogether, these high-quality males may be the most successful infant defenders. The proportion of unimale/multifemale groups is variable in our population (26–48%) (Saj et al. 2005; Holmes 2011). During their lifetimes, few males show the strength to be able to exclude other males from their groups for an extended period of time (only 8.5% of adult males observed over more than 12 years in our research groups have resided as the single male in a unimale group, Teichroeb JA, Wikberg EC, unpublished data), and tenure, although variable, tends to be short (22.3 months, $N = 8$, Teichroeb et al. 2011). Therefore, displaying high male quality does not appear to be directly related to male age nor is it attainable by all males.

In this article, we used data from 7 study groups from 2004 to 2010 to investigate the impact of group composition on the risk of infanticide for *C. vellerosus* at BFMS. We examined the influence of absolute female group size, absolute male group size, and relative male group size on 4 increasing levels of infanticide threat (Table 1): number of male immigrants, the rate of takeovers and changeovers (a change in the dominant male of the group), the rate at which infants were attacked by different males, and the overall infanticide rate (number of infants killed by males per infant born). We also further investigated the notion that resident males of unimale/multifemale were of better quality than resident males of multimale/multifemale groups, which could influence infanticide risk. We based our hypotheses on the theoretical level of infanticide risk that folivorous animals undergo at various group sizes (Figure 1, Crockett and Janson 2000). We hypothesized that all the levels of infanticide risk would increase with increasing female group size because outside males should be more attracted to larger female groups (Teichroeb et al. 2011), leading to challenges to the alpha male position, more attacks on infants by these new males, and greater infanticide rates (Table 1). However, with the caveat that attacks on infants and infant deaths would increase with increasing female group size only to the point where groups become multimale, then, because of the protection afforded by having several males (discussed above), rates of attacks on infants and infant deaths would decrease. For increasing male group size, we hypothesized that the first level of risk, male immigration, would show a negative relationship with increasing male group size because outside males should cue in to the adult male:adult female ratio of a group and preferentially attempt to immigrate into groups with a favorable ratio and therefore fewer males. Potential immigrant males may also be deterred from entering groups with several resident males when these males form coalitions to exclude them (Teichroeb et al. 2011). However, in multimale groups, the second level of risk, changes to the alpha male position, may occur frequently because males in multimale groups are unable to evict one another and thus may be closely matched in fighting ability, allowing them to successfully challenge one another (Teichroeb and Sicotte 2010). As male group size increases, we predicted that infant attack rates and infanticide rates should decrease because of lower mating and reproductive skew among males, and the availability of sires to defend infants (Janson and van Schaik 2000; Ostner et al. 2008).

MATERIALS AND METHODS

Study site and species

This research was conducted at BFMS in central Ghana (7°43′N and 1°42′W), a dry semideciduous forest, 192 ha in

Table 1

Behaviors used to evaluate increasing levels of infanticide risk

Increasing levels of infanticide risk	Behavior	Increase of infanticide risk	Resident male response in *C. vellerosus*	Resident female response in *C. vellerosus*	Predicted relationship with increasing group size		Observed relationship with increasing group size	
					♂	♀	♂	♀
1	New male(s) immigrate	New males often have not mated with resident females, so may kill infants to gain access to estrus females	Residents resist male immigration but are unsuccessful[a]	Females without infants may emigrate[b]	↓	↑	↑	↑
2	New immigrant male(s) become high ranking[c]	Infanticide is most beneficial to high-ranking males because they are likely to get sexual access to the mother afterwards	Some or all resident males may be evicted[b]	Females with infants may emigrate with ousted males[d]	↑	↑	NS	NS
3	New immigrant male(s) attack infants or infants are attacked by extragroup male(s)	Escalation of the situation to where male(s) attempt to kill an infant (although they may not always be successful)	Remaining resident males may defend the infants[b]	Females, in coalitions with the mothers may defend infants[e]	↓	↑*	NS	NS
4	Infanticidal male(s) (intra- or extragroup) successfully kill infants	Male(s) succeed in their goal, killing the infant and bringing the mother back into estrus sooner	Sires, whose infants are killed, may emigrate[f]	Mother mates with infanticidal male[b]	↓	↑*	↑**	NS

NS, relationship was not significant.
[a]Teichroeb et al. (2011).
[b]Teichroeb and Sicotte (2008a).
[c]Lower ranking males may attack infants if their prospect of becoming high ranking is good, Teichroeb and Sicotte (2008a).
[d]Bădescu I (unpublished data).
[e]Teichroeb JA (personal observation)
[f]Teichroeb et al. (2009).
*Infanticide risk increases with greater female group size but only to the point where the group becomes large enough to be multimale, then infanticidal attacks and deaths decrease due to paternity confusion. **Infanticide rates increased in groups with relatively more males but not absolutely more males, showing the importance of male quality in infant defense because a greater number of adult males:adult females indicates that these males are unable to exclude one another from the group and have low fighting ability (see text).

