Even Adult Sex Ratios in Lemurs: Potential Costs and Benefits of Subordinate Males in Verreaux’s Sifaka (Propithecus verreauxi) in the Kirindy Forest CFPF, Madagascar

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ABSTRACT Optimal group size and composition are determined by both the costs and benefits of group living for the group’s members. Verreaux’s sifakas (Propithecus verreauxi), a diurnal lemur, form multimale multifemale groups with the tendency toward even adult sex ratios despite a small average number of females per group. The unexpected presence of multiple adult males may be explained by tolerance of other group members if subordinate males provide benefits to the group that outweigh the costs associated with their presence. Results based on both demographic data collected over a 13-year period and behavioral observations suggest that subordinate males provide no benefits in terms of infant survival and defense against group takeover by outside males. Although groups with more males are more likely to win intergroup encounters, subordinate males do not participate in these encounters more often than expected. Subordinate males are not costly to other group members in terms of direct intragroup feeding competition, but aggression rates between dominant and immigrated subordinate males increase in the mating season. Even though subordinate males provide very few benefits to the group, they are not very costly either and thus may be tolerated by resident females and dominant males. This tolerance may help to partially explain the tendency towards their unusual adult sex ratio. Am J Phys Anthropol 000:000–000, 2009. © 2009 Wiley-Liss, Inc.
multimale groups depends on both the number and temporal distribution of fertile females and reflects the outcome of male contest competition for mates and female counter-strategies (Altmann, 1990; Mitani et al., 1996; Kappeler, 1999; Nunn, 1999).

In contrast to most group-living anthropoid species (Andelman, 1986; Cords, 2000), the formation of multimale groups in diurnal lemurs, despite small average female group size, is the norm (e.g., Lemur catta: Pereira, 1991; Sauther and Sussman, 1993; Eulemur fulvus rufus: Overdorff et al., 1999; Ostner and Kappeler, 2004; Propithecus verreauxi: Richard, 1974; Propithecus edwardsi: Pochron and Wright, 2003, reviewed in Kappeler, 2000), resulting in a tendency toward on average even adult sex ratios. Various hypotheses have been postulated to explain this discrepancy in operational sex ratio between lemurs and other primates, focusing on high female mortality, male transfer tactics, or fitness benefits to both females and males connected with the presence of additional males (reviews in van Schaik and Kappeler, 1996; Kappeler, 2000). If benefits are provided by additional males, these benefits must more than compensate the costs associated with increased group size (van Schaik and van Hooff, 1983; Kappeler, 1999). Such costs include repressed reproduction, competition with other group members for food and mates, and increased conspicuousness to predators (Alexander, 1974; Bertram, 1978; Pulliam and Caraco, 1984; Janson, 1988).

Several benefits may be derived from the presence of multiple males within a group that serve to increase the fitness of both resident females and males, including increased infant survival due to help in rearing young (Goldizen, 1987; Sussman and Garber, 1987; Koenig, 1995; Treves, 2001) and increased vigilance toward predators and potentially infanticidal conspecific males (Bad[ID]

In lemurs, although males contribute to group vigilance levels, there are generally no sex differences in vigilance (Sherry and Gould, 1986; Kappeler, 2000). Yet, their presence can serve to decrease the per capita risk of predation due to dilution effects (Pulliam, 1973). In addition, the presence of now extinct large eagles (genus Polyboroides radiatus (Karpanty and Goodman, 1999; Brockman, 2003), and the fossa, Cryptoprocta ferox (Rasolofarison, 1995; Wright et al., 1997), are known to regularly prey upon sifaka. Because they have alarm calls for both predators (Fichtel and Kappeler, 2002), subordinate males could provide survival benefits to their group mates by warning them. Secondly, intergroup encounters are common at feeding sites within overlapping areas of home-ranges (Lewis, 2004a; Benadi et al., 2008). Therefore, there is a potential for males to defend resources from other groups. Thirdly, infanticide by strange males has been observed in this species (Lewis et al., 2003), and thus defense against group takeover and social vigilance could be important potential benefits provided by subordinate males. Indeed, subordinate males have been observed to sometimes form coalitions with the dominant male to keep extra-group males out and to prevent them from mating with resident females (Lewis and van Schaik, 2007). Paternal care benefits are not relevant as male P. verreauxi have not been observed to engage in extensive infant care (Lewis, 2004a).

