

## RESEARCH ARTICLE

# The Influence of Male Takeovers on Female Dispersal in *Colobus vellerosus*

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Male takeovers affect male tenure, female mate choice and ultimately, individual reproductive success in group-living primates. In social systems with female philopatry and high male reproductive skew, male takeovers largely determine female mate choice, whereas in species with female dispersal, females have the option of deserting a new male. We focused on a species with facultative female dispersal to investigate which factors promote female desertion of males after takeover, using 15 cases (12 for which we have complete data on the takeover process and the female dispersal outcome). These cases took place in nine groups of *Colobus vellerosus* between 2001 and 2013 at the Boabeng-Fiema Monkey Sanctuary, Ghana. Quick takeovers were usually achieved by single adult males and were never followed by female dispersal. Slow takeovers involved several males, and these takeovers were regularly accompanied by female emigration. Infant attacks and infanticide by males occurred during both kinds of takeovers, but females with dependent offspring never dispersed, regardless of whether their infant was attacked or killed by the new male(s). Subadult females, who were not constrained by the presence of infants, dispersed more often after slow takeovers than after quick takeovers. Whether female dispersal post-takeover is an expression of female mate choice, or occurs to avoid the social upheaval surrounding slow takeovers, remains to be investigated. *Am. J. Primatol.* 79:e22436, 2017. © 2015 Wiley Periodicals, Inc.

**Key words:** colobines; female dispersal; male takeovers; male infanticide

## INTRODUCTION

Male takeovers (sometimes known as “alpha male replacements”) occur when an extra-group male(s) ousts the resident male(s) of a group. They have been documented in a wide range of animal species [Birds: Freed, 1986; Ridley, 2012; Carnivores: Packer & Pusey, 1983a; Ungulates: Feh & Munkhtuya, 2008; Rubenstein and Nuñez, 2009; Rodents: Hackländer and Arnold, 1999; Primates: Butynski 1982; Clarke, 1983; Clarke et al., 1994; Fairgrieve, 1995; Fedigan, 2003; Harris & Monfort, 2003; Kappeler, 2000; Onderdonk, 2000; Reena & Ram, 1992; Ross, 1993; Sterck and van Hooff, 2000; Wolfe & Fleagle, 1977]. Male takeovers reduce the tenure of resident males [Primates: Beehner et al., 2009; Steenbeek et al., 2000; Wich et al., 2007; Ungulates: Rubenstein & Nuñez, 2009] and infanticide by new males often occurs [Hrady, 1974; Packer & Pusey, 1983b; van Schaik and Janson, 2000; Fedigan, 2003; Teichroeb & Sicotte, 2008], which decreases the reproductive success of both mothers and fathers [Palombit, 2012].

In social systems with predominant female philopatry and strong male reproductive skew,

male takeovers largely determine female mate choice [Fedigan, 2003]. In species with female dispersal, females have the option of expressing direct mate choice by staying with or deserting the new male, or by leaving when the resident male is the target of harassment by extra-group males [Sterck, 1997; Steenbeek et al., 2000; Steenbeek & van Schaik, 2001; Robbins et al., 2009]. Natal and secondary female dispersal occur in several primate species [Moore, 1984]. When parous females disperse, they generally do not have a dependent offspring [i.e., their previous infant is weaned, *Semnopithecus entellus*: Hrady, 1977; *Gorilla b. beringei*: Sicotte,

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2000, 2001; *Colobus vellerosus*: Teichroeb et al., 2009; *Presbytis thomasi*, Sterck, 1997; meta-analysis: Sterck & Korstjens, 2000: 309]. Females with infants face an increased risk of infanticide by males during takeovers, whether they choose to disperse or not [van Schaik & Janson, 2000; Teichroeb & Sicotte, 2008]. Group fission, when a subset of females leave with the former alpha male, may be the best solution in the short term if it means continued protection from the sire of the females' infants [Hrdy, 1974; Sterck & Korstjens, 2000; Zhao et al., 2011], but this also involves risks, as the alpha male's inability to prevent the takeover suggests that he may be waning in strength [Steenbeek, 1999]. Group fission may also involve costs associated with establishing and defending a new home range [Isbell & Van Vuren, 1996]. Thus, female mate choice (i.e., whether females remain with the new male(s), or disperse with the former alpha or elsewhere) in species exhibiting male takeovers and male infanticide should be influenced by the presence of dependent offspring and by whether the resident male can offer infanticide protection [Sterck & Korstjens, 2000; Teichroeb & Sicotte, 2008]. Therefore, females without infants may be the least constrained when it comes to dispersing after a takeover.

In *Colobus vellerosus* (ursine or white-thighed colobus), all males disperse from their natal group, whereas some females disperse and others reproduce in their natal group [Teichroeb et al., 2009, 2011; Wikberg et al., 2012]. *C. vellerosus* is therefore an interesting species in which to study female mate choice after male takeovers because females have the option of deserting a new male(s). Groups can be uni-male or multi-male [Wong & Sicotte, 2006], and the number of resident males may affect the group's competitive ability during intergroup encounters as well as infant protection against infanticide [Teichroeb et al., 2011, 2012]. Single males are better able to resist male immigration, and are thus presumably better at defending infants against infanticide by incoming males, compared to males in multi-male groups [Teichroeb & Sicotte, 2010; Teichroeb et al., 2012; see also Dunbar, 1987]. Males in uni-male groups also perform more energetically expensive displays and are dominant over males in multi-male groups during intergroup encounters [Teichroeb & Sicotte 2010; Teichroeb et al., 2012]. In primates, male takeovers can be quick or they can take several months to complete [Dunbar, 1987; Oates, 1977; Sterck & van Hooft, 2000]. In a subset of our data, three single males performed quick takeovers, whereas six coalitions of males performed slow takeovers [Teichroeb et al., 2011]. Thus, takeovers by single males may be associated with shorter periods of social upheaval.