size. BFMS is located at an altitude of 350 m in the Nkoranza district of the Brong-Ahafo Region. It is surrounded by farmland but connects by a narrow riparian forest to several smaller forest fragments that also contain ursine colobus populations. The vegetation is a mosaic of primary forest,
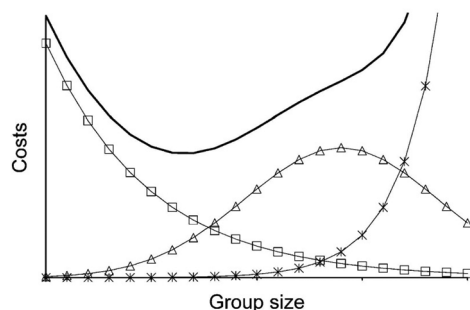

Figure 1
Theoretical costs of predation (squares), infanticide risk (triangles), and food competition (asterisks) at various group sizes. The solid dark line represents the combination of all 3 costs and shows where total costs are minimized. (A correction factor was used so that lines did not overlap. Reproduced with permission from Robbins et al. [2009], adapted from Crockett and Janson [2000] and Chapman and Pavelka [2005]).

regenerating farmland (secondary forest), and woodland (Fargey 1991; Saj et al. 2005).

Ursine colobus monkeys (*C. vellerosus*) at BFMS have been studied under the supervision of PS since 2000. They are mainly folivorous (annual diet: 74% leaves, Saj et al. 2005), and group sizes vary (range: 9–38, mean: 15.0, *N* = 15; Wong and Sicotte 2006) as does group composition, which can be multimale/multifemale, unimale/multifemale, or all-male bands (AMBs) (Saj and Sicotte 2005; Saj et al. 2005; Holmes 2011). Several infanticides have been observed after new males have immigrated, and infanticide accounted for 38.5% of infant mortality in the study population for the period from 2000 to 2005 (Teichroeb and Sicotte 2008a). If incoming males do not evict them, putative sires may aid females in infant defense (Saj and Sicotte 2005; Teichroeb and Sicotte 2008a, 2008b). Between-group encounters, defined as 2 groups coming to within 50 m of one another (Oates 1977), are usually aggressive, with adult males as the main participants. Male incursions also occur when group males, solitary males, or males in AMBs approach to within 50 m of a bisexual group, sometimes attacking individuals in the group (Sicotte and MacIntosh 2004; Teichroeb et al. 2011). Targeted aggression toward infants also occurs during both between-group encounters and male incursions (Sicotte and MacIntosh 2004; Saj and Sicotte 2005).

Our observations have shown that groups go through periods of stability, without infanticide or male immigrations, when their high-ranking males are strong and close to prime age. When their males are weakening or aging, new males immigrate and may takeover the alpha male position (slow or fast takeovers, Teichroeb et al. 2011). Thus, all groups go through unstable periods of changes in male composition, sometimes accompanied by female emigrations and infanticide (Teichroeb and Sicotte 2008a; Teichroeb et al. 2009), before a prime-aged male emerges as dominant and the group becomes stable again. Not all prime-aged males become resident of a unimale group.

Study subjects and data collection

To determine the most important factors influencing infanticide risk for *C. vellerosus*, we used data on group composition, male immigration, observed attacks on infants, and infanticides from 7 research groups collected from 2004 to 2010. Groups were followed for varying amounts of time, and all adult and subadult individuals could be recognized by features of the face and tail. When researchers were present at the site, each study group was followed for at least 1 day per month (range: 1–22 days, mean 4.57 days/month) for 7–12 h per day (Table 2). Behavioral observations were done using 10-min focal samples (Altmann 1974) that were alternated among adult and subadult males and females, with no individual sampled more than once per hour. Focal data used for male quality assessment were collected in 2004–2005 by JAT on 4 groups, RT, B2, DA, and WW (202 follow days, 433.3 focal hours).

Each observation day, observers recorded demographic information on the study groups. New immigrants, births, or infant disappearances were noted. Males may commit infanticide up to 4 months after immigrating (Teichroeb and Sicotte 2008a). Therefore, we consider males as new immigrants during the first 4 months of group residency. Takeovers were defined as a complete change in male group membership, meaning that all the resident males emigrated within a few months of new male(s) immigrating. Changeovers were defined as changes of the alpha position, without the emigration of all the resident males. We lumped takeovers and changeovers in our models because in this population, both these processes are a result of immigrant males, who are potentially infanticidal, becoming alpha. At this point, we do not have evidence that young males enter a group and slowly become high ranking (inside takeovers, Clarke et al. 2009; e.g. *P. cynocephalus*, Collins 1984; *Macaca fuscata*, Sprague et al. 1998; *M. fascicularis*, van Noordwijk and van Schaik

2001). High rank is usually achieved through fast or slow takeovers (Teichroeb et al. 2011) of another group. In the following analyses, takeover/changeover rates were calculated as the number of these events per observation hour and month. Male dominance relationships were determined from the direction of aggression, displacements, avoidance, and submissive behaviors during focal samples and ad libitum observations. Instances of unstable male rank relationships, where the same male reacquired the alpha position several times within a few months, were counted as a single changeover.

During contact hours, events such as attacks on infants were recorded ad libitum (Altmann 1974). The death of an infant was considered infanticide if a male directed aggression (chases and contact aggression) toward an infant or a mother–infant pair before the infant disappeared or died from its wounds. We also included suspected infanticides in our analyses, which were cases where apparently healthy infants disappeared at the same time as a takeover or changeover and/or the infant's body was found with wounds that appeared to be caused by canines (following Watts 1989; Teichroeb and Sicotte 2008a). Larger predators at BFMS have been extirpated and people are forbidden from owning dogs (Teichroeb and Sicotte 2012), so there are no other animals to which these canine wounds could belong. When used in analyses, multiple attacks by the same male on the same infant within a few months were only counted once as a "set of attacks on infants." Rates of attacks on infants were then calculated as sets of attacks per month or per hour. The infanticide rate in each group during each time period was calculated as the number of infants killed divided by the number of infants born.