In this study, we examine the tendency toward even or male-biased adult sex ratios in sifakas by examining whether adult subordinate males provide benefits to the group. We test the predictions that the presence of subordinate males 1) has a positive effect on infant survival, 2) decreases the chance that a group will be taken over by intruding males, 3) increases the probability of winning an intergroup encounter, and 4) does not incur costs...
for other group members in relation to intragroup feeding competition and intermale aggression. In answering these questions, we hope to illuminate some of the evolutionary forces shaping the social organization of this species that could then be extrapolated to and tested in other lemur species.

**METHODS**

**Study site and population**

This study is part of an ongoing long-term study conducted in Kirindy Forest CFPF, a dry deciduous forest located in central western Madagascar, 60 km north of Morondava (Sorg et al., 2003). The site is operated by the Centre de Formation Professionnelle Forestière (CFPF) Morondava and our research was approved by the Malagasy Ministère de l’Environnement et des Eaux et Forêts (2005, 2006, 2007, 2008). The German Primate Center has established a field station with three study areas within the forestry concession, where ongoing research has been conducted since 1993. Since 1995, all individuals in the study groups have been habituated and individually marked with either nylon collars and unique pendants or radio collars (Kappeler and Schäffler, 2008). This study population has been censused several times each week since 1995. All births, deaths, and dispersal events were recorded and timed to within a few days. The number of groups within the study population and their size and composition (based on adult group members) varied over the years and is summarized in Table 1. From these long-term data, several demographic variables could be estimated.

**Behavioral data**

Behavioral data from ten social groups were collected by V.M. and one Malagasy field assistant during three sampling periods from September to March 2005–2006, 2006–2007 and 2007–2008 using continuous focal animal sampling. Adult females who had previously reproduced (n = 12) and dominant males (n = 10) were observed during the first and second sampling period. Subordinate adult males (n = 12) were observed during the second and third sampling period. Males were classified as dominant (D), nonnatal subordinate (NN), natal subordinate (N), and related (R). R males are defined as males that are related to the D male but not the group females. Male classifications were established genetically (Kappeler and Schäffler, 2008) and based on the outcome of decided agonistic interactions in both this and previous studies (Kraus et al., 1999; Lewis, 2004a). Males and females were considered adult at 3 years of age, as males have been observed to mate successfully at this age (Rümnap, 1997; Kraus et al., 1999; Richard et al., 1991, 2002) and females to actively participate in group defense (Mass, personal observation). Each focal observation session lasted 1.5 h and four focal individuals were observed by each observer per day yielding a total of 2,808 h of focal animal observation (Table 1).

During each observation session, the activity (foraging, resting, and locomotion) of the focal animal was continuously recorded. For aggressive and submissive behaviors (sensu Brockman, 1994), the context (i.e., activity) the focal animal was engaged in and whether the interaction had a decided outcome, denoted by a clear submissive signal (Pereira and Kappeler, 1997), were recorded. If a series of aggressive and submissive events between the same dyad took place, the series was considered one event. Aggressive intergroup encounters (sensu Cheney, 1987) were sampled ad libitum. The participating groups, identities of participants (individuals who engaged in chasing behavior and/or aggressive approaches of members of the rival group), and whether there was a clear winner (defined by retreat of one group within 10 min of the cessation of active agonism) or undecided outcome were recorded.