Assessment of male quality

Colobus vellerosus males perform several agonistic display behaviors that appear to function in male–male competition (Teichroeb and Sicotte 2010). Two of these behaviors, loud calls and stiff-leg displays, decrease in vigor over time during a single display and thus appear energetically costly (Teichroeb and Sicotte 2010). Stiff-leg displays involve individuals holding their legs straight out from a branch, where they may be held for varying lengths of time (as described for *C. guereza*, Oates 1977). Loud calls involve multiple roars ("rurr rurr rurr rurr") produced in several repeated bouts while leaping through the canopy (jump display). Loud calls occur in the morning in contagious choruses with other groups and at other times of the day. Usually all the adult males in a group roar in relative synchrony, although some males produce more roars per bout or more bouts of roaring, and/or

Table 2

Study group summary for the years of analysis

Group	Years of observation included in analyses	Contact hours	Follow days	Mean no. of adult females	Mean no. of resident adult males	Mean no. of male immigrants/ month	Takeover and changeover rate/month	Mean no. of sets attacks on infants/ month[a,b]	Infanticide rate/infant born/month
SP	2006–2010	697.6	435	3.40	1.00	0.03	0	0.03	0
B2	2004–2010	1220.8	369	5.00	1.33	0.15	0.09	0.11	0.009
OD	2006–2010	732.2	326	5.60	1.00	0.15	0.03	0	0
RT	2004–2010	1462.0	455	6.00	1.50	0.08	0.04	0	0
DA	2004–2010	1240.9	374	7.70	3.42	0.43	0.1	0.15	0.002
BO	2006–2010	400.1	73	8.00	1.00	0	0	0	0
WW	2004–2010	1698.3	585	8.38	2.88	0.19	0.13	0.23	0.003

[a]Attacks by the same male on the same infant were counted as 1.
[b]Attacks by extragroup males are included.

tend to participate more often (Teichroeb and Sicotte 2010). Bouts of roaring within a loud call are usually separated by several seconds and therefore roars and bouts can be counted easily. Because loud calls and stiff-leg displays appear energetically costly, they may act as honest indicators of male quality. Males of greater quality should be able show their superiority by producing more displays or displays of longer duration (Zahavi 1975, 1977).

For 13 months of observation in 2004–2005, data were collected on male display output by JAT. Here, we use these data to compare males in 1-male groups and males in multimale groups in their performance in stiff-leg and loud call displays. When loud call bouts occurred, they were recorded on a handheld tape recorder (Sony TCM-400DV) and the observer (JAT) dictated during each bout the identity of the calling male(s). In multimale groups, when several males called together, observations focused on a single male (this was possible in 60% of choruses, $N = 45/75$) to determine his contribution to the chorus. During the study, only 1 focal group (RT) had a single adult male and one other group (B2) went through a stage with 1 male. We, thus, included other, nonresearch, unimale groups that were nevertheless habituated to human presence ($N = 4$), and we recorded the roaring of these males to allow comparisons with males in multimale groups. The number of bouts and number of roars were extracted from recordings, and the duration of roaring per call was timed. The rates and durations of stiff-leg displays were recorded during focal samples on study groups, so measures were only available from 2 males in 1-male groups to compare with all adult males in multimale groups. The measures of display behaviors compared below include 1) the mean number of roars per loud call, 2) the mean duration of roaring per call (s), 3) the mean number of roaring bouts per call, 4) the mean number of roars per bout, 5) the rate of stiff-leg displays (number/min.), and 6) the mean duration of stiff-leg displays (s). Because only one male was the focus of observations during loud call choruses, accurate rates of loud call participation for each male could not be calculated.

Between-group encounters and male incursions in *C. vellerosus* overwhelmingly involve male participation (100% of encounters, Sicotte and MacIntosh 2004); thus, like *C. guereza* (Harris 2010), intergroup conflict often becomes a battle between the males of 2 groups. During the same period that display performance was assessed (2004–2005), the outcomes of between-group encounters and male incursions between groups were recorded. This allowed us to examine the outcome of encounters between groups with a single male versus those with multiple males. Encounters separated by at least 1 h were considered distinct. If more than 1 encounter between the same groups occurred in a single day, only the first was used in analyses. The "winners" of encounters were defined as the group that displaced or forced the other group to retreat or change direction (Fashing 2001; Harris 2005). A clear winner could only be determined for 50.4% (122/242) of encounters.

Data analyses

To investigate how male and female group size affects infanticide risk, we used 3 generalized estimating equation (GEE) models: 1 model to examine the influence of female group size on the 4 increasing levels of infanticide threat and 2 models to examine the effect of male group size. GEEs are a type of generalized linear model that controls for the temporal autocorrelation that is present when repeated measures are taken on the same groups longitudinally (Fitzmaurice and Verbeke 2009; Zuur et al. 2009). GEEs were more applicable to our case than generalized linear mixed models (GLMM)

because they allow dependent variables to be correlated, which GLMMs do not (Ghisletta and Spini 2004). GEEs also tend to be more conservative (Walker et al. 2009).