**Data analyses**

Although infant mortality can be due to different factors, such as disease and inadequate mothering, the presence of nonreproductive group members may benefit the group in terms of improving infant survival via increased vigilance and defense against infanticidal takeovers (Robinson, 1988; Baldellou and Henzi, 1992; van Schaik, 1996; Treves, 2001). This is especially the case in lemurs, as this group of primates tends to suffer more losses due to predation than most other primates (Wright, 1999). Therefore, we predicted that infant survival rate would be higher in groups with more adult subordinate males. Infants were operationally defined as

<table>
<thead>
<tr>
<th>Group</th>
<th>Years in study population</th>
<th>Group size</th>
<th>Females</th>
<th>Males</th>
<th>Male class</th>
<th>Sex ratio (M:F)</th>
<th>Observation hours</th>
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<td>Natal males</td>
<td>Nonnatal males</td>
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<td>A°</td>
<td>12</td>
<td>3.89</td>
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<td>B°</td>
<td>13</td>
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<td>C°</td>
<td>13</td>
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<td>D</td>
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<td>13</td>
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<td>F°</td>
<td>13</td>
<td>3.63</td>
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<td>F1°</td>
<td>2</td>
<td>4.96</td>
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<td>G°</td>
<td>11</td>
<td>4.30</td>
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<td>H°</td>
<td>10</td>
<td>2.90</td>
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<td>J°</td>
<td>9</td>
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Mean ± SD – 3.87 ± 0.84 1.70 ± 0.54 2.15 ± 0.56 0.41 ± 0.40 0.48 ± 0.42 0.31 ± 0.65 1.083 ± 2808
0–12 months of age, as this is the time when they are most vulnerable to both predation and infanticide. For each group and each birth season, we calculated the proportion of infants that survived from birth to 12 months of age and defined this period as a group year. The mean adult group size and number of subordinate males were calculated for this period by averaging the group size and composition for each month. This takes into account changes in both size and number of subordinate males in the group over the year period. Infants that disappeared within the first 12 months of life can be assumed dead, as sifakas less than 36 months old have never been seen to disperse voluntarily and have never been relocated in other groups after disappearing from their natal group (Richard et al., 1993; Kappeler, unpublished data for study population). Group years in which no infants were born were not included in this analysis.

To assess whether either overall group size and/or the presence of subordinate males affects infant survival, we fit a generalized linear model (GLM) with binomial error structure to the 79 group years for which demographic data were available. To test for a potential effect of overall group size on the proportion of infants that survived, we entered average group size (as defined above) as the first explanatory variable to our model and reported the difference in deviance ($\Delta D$) to the null model. To check for an additional effect of the number of subordinate males, we then entered the average number of subordinate males as a second explanatory variable and reported the difference in deviance to the model already containing group size. $\Delta D$ is $\chi^2$-distributed with $p-q$ degrees of freedom, where $p$ and $q$ are the numbers of parameters in the more complex and in the simple model, respectively (Dobson, 1990).

A group takeover was defined as when an immigrant male comes into a group and assumes the D position and the former D male leaves within 1 month of this immigration event. Peaceful male immigrations were not considered takeovers, as they did not result in the eviction of resident males or in the change of status of the D male. Using the demography data, we calculated an overall population takeover rate by dividing the total number of takeovers that occurred in the population by the number of years the population was censused. To test the prediction that groups with a lower chance of being taken over as the number of subordinate males within a group increases, we fit a logistic regression model. For each group year (where, in this analysis, group year was defined as the period from mating season to mating season), the occurrence or absence of a takeover was regressed against the minimum number of males present in the respective group year or against the number of males present during a takeover, if a takeover occurred.

Based on observed intergroup encounters during the study period, we used Chi-squared tests to determine whether groups with a higher proportion of males win intergroup encounters more often and if bigger groups in general win encounters more often than would be expected by chance. Only intergroup encounters including known marked groups with a clear winner were included in this analysis.

To examine the frequency of adult male and female participation in intergroup encounters, we compared observed versus expected participation using Chi-squared tests. Derived expected values take into account both the frequency of each group’s participation in intergroup encounters and group composition as all groups did not participate equally nor were all participant classes equally represented within the study groups.