In the first GEE model used to determine the effect of female group size on the 4 increasing levels of infanticide risk, the independent variable "number of resident adult females" was examined for its effect on 4 dependent variables: "number of new male immigrants," "takeover/changeover rate," "infant attack rate," and "infanticide rate." The data set was organized with a new entry for each group, each study year, or each time adult female group size changed. To visualize this large data set, we provide a figure (Figure 2) that divides the data into groups with less than 7 versus 7 or more females and summarizes the monthly rates of male immigration, takeover/changeover, sets of attacks on infants, and infanticide per infant born. We chose a cutoff of 7 females for this figure because the mean number of females in the groups was 6.4.

The data set used to analyze the effect of male group size on infanticide risk was set up a little differently than the previous data set. Because the number of resident males changed so often, it was important to take into account the length of the periods of stability with no threats to infants. Thus, for these analyses, we constructed a database with a new entry for groups every 4 months or each time resident adult male group size changed. We chose 4 months as the time period for new entries because this is the time period after which new immigrant males seem to no longer be an infanticide threat (Teichroeb and Sicotte 2008a) and are considered "resident."

Analyses of the effect of the number of resident males on infanticide risk were performed in 2 ways using 2 GEE models. First, a GEE model was done in exactly the same way as the model for female group size, with "number of resident adult males" as the independent variable and dependent variables for each of the 4 increasing levels of infanticide threat ("number of new male immigrants," "takeover/changeover rate," "infant attack rate," and "infanticide rate"). This analysis did not control for the strong influence of the number of resident females on the number of resident males (Nunn 1999; Teichroeb et al. 2011) and thus represents the effect of the *absolute* number of males in a group on infanticide risk. To visualize this large data set on the effect of male group size on infanticide risk, we provide a figure (Figure 3) comparing monthly rates of male immigration, takeover/changeover, sets of attacks on infants, and infanticide per infant born for groups with 1 versus more than 1 resident male.

The second GEE model on the influence of male group size accounted for the effect of the number of resident females on the number of resident males by using the independent variable "adult male:adult female ratio" with the same 4 dependent variables: "number of new male immigrants," "takeover/changeover rate," "infant attack rate," and "infanticide rate". Adult male:adult female ratios were calculated for each 4-month entry into the data set as number of resident adult males over the number of resident adult females. Thus, this model examines the effect of the *relative* number of resident males on infanticide risk. For this data set, Figure 4 shows monthly rates of male immigration, takeover/changeover, sets of attacks on infants, and infanticide per infant born for groups with adult male:adult female ratios less than 0.4 and greater than or equal to 0.4 (mean adult male:adult female ratio was 0.32).

Rates in the models were calculated per hour of observation. For all 3 GEE models, we used the frequency rather than the rate of male immigration because new immigrant males would have been noted regardless of the number of hours of observation on a group. The dependent variables in the first 2 GEEs were counts, so they were analyzed using
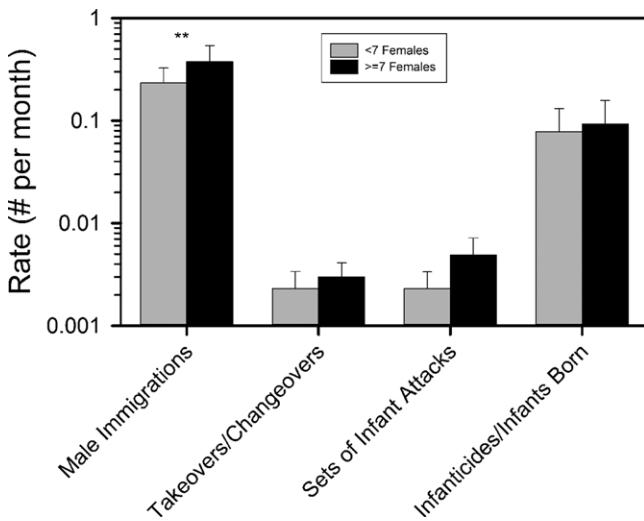
Figure 2

Summary of the data analyzed in Table 3 examining the effect of larger female group size on infanticide risk. Log-transformed monthly rates of male immigrations, takeovers/changeovers, attacks on infants by males, and infanticides by males/infants born for groups with less than 7 resident females and those with 7 or more resident females. Error bars show standard error. **Male immigrations occurred significantly more often in larger female groups ($P = 0.009$).
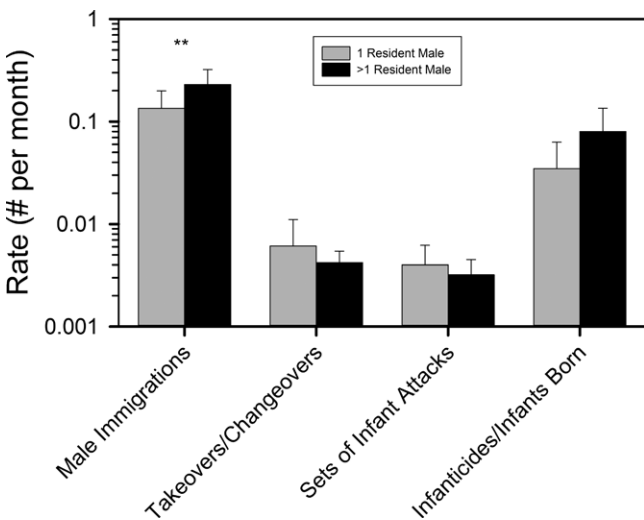

Figure 3

Summary of the data analyzed in Table 4 examining the effect of larger *absolute* male group size on infanticide risk. Log-transformed monthly rates of male immigrations, takeovers/changeovers, attacks on infants by males, and infanticides by males/infant born for groups with 1 resident male and those with multiple resident males (mean = 3.16 males). Error bars show standard error. **Groups with more than 1 resident males had significantly more male immigrations ($P = 0.002$).

Poisson distributions. For the third model, the dependent variable (adult male:adult female ratio) was ordinal so a multinomial distribution was used. Those models with the lowest corrected and uncorrected quasi likelihood under independence model criterion (QICC and QIC) were considered to have the best goodness of fit (QIC is akin to Akaike information criteria, Hardin and Hilbe 2002). Comparisons of several aspects of loud call and stiff-leg performance for males in unimale versus those in multimale groups were done using
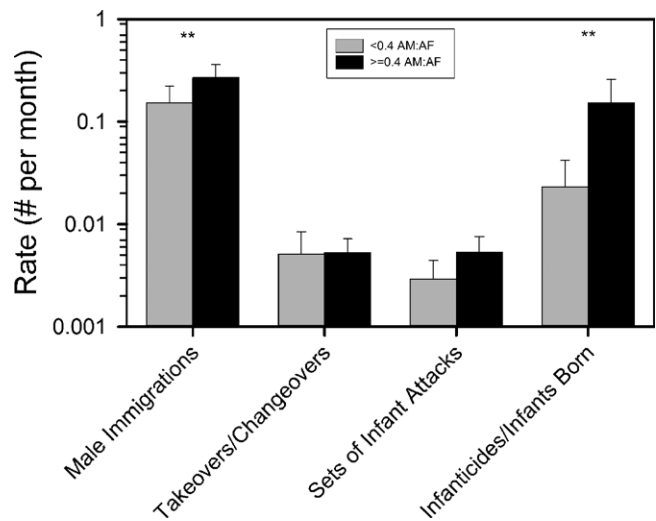

Figure 4

Summary of the data analyzed in Table 5 examining the effect of larger *relative* male group size on infanticide risk. Log-transformed monthly rates of male immigrations, takeovers/changeovers, attacks on infants by males, and infanticides by males/infant born for groups with an adult male:adult female ratio of less than 0.4 (relatively fewer males) and greater than or equal to 0.4 (relatively more males). Error bars show standard error. **Groups with relatively more resident males had significantly more male immigrations ($P = 0.006$) and more infanticides/infants born ($P = 0.001$).

Mann–Whitney U tests. For all analyses, significance was set at 0.05. Models and statistics were run using SPSS/PASW 17.0.

RESULTS

The effect of resident adult female group size on infanticide threat

The GEE model for resident female group size showed that for the 7 study groups, a greater number of resident adult females had a positive effect on the number of new male immigrants ($\beta = 0.052$, $P = 0.009$). Larger female group size did not show a significant effect on takeover/changeover rates ($\beta = -18.694$, $P = 0.422$), infant attack rates ($\beta = 8.542$, $P = 0.459$), or infanticide rates ($\beta = 0.111$, $P = 0.683$) (Table 3). Monthly rates of each behavior associated with the 4 levels of infanticide risk for groups with less than 7 resident females and groups with 7 or more females are displayed in Figure 2.

The effect of resident adult male group size on infanticide threat

The second GEE model examining the effect of the *absolute* number of resident males on infanticide risk showed that a greater number of resident adult males had a positive effect on the number of new male immigrants ($\beta = 0.082$, $P = 0.002$). However, having absolutely more males did not significantly affect takeover/changeover rates ($\beta = -5.180$, $P = 0.316$), infant attack rates ($\beta = -7.996$, $P = 0.421$), or infanticide rates ($\beta = 0.287$, $P = 0.508$) (Table 4). A visual representation of this data set is provided in Figure 3 for months when groups had 1 resident male versus when they had more than 1 resident male.

Results of the third GEE model for the *relative* number of resident adult males showed that having a greater number of resident adult males to adult females (adult male:adult female ratio) had a positive effect on the number

Table 3

GEE for effect of resident adult female group size on levels of infanticidal threat

Level of infanticidal threat	β	Wald chi-square (df = 1)	P level
Number of male immigrants	0.052	6.82	0.009*
Takeover/ changeover rate	−18.694	0.64	0.422
Infant attack rate	8.542	0.55	0.459
Infanticide rate	0.111	0.17	0.683

*Significant results.

Table 4

GEE for effect of absolute resident adult male group size on levels of infanticidal threat

Level of infanticidal threat	β	Wald chi-square (df = 1)	P level
Number of male immigrants	0.082	9.60	0.002*
Takeover/changeover rate	−5.180	1.01	0.316
Infant attack rate	−7.996	0.65	0.421
Infanticide rate	0.287	0.44	0.508

*Significant results.

of new male immigrants (β = 0.256, P = 0.006) and infanticide rates (β = 2.254, P = 0.001). However, having relatively more resident males did not significantly affect takeover/ changeover rates (β = −17.368, P = 0.222) or infant attack rates (β = −73.728, P = 0.072) (Table 5). Monthly rates for these behaviors when the adult male:adult female ratio was less than 0.4 (relatively fewer males) and when it was 0.4 or greater (relatively more males) are provided in Figure 4.