Finally, we measured two costs, intragroup feeding competition and intermale aggression rates. Although feeding competition is expected to be low in small groups of folivorous primates (Isbell, 1991; Janson and Goldsmith, 1995), sifakas live in an environment where food availability is highly seasonal and are subject to periods of food scarcity. This is reflected in significant changes in body mass and body fat, as their diet shifts from new leaves and fruit to mainly mature leaves (Lewis and Kappeler, 2005). To determine if subordinate males increase intragroup feeding competition beyond increased scramble competition, we calculated the proportion of agonistic interactions in a feeding context (where at least one member of the dyad was either feeding or foraging) that were either won by subordinate males or females or were undecided outcomes. As a control, we also calculated proportions of agonistic interactions won by either D males or females in a feeding context. Additionally, we used Chi-squared tests to examine in which type of dyad (D male–female, subordinate male–female and female–female) the majority of aggressive interactions within a feeding context occurred. Expected values were derived that take into account the number of dyads of each type that are present within the study population.

High glucocorticoid output, a measure of stress, is a physiological cost faced by D males in the mating season (Fichtel et al., 2007) and can be influenced by aggression. Additionally, aggression itself is a costly behavior due to risk of injury. We compared overall aggression rates between D–NN male, D–N male, and D–R male dyads using a Kruskal–Wallis test. Wilcoxon matched-pairs tests were used to test the prediction that aggression rates would increase in the mating season when compared to the nonmating season in D–NN male and D–R male dyads but not in D–N male dyads. The mating season was defined as the onset of the first female’s fertile phase in the study population to the termination of the last. Fertile phases were determined via hormone analysis of fecal progesterone levels as described in Mass et al. (in press).

The GLM and logistic regression were performed in R version 2.5.1. All other data analyses were preformed using STATISTICA (StatSoft, version 6.0, 2001). The significance level was set at $P < 0.05$.

RESULTS

Infant survival

Between July 1995 and June 2007, a total of 106 infants were born in the study population. Of these, only 57 survived 1 year, a proportion similar to that for another population of Verreaux’s sifaka at Beza Mahafaly in southwest Madagascar (Richard et al., 2002). Of the 49 infant deaths, several could be attributed to fossa predation based on the state of the remains when found. Mean ± SD group size and number of nonnatal subordinate males within groups during this period were $3.87 ± 1.14$ (range 2–9) individuals and $1.02 ± 0.63$ (range 0–3) individuals, respectively. Group size did not significantly affect the proportion of infants that survived 1 year of age ($\Delta D = 0.791$, $df = 1$, $P = 0.374$). When we added the number of subordinate males as an additional explanatory variable, as compared to the model containing group size only, number of subordinate males also
did not significantly reduce the deviance ($\Delta D = 0.089, df = 1, P = 0.765$). These results indicate that there is no effect of either group size or number of subordinate males on infant survival. A summary of the estimates ($\pm SE$) of the model is provided in Table 2.

### Group takeovers

A total of eight takeovers over 12 study groups were recorded between 1995 and 2008 ($n = 113$ group years). These takeovers do not include three instances where resident subordinate males rose in rank to become dominant due to the death of the D male ($n = 2$), most likely due to fossa predation, and the eviction of the D male by resident females ($n = 1$). Seven takeovers occurred when there was one or more subordinate male present within the group and only one when there were no subordinates present. The average population takeover rate was 0.6 takeovers per year. The number of males present during a group year had no significant effect on the probability of whether a takeover occurred or not ($b_{\text{males}} \pm SE = 0.44 \pm 0.42, z = 1.05, P = 0.29$).

### Resource defense

During the three sampling periods, a total of 134 intergroup encounters were observed. Out of this total, 81 encounters with known groups and decided outcomes could be used for the analysis of intergroup encounter winners. Bigger groups won more often (66% of encounters) than expected by chance (Chi-squared test: $\chi^2 = 5.59, df = 1, P = 0.018$). Groups with the same total group size as their opponents ($n = 11$) but with a higher proportion of males also won (79% of encounters) significantly more often (Chi-squared test: $\chi^2 = 4.57, df = 1, P = 0.033$).