Display performance and encounter wins for males in unimale versus multimale groups

During morning loud calls, males in unimale groups performed more roars per call ($N_{unimale}$ = 5, $N_{multimale}$ = 11, Z = 1.93, P = 0.05), roared for longer duration per call ($N_{unimale}$ = 5, $N_{multimale}$ = 7, Z = 1.95, P = 0.05), and had a tendency for more roaring bouts per call ($N_{unimale}$ = 6, $N_{multimale}$ = 13, Z = 1.8, P = 0.07) compared with all males in multimale groups. There was no difference in the mean number of roars per bout produced by males in unimale

Table 5

GEE for effect of adult male:adult female ratio on levels of infanticidal threat

Level of infanticidal threat	β	Wald chi-square (df = 1)	P level
Number of male immigrants	0.256	7.46	0.006*
Takeover/ changeover rate	−17.368	1.49	0.222
Infant attack rate	−73.287	3.24	0.072
Infanticide rate	2.254	10.88	0.001*

*Significant results.

and multimale groups ($N_{unimale}$ = 6, $N_{multimale}$ = 13, Z = −0.57, P = 0.57).

When males in unimale groups were compared with the alpha males of multimale groups, no differences emerged, however (number of roars per call: $N_{unimale}$ = 5, $N_{multimale}$ = 5, Z = −0.63, P = 0.52; duration: $N_{unimale}$ = 5, $N_{multimale}$ = 3, U = 4.0, P > 0.05; number of bouts: $N_{unimale}$ = 6, $N_{multimale}$ = 5, Z = 1.55, P = 0.12). Alpha males in multimale groups actually showed a tendency to produce a greater mean number of roars per bout than single males of unimale groups ($N_{unimale}$ = 6, $N_{multimale}$ = 5, Z = −1.92, P = 0.055; Table 6).

Mean stiff-leg display duration was not significantly different between males in unimale groups (mean = 14.4 s, N = 2 males) and all males in multimale groups (mean = 10.6 s, N = 17 males) ($N_{unimale}$ = 2, $N_{multimale}$ = 17, U = 8.0, P > 0.05) or the alpha males of multimale groups (mean = 8.9 s, N = 7 males) ($N_{unimale}$ = 2, $N_{multimale}$ = 7, U = 2.0, P > 0.05). Rates of stiff-leg displays were also not significantly different between the single males of unimale groups (0.03/min, N = 2) and all males in multimale groups (0.04/min, N = 22) ($N_{unimale}$ = 2, $N_{multimale}$ = 22, U = 24.0, P > 0.05) or the alpha males of multimale groups (0.07/min, N = 5) ($N_{unimale}$ = 2, $N_{multimale}$ = 5, U = 8.0, P > 0.05).

Of all decided between-group encounters and male incursions (N = 71 encounters) between 1-male (N = 4 groups) and multimale (N = 5 groups) groups, unimale groups were defined as winning the encounter in the majority of cases (69%, 49/71). Yet, these data were skewed by 1 large multimale group (WW) that often appeared to win encounters based on group size rather than on male participation. When WW is removed for the data set, unimale groups overwhelmingly won their encounters against multimale groups (93.2%, 41/44).

DISCUSSION

Absolutely larger female and male group size increased infanticide risk in groups of ursine colobus monkeys (*C. vellerosus*)

Table 6

Comparison of loud-calling performance for males in unimale versus multimale groups

Measure	Males in unimale groups (N = 6)	Males in multimale groups (N = 13)	Alpha males of multimale groups (N = 5)*
Mean no. of roars per call	91.5 (101, 23.6)	61.9 (55, 39.0)	88.3 (70, 30.0)
Mean roaring duration per call	44.6 s (40, 4.1)	24.7 s (31, 10.3)	38 s (41, 14.0)
Mean no. of roaring bouts per call	12.6 (7, 6.0)	4.6 (4, 4.8)	5.1 (4, 3.3)
Mean no. of roars per bout	13.6 (11, 6.0)	16.3 (13, 9.4)	21.6 (23, 15.0)

Median and interquartile range provided in parentheses.
*Data from these alpha males is also included in the column on all males in multimale groups.