All observed intergroup encounters ($n = 134$) were included in the analysis of intergroup encounter participants. D males ($n = 10$) participated in intergroup encounters more often than expected (Chi-squared test: $\chi^2 = 12.48, df = 1, P < 0.0001$), whereas R males ($n = 7$) participated less often than expected by chance (Chi-squared test: $\chi^2 = 7.56, df = 1, P = 0.006$). There was no difference between observed and expected participation frequencies for dominant females ($n = 10$), adult females ($n = 9$), NN males ($n = 4$), and N males ($n = 10$) (Fig. 1).

### Intrigroup feeding competition

A total of 383 agonistic interactions in a feeding context were observed over the three sampling periods between adult females and males. Females won these interactions 86% of the time. Males won agonistic interactions only 4% of the time (15 out of 383) and of these subordinate males only won one encounter in a feeding context. The remaining 10% (38 out of 383) were interactions with an undecided outcome. Thirteen D male wins occurred during interactions with adult subordinate females. Between D and subordinate males, 67 agonistic interactions in a feeding context were observed. As would be expected due to stable dominance hierarchies, D males won 99% of these interactions (66 out of 67). When aggressive interactions between females were included, a total of 425 interactions were observed. Aggressive interactions within a feeding context occurred more often than expected between D male–female dyads ($n = 18$) (Chi-squared test: $\chi^2 = 115.84, df = 1, P < 0.0001$) and less often than expected between both subordinate male–female dyads ($n = 30$) (Chi-squared test: $\chi^2 = 41.04, df = 1, P < 0.0001$) and female–female dyads ($n = 9$) (Chi-squared test: $\chi^2 = 30.29, df = 1, P < 0.0001$).

### Intermale aggression

There was no difference in overall aggression rates per hour between D males and all three classes of subordinate males (Kruskal–Wallis: $H = 2.46, n = 23, P = 0.29$; median$_{\text{NN}} = 0.2$, range $= 0.06–0.43$; median$_{\text{N}} = 0.09$, range $= 0.02–0.18$; median$_{\text{D}} = 0.15$, range $= 0–0.31$). Using results from hormone analyses (Mass et al., in press), we were able to divide the sampling period into mating season and nonmating season based on female fertile phases. The rate of aggression per hour increased significantly in the mating season between D–R male dyads (Wilcoxon-test: $T = 3, n = 9, P = 0.036$; median$_{\text{mating season}} = 0.18$, range $= 0–0.31$; median$_{\text{nonmating season}} = 0.07$, range $= 0–0.2$) but not between D–N male dyads (Wilcoxon-test: $T = 15, n = 10, P = 0.2$; median$_{\text{mating season}} = 0.04$, range $= 0–0.3$; median$_{\text{nonmating season}} = 0.1$, range $= 0–0.21$). Although we could not test for differences between the mating and nonmating season rate of aggression for D–NN male dyads due to low sample size ($n = 4$), the data suggest an increase in aggression rate in the mating sea-
Our results demonstrated that sifaka subordinate males provide few of the predicted benefits to the group but are also not too costly to D males or females in terms of intragroup feeding competition. Additionally, subordinate males are not very costly to the D male in terms of lost reproduction (Kappeler and Schäffler, 2008). The presence of subordinate males in a group did not affect infant survival nor did it deter strange males from taking over the group. Although groups with a higher proportion of males won intergroup encounters more often, subordinate males did not participate in encounters more often than would be expected by their representation in groups. However, these males may have participated at sufficient levels to increase the probability that their group won the encounter. Bigger groups won intergroup encounters more frequently but group size is most often a function of the number of males in a group as the number of females tends not to vary greatly. Although subordinate males provided few benefits, the D male faced some costs associated with the presence of NN and R subordinate males but not N subordinates in the form of increased mating competition as aggression rates increased when females were receptive. Thus, costs for D males in the form of increased male–male aggression may be offset by the benefits gained by females in terms of securing food resources contested between groups.

### Infant survival

If males provide protection from both predators and potential infanticidal males, then groups with more males should have higher infant survival (Robinson, 1988; Koenig, 1995; Treves, 1998, 2000). Moreover, D males may benefit from the presence of subordinates if the loss in numbers of infants sired is outweighed by increased infant survival (van Schaik and Hörstermann, 1994). Results from this study indicate that infant survival in sifakas was not affected by either group size or the number of subordinate males present within the group. This result is in concordance with other group-living lemurs exhibiting even adult sex ratios, e.g., *L. catta* (Takahata et al., 2006) and *P. edwardsi* (Pochron and Wright, 2003; Pochron et al., 2004), but not with *Cebus olivaceus* or *Alouatta* spp. In these species, female reproductive success and juvenile survival appear to be affected by the presence of males where females can maximize offspring survival by reproducing in a group that contains a high proportion of males (Robinson, 1988; Treves, 2001).

This discrepancy between lemurs and some anthropoid species could be due to differences in male vigilance effort. In both sifakas and *L. catta*, males in general were not more vigilant or likely to detect predators than females (Hussmann, 1996; Gould et al., 1997), whereas males in a number of anthropoid species tend to be more vigilant than females (van Schaik and van Noordwijk, 1989; Rose and Fedigan, 1995). Sifaka males have been found to increase scanning behavior just prior to and during the mating season (Lewis, 2004a), which suggests an additional social function of male vigilance. Thus, the presence of extra subordinate males may only lower the per capita predation risk in general (Hamilton, 1971), which can be a particularly important benefit in small groups.

### Group takeovers

Additional males may confer fitness benefits to both D males and resident females by ensuring defense against infanticidal takeovers. Infanticide has been observed in *P. verreauxi* and *P. diadema* (Erhart and Overdorff, 1998; Lewis et al., 2003). In contrast to what was reported for *E. f. rufus* (Ostner and Kappeler, 2004), *Alouatta seniculus* (Pope, 1990), and *Artibeus jamaicensis* (Ortega and Arita, 2002), the presence of subordinate males in Verreaux’s sifaka does not deter strange males from taking over the group. Subordinate male sifakas do not face the same risk posed by potential infanticidal males in terms of decreased fitness, as they are not receiving a large share of reproduction (Kappeler and Schäffler, 2008) and thus there may be no payoff that outweighs the risks and costs of helping to defend the group from being taken over. Variable participation by subordinate males in encounters with conspecific males has also been reported for *Alouatta pigra*, a species in which infanticide after takeover also occurs (Kitchen, 2004).
Thus, although groups are predicted to contain multiple males if infanticide is a serious threat (van Schaik, 2000), the presence of multiple males in Verreaux's sifaka groups did not deter takeovers and thus this male benefit cannot explain the presence of subordinate males within this species. Alternatively, the presence of multiple males may serve to reduce the risk of infanticide via paternity confusion. Although reproduction is highly skewed toward dominant individuals (Kappeler and Schäfler, 2008), this may not reflect the actual mating skew. Female sifakas at Beza Mahafaly have been observed to mate with both extra-group males and within-group subordinate males (Brockman, 1999). Thus, even though it is not possible to quantify the mating skew for the population of sifakas at Kirindy as mating is rarely observed, paternity confusion as a female benefit of multiple males within a group cannot be ruled out.