at BFMS by attracting greater numbers of immigrant males. Additionally, when there were relatively more males in a group (a greater adult male:adult female ratio), not only were male immigration rates higher but infanticide rates increased. This result is congruent with findings from Hanuman langurs (*Semnopithecus entellus*, Borries 1997; Borries and Koenig 2000) but contrasts with findings in other primate species that showed a decreased threat of infanticide in groups with multiple males (*P. rufomitratus*, Leland et al. 1984; *S. entellus*, Newton 1986; *G. b. beringei*, Robbins 1995; *A. seniculus*, Crockett and Janson 2000; *P. ursinus*, Palombit et al. 2000). The protection afforded by having multiple males in these species presumably derives from paternity confusion and from the presence of male defenders who remain in the group even after the death or eviction of the dominant male (reviewed in Janson and van Schaik 2000). Indeed, in some species with multimale groupings, there are large age and rank differences between resident males and new immigrants (Broom et al. 2004). Males immigrate and remain at the bottom of the hierarchy for several years, slowly working their way up in rank (e.g. *M. fuscata*, Sprague et al. 1998; *M. fascicularis*, van Noordwijk and van Schaik 2001; *P. cyncephalus*, Collins 1984). These low-ranking new males have little incentive or opportunity to commit infanticide initially, and once they become high ranking, females have had time to mate with them and infanticide is thwarted through paternity confusion (Hrdy 1979; van Schaik et al. 2000). Alternatively, natal males may stay in their groups and inherit the alpha male position in the case of the death of the dominant male, thus reducing the risk of a group dissolution that would leave infants vulnerable to infanticide by extragroup males (Robbins 1995, 2001). These arguments for the benefits of multimale groups do not seem to hold for *C. vellerosus*. In this species, new males can immigrate and immediately become high ranking in both unimale and multimale groups (Teichroeb et al. 2011; also observed in: *S. entellus*, Borries 2000; *P. cynocephalus*, Alberts and Altmann 1995; *P. leo*, Packer and Pusey 1983). Though resident *C. vellerosus* males who remain in the group may defend infants, defense is rarely successful (Teichroeb and Sicotte 2008a). We suggest that there are 2 explanations to explain the fact that groups with relatively more males may have increased infanticide rates: 1) most males in multimale groups are lower quality males than those in unimale groups and 2) a collective action problem is occurring in multimale groups.

If most of the males in multimale groups are individually weak, this would explain why they are unable to evict other resident males (Teichroeb and Sicotte 2010), are incapable of preventing male immigration, and are often unable to prevent infanticide (Teichroeb and Sicotte 2008a). Indeed, we found that males in multimale groups perform energetically costly roaring during loud calls with less vigor than males in unimale groups. Males in multimale groups also often lost between-group encounters and male incursions to males from unimale groups. Although males in multimale groups may be physically weak because they are young and small in size or old and past their prime, age does not seem to be the only determinant of male quality because few males can achieve the status of resident male in a unimale group. Though males in multimale groups sometimes form coalitions and jointly direct aggression at newcomers, they are rarely successful in excluding new males (Teichroeb et al. 2011). Indeed, in a census of ursine colobus groups in BFMS and surrounding fragments, Holmes (2011) found that the proportion of adult females to adult males was higher in unimale groups than in multimale groups. More work is necessary to understand why male coalitions in multimale groups are not stable and/or reliable enough to deter new male immigration or infanticide.

The single resident males of unimale groups are fully adult and usually prime aged and are able to defend against the immigration of new and potentially infanticidal males, evict other males (Teichroeb and Sicotte 2010), defend infants during between-group infanticidal attacks (Teichroeb and Sicotte 2008a), and win more encounters (this study). Thus, male quality, rather than male number, is important in decreasing the risk of infanticide in *C. vellerosus*. Further, we suggest that because our results show that male immigration increases in groups with absolutely and relatively more males in *C. vellerosus*, the mere presence of multiple males may act as a signal to extragroup individuals that the group does not have a strong alpha male and is therefore vulnerable to takeover.

A link between male quality and infanticide risk has also been documented in Thomas langurs (*Presbytis thomasi*), a colobine with a similar social system as ursine colobus but in which female dispersal seems more prevalent, groups are less permanent, and male quality is based largely on male age. Bisexual groups in Thomas langurs normally form as females join a young male in his early tenure and are generally stable through the middle tenure phase when females reproduce. Females begin to leave males when they are weakening in their late tenure phase, until the male is left with his immature male (and occasionally female) offspring in an AMB (Steenbeek 1999a, 1999b). Therefore, the lifespan of groups is directly tied to the quality of the reproductive male (Steenbeek 2000), as also appears to the case for unimale groups of gorillas (*G. b. beringei*, Watts 1989; Robbins 2001; *G. gorilla gorilla*, Robbins et al. 2004). For *P. thomasi*, female transfer in the late tenure phase coincides with the fact that a female's group shows increased avoidance of extragroup males during ranging (Steenbeek 1999b), is targeted by extragroup males, and suffers an increase in infant mortality (Steenbeek 2000). Although male quality may influence female dispersal decisions in our study population, female group membership is usually stable over several male takeovers. Therefore, a group's lifespan and very existence in *C. vellerosus* is not directly linked to the presence of a given male as in *P. thomasi*.

For another black-and-white colobus species (*C. guereza*), which is closely related to *C. vellerosus* (Ting 2008), males in 1-male groups also had superior fighting ability compared with males in multimale groups during between-group contest competition; the former were more likely to initiate encounters, engage in high-intensity aggression, and win encounters (Harris 2010). However, for *C. guereza* there was stronger evidence that males competed to defend feeding areas for females between groups (Fashing 2001; Harris 2006, 2010) rather than to defend infants (Harris 2010). For *C. vellerosus*, the weight of evidence so far suggests that female and infant defense by males is more important than food defense because infanticide occurs relatively more often than for *C. guereza* (Harris and Monfort 2003; Sicotte and MacIntosh 2004; Teichroeb and Sicotte 2008a). Whether or not this difference is driven by local ecological and demographic conditions or results from interspecific differences remains to be investigated.