**Resource defense**

Our results indicate that, in concordance with other primate species, e.g. *Eulemur macaco macaco* (Bayart and Simmen, 2005) and *Cebus olivaceus* (Robinson, 1988), groups with a higher proportion of males win intergroup encounters more often and thus support the idea that an increased number of males within groups leads to increased intergroup dominance (Wrangham, 1980). In many species of primates, males are the primary participants in encounters (Cheney and Seyfarth, 1977; Harcourt, 1978; Fashing, 2001), which may be explained if encounters are primarily about mate defense instead of food resource defense (Cheney, 1987). The fact that D male sifakas were the only individual class that participated more than expected may be explained by the fact that participating in intergroup encounters can be both costly and risky and thus participation may be related to greater reproductive benefits (Cheney and Seyfarth, 1977; Cheney, 1987). As subordinates are not receiving a large share of reproduction (Kappeler and Schäfler, 2008), the fact that they do not participate more often than would be expected by chance is therefore not surprising. Alternatively, subordinate males may participate at levels that allow them to be tolerated as group members but that are not high enough to be conceded a share of reproduction.

**Costs**

Aggressive interactions in animals can stimulate the release of glucocorticoids (Balm, 1999), which are an important component of the stress response (Munck et al., 1984). Fichtel et al. (2007) found that D male sifakas exhibit higher glucocorticoid levels than subordinates during the mating season. Additionally, in several primate species including sifakas (Brockman et al., 1998; Kraus et al., 1999), males living in multimale groups exhibit higher testosterone levels, a measure linked with heightened aggression, in the mating season due to within-group reproductive competition (Gould and Ziegler, 2007; Ostner et al., 2008). Increased aggression can be costly due to an increase in the risk of injury while engaged in aggressive interactions. Thus, although there is a cost to D males associated with the presence of males who are not related to group females, this cost may not be high enough to engage in fierce combat to evict them. Sifakas are highly seasonal breeders with females exhibiting a very short receptive period (Brockman, 1999), and thus, high aggression rates should only be sustained over a short period of time.

**Socioecological theory and even adult sex ratios**

Based on the assumptions of sexual selection theory and socioecological theory, we predicted successful monopolization of small groups of females by D male sifakas as is observed in cercopithecine primates with similar life history traits (Andelman, 1986). The fact that sifaka group composition is highly variable, even within the same population (Richard, 1985; Kubzdela, 1997; Pochron and Wright, 2003), but tends on average toward an even or male-biased adult sex ratio (Lewis and van Schaik, 2007), shows that D males are not excluding potential rival males. This pattern has also been found for the population of Verreaux's sifaka at Beza Mahafaly (Brockman, 1999). The deviation from the predictions of these two fundamental theories has been explained in several Old and New World primate species in relation to benefits provided to the group by subordinates (van Schaik and Hörstermann, 1994; Mitani et al., 1996). Additionally, it has been suggested that if D males profit in their associations with same-sex conspecifics, subordinates should receive a share of reproduction as an incentive to stay in the group (Vehrencamp, 1983; Keller and Reeve, 1994; Johnstone, 2000).

The results of this study reveal that, overall, subordinate males are not providing many benefits to the group although their presence within a group does contribute to intergroup dominance over feeding sites and a reduced per capita predation risk. Although male services have been suggested to be exchanged for mating opportunities (Duffy et al., 2007), group membership instead of reproduction could also be a commodity provided for services (van Schaik and van Noordwijk, 1989; Gould, 1996a). Therefore, an increase in intergroup dominance may be enough for females to tolerate the presence of subordinates and allow them group membership but may be too low for D males to provide them with a share of reproduction. This has also been shown for *Alouatta seniculus* (Pope, 1990) and *Artibeus jamaicensis* (Ortega and Arita, 2002).

An advantage over other groups with respect to access to feeding sites in the overlapping areas of home ranges is of relatively more importance to females (Wrangham, 1980). This is especially true for a Malagasy primate living in a harsh seasonal environment where there are periods of severe food scarcity (Wright, 1999). Although there is evidence to suggest that female reproductive success may be negatively affected with increasing group size due to intragroup feeding competition (Harcourt, 1987; Koenig, 2000; Koenig and Borries, 2002), results of this study indicate that D, not subordinate, males are more costly to females in relation to intragroup feeding competition. Thus, the presence of subordinate males should not increase intragroup feeding competition per se for females. Moreover, Wrangham (1980) proposed that multimale groups may have evolved as a means for females to compete more successfully for dominance over food resources with other groups.