It is important to note, however, that males in unimale *C. vellerosus* groups did not perform more vigorous displays compared with the alpha males of multimale groups, despite winning more often in between-group contests against multimale groups (although this may be an artifact of our small sample size). This indicates that a collective action problem plays a role in explaining why males in multimale groups do not often win against males in unimale groups. Range defense by a social group provides collective benefits, and in these situations, free riders often emerge that take advantage of the benefits and do not contribute to the costs (e.g. *P. leo*,

Heinsohn and Packer 1995; *Lemur catta*, Nunn and Deaner 2004). A collection action problem occurs when free riding causes a decrease in the collective benefit (Olson 1965; van Schaik 1996; Nunn 2000). In encounters between *C. vellerosus* groups, some males in multimale groups often did not participate, nor were alpha males always primary participants (Teichroeb JA, Wikberg EC, Bǎdescu I unpublished data). For *C. guereza*, Harris (2010) also found evidence of a collective action problem among males in multimale groups. Males in unimale groups were more likely to win against males in multimale groups, even when they were smaller than the alpha male of the multimale group (body size determined by using the correlation between formant dispersion in loud calls and body size, Harris et al. 2006). Harris (2010) suggested that dominant males of multimale groups participated less in between-group encounters, often staying back with the females and mate-guarding them from the other males in the group. Mate-guarding and the guarding of infants (Teichroeb JA, unpublished data) may explain the collective action problem in *C. vellerosus*, but this awaits further investigation.

Sexual conflict over group size, group composition, and the mating system in *C. vellerosus*

In group-living species, where groups represent a concentration of potential mates, sexual conflict over group size and composition is often linked to struggles over mate choice and over the optimal mating system for each sex (birds: Davies 1989, 2000; Thomas et al. 2007; mammals: Pradhan and van Schaik 2008; Palombit 2010; King et al. 2011; Möller 2011). For instance, in some species, females benefit from living in groups with sex ratios skewed toward males because these groups are at lower risk of male takeover and allow females to mate polyandrously while male reproductive success increases when there are fewer male competitors in the group (van Schaik et al. 2004; *Alouatta* sp., Treves 2001; Ryan et al. 2008; van Belle and Estrada 2008; *Cebus capucinus*, Fedigan and Jack 2011). A pattern of both intersexual and intrasexual conflict over optimal group composition is in fact occurring in *C. vellerosus* in regard to infanticide risk. Female strategies do not seem to be at odds with the strategies of prime, high-quality, dominant males, as both benefit from female group sizes small enough to allow 1 male to monopolize the group (though male quality will determine the size of the female group that a male can monopolize). However, prime males and females have an optimal group composition different from that of nonprime males. Larger female groups often cannot be monopolized by a single male, and they attract more immigrant males (Teichroeb et al. 2011). These males may be lower quality males, and males in multimale groups may suffer from collective action problems, leading to greater infanticide risk for mothers and sires. Not only then are males in these groups competing for a finite number of fertilization opportunities (van Hooff and van Schaik 1994), but the chances of survival of the sired infants are also lower than in unimale groups. However, these multimale groups seem to be the only way for nonprime males to reside in a bisexual group and have at least some consistent access to females for mating. This sets up conflict between males when prime males strive to evict others and nonprime males attempt to immigrate into bisexual groups (Teichroeb and Sicotte 2010). It also causes conflict between females, as groups grow naturally through births and quickly become suboptimally large for a single male to monopolize them. Thus, female aggression may escalate in large female groups prior to forced emigration of new breeding females (Teichroeb et al. 2009).

Data from *C. vellerosus* then contrast with that from some other primates (c.f., Ryan et al. 2008; Fedigan and Jack 2011) in that females prefer to live in unimale groups with a prime male as opposed to multimale groups with polyandrous mating, despite the infanticide-reducing benefits of paternity confusion. These results support Pradhan and van Schaik's (2008) model of intersexual conflict when infanticide is present, which showed that female preference for multimale groups should decrease as dominant males increase in strength relative to their rivals. However, female *C. vellerosus* may still attempt to use polyandrous mating as a counterstrategy to infanticide. Indeed, females not only mate with several males in multimale groups but also actively seek extragroup copulations in unimale groups (Teichroeb et al. 2005; Teichroeb JA, Wikberg EC, Bǎdescu I, unpublished data), probably so they can reside with a single prime male and still confuse paternity among outside males that have the potential to take over the group. Thus, females and prime males may have some intersexual conflict in mating allocation, but in terms of group composition and relative group size, their strategies are aligned (e.g. Clarke et al. 2009). Nonprime males show both intersexual and intrasexual conflict over optimal group composition with prime males and females.

CONCLUSIONS

This study provides another example for how infanticide risk may select for smaller group size in some animal species (Crockett and Janson 2000; Steenbeek and van Schaik 2001). Although having multiple males leads to decreased infanticide threat in certain species (but see Borries 1997; Borries and Koenig 2000), in *C. vellerosus*, a larger adult male:adult female ratio appears to signal that males in the group are weak and/or are not in a strong coalition and that the group is an easy target for takeover. Thus, smaller groups are advantageous in decreasing infanticide risk. Females can control group size to some degree in this species (e.g. Nunn and van Schaik 2000) by dispersing, evicting maturing females, and resisting new female immigration (Teichroeb et al. 2009).

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