Aside from intergroup dominance over contested food resources, female primates seem to prefer to live in groups with several males (Altmann, 1990). Several benefits to females include mating with many males as a means to avoid genetic incompatibilities and to reduce
the risk of infanticide through paternity confusion, enhancing parental care, receiving good sperm, and the facilitation of cryptic female choice (reviewed in Wolff and Macdonald, 2004). Female Verreaux’s sifakas have been observed to actively evict D males from the group but do not prevent and may even facilitate the residency and immigration of new subordinate males (Richard et al., 1993; Brockman, 1999; Lewis, 2004a, 2008). Indeed, several studies have shown that female sifakas actively recruit subordinate males into the group (Brockman et al., 2001; Lewis, 2008) and are responsible for maintaining proximity with subordinate but not D males (Lewis, 2004b). Moreover, females have been observed to have facilitated copulation with both the D and subordinate males (Lewis and van Schaik, 2007). Thus, female sifakas may be playing an active role in regulating group composition and regulating male residency in favor of more males that may be facilitated by their dominant status (Richard, 1987; Lewis, 2004b, 2008). The impact of female reproductive strategies on the evolution of even adult sex ratios in sifakas should therefore be studied in more detail.

Although variance in male mating success is generally positively correlated with dominance rank, e.g., Cervus elaphus (Clutton-Brock et al., 1982), Felis catus (Say et al., 2001), Pan troglodytes (Constable et al., 2001) and Eulemur fulus mayottensis (Gachot-Neveu et al., 1999), a decrease in reproductive success is predicted if female group size increases as is seen in both Alouatta palliata (Ryan et al., 2008) and E. fulus rufus (Kappeler and Port, 2008), as D males may not be able to exclude rivals from access to receptive females especially if females are receptive synchronously (Emlen and Oring, 1977; Ims, 1988; Mitani et al., 1996; Nunn, 1999). The fact that female group size in sifakas rarely exceeds four individuals and that females are receptive asynchronously within groups (Mass et al., in press) may allow D males to monopolize reproduction. Possible monopolization mechanisms include mate-guarding (Brockman, 1999; Lewis and van Schaik, 2007, Mass et al., in press) and physiological suppression of testosterone in subordinates by D males (Kraus et al., 1999). As a result, the presence of subordinate males is not a threat to D males in terms of lost reproduction and therefore may be tolerated by him especially if these subordinate males are N males. Moreover, although there were no direct benefits provided to the D male, D males may benefit indirectly from increased intergroup competitiveness, because females that are heavier at the time of mating are significantly more likely to give birth the following birth season than lighter females (Richard et al., 2000).

Although tolerance of subordinate males by D males and active recruitment by females (Lewis, 2008) can lead to the evolution of even adult sex ratios in sifakas, subordinate male reproductive strategies also need to be considered, as changes in group composition are mainly a result of their dispersal decisions. Thus, a combination of delayed natal dispersal and males immigrating into subordinate positions to queue for the dominant position (Kokko and Johnstone, 1999; Cant and English, 2006) also play a role in shaping Verreaux’s sifaka social organization.

In conclusion, the tendency toward even or male-biased adult sex ratios in Verreaux’s sifaka despite small female group size and estrous asynchrony within groups can be partially explained by social tolerance through benefits provided by subordinate males. These small benefits, namely dominance in intergroup competition, may be enough for females to prefer to reside in multimale groups and for D males to tolerate subordinate males as group members but insufficient to grant them a share of reproduction. This unusual form of social organization must be seen as the outcome of the interplay of dominant male, female, and subordinate male reproductive strategies. A deeper understanding of the factors that play a role in subordinate male dispersal decisions is needed to fully comprehend not only why subordinate males use different reproductive strategies, but the evolutionary forces that shaped them.

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LITERATURE CITED