We investigated the factors that promote retention of, or desertion by, females after male takeovers in *C. vellerosus* at the Boabeng-Fiema Monkey

Sanctuary (BFMS), Ghana. Our sample consisted of 15 cases of successful takeovers. Ten of these cases are partially published in papers describing the events leading up to male takeovers, male dispersal patterns, and the conditions under which infanticide occurs (Table I). In this paper, we combine the previously reported cases with newly observed cases of takeover, with the aim of understanding how male takeover affects female dispersal in our study population, a topic not previously investigated.

First, we verified whether the previously suggested relationship between the number of invading males and the duration of takeovers [Teichroeb et al., 2011] remained valid with our larger sample size (which now allows for statistical analysis). Second, we examined whether the number of males taking over the group or the duration of the takeover was associated with the occurrence of female dispersal. Because females should favor resident males with high competitive ability [Sterck & Korstjens, 2000; Teichroeb & Sicotte, 2008] and single males are better competitors than males in all-male bands or multi-male groups in our population [Teichroeb & Sicotte, 2010; Teichroeb et al., 2011, 2012], we expected that takeovers by single adult males would be associated with more female retention than takeovers by several males. We also expected that slow takeovers with prolonged periods of social upheaval would be associated with more female dispersal than quick takeovers. Third, we investigated how female reproductive status affected the likelihood of post-takeover dispersal. We predicted that dispersal, as a form of mate choice, would be an option for females without vulnerable infants but not for females with infants. We did not expect females with infants to disperse, except if these females could emigrate in parallel with their previous resident male(s), which might protect their infants against infanticide [Hrdy, 1974; Jack & Fedigan, 2009; Sterck & Korstjens, 2000; Zhao et al., 2011]. Finally, male takeovers create conditions in which infanticide can occur. We did not expect a difference in the occurrence of infanticide depending on the type of takeover (slow vs. quick). After infant loss to infanticide, a female's dispersal options are no longer constrained and her dispersal decision likely depends on the same factors as a female who did not have a dependent infant at the onset of the takeover. Therefore, we predicted that females who lost their infant to infanticide would stay with single males performing quick takeovers and disperse where slow takeovers occurred by several males.

## METHODS

### Study Species and Population

Black and white colobus are arboreal, folivorous monkeys that often live in relatively small uni-male/

TABLE I. List of Takeover Cases in the *Colobus vellerosus* Study Population at BFMS (2001–2013)

Case	Group	Start date	Quick or slow?	# of males in TKV event <sup>e</sup>	# Males in target group <sup>e,f</sup>	# Females at onset of TKV <sup>g</sup>	# Infants at onset of TKV	Female dispersal <sup>g</sup>	Duration (Mo.)	Infanticide <sup>i</sup>
1 <sup>a,c</sup>	BS	Apr. 01	S	7–9 SM	1 AM	2 PF, 1 NF	1	No	5 <sup>h</sup>	Attempted
2 <sup>b</sup>	BS	Sept. 04	Q	1 AM	3 AM & 4 SM	4 PF, 1 NF	2	No	1	No
3 <sup>b,c</sup>	BS	Dec. 04	Q	1 AM	1 AM & 3 SM	4 PF, 1 NF	2	No	1	Yes
4 <sup>b</sup>	BS	May 10	S	1 AM & 3 SM	1 AM & 5 SM	6 PF, 1 NF	4	No	3	Yes
5 <sup>b,c</sup>	DA	Sept. 04	S	2 AM & 4 SM	3 AM & 3 SM	10 PF, 3 NF	5	1 PF & 2 NF	8	Yes
6	NP	May 11	S	2 SM	(1AM & 3 SM)	4 PF, 3 NF	0	No	4 <sup>h</sup>	N/A
7 <sup>b</sup>	OD	May 07	S	5 AM & 1 SM	1 AM & 1 SM	6 PF, 6 NF	1	3 PF	4	No
8 <sup>b,c,d</sup>	RT	July 03	Q	1 AM & 1 SM	1 AM	5 PF, 1 NF	3	No	1	Yes
9 <sup>b</sup>	RT	May 06	?	2 AM & 2 SM	1 AM & 1 SM	6 PF, 0 NF	0	No	?	N/A
10 <sup>b</sup>	RT	May 10	S	1 AM & 1 SM	(2 AM & 2 SM)	5 PF, 3 NF	2	2 NF	3–5	Suspected
11 <sup>b,c</sup>	WW	Sept. 04	Q	1 AM	6 AM & 2 SM	10 PF, 3 NF	5	No	1	Yes
12	WW	May 08	S	2 AM	(2 AM & 2 SM)	9 PF, 2 NF	2	2 PF	12	Yes
13	WW	May 11	?	1 AM	(2 SM & 2 SM)	8 PF, 2 NF	1	1 NF	?	Suspected
14	RT	Sept. 13	Q	1 AM	1 AM & 3 SM	5 PF, 0 NF	4	No	1	Suspected
15	SP	May 13	S	1 AM & 6 SM	(1 AM & 3 SM)	5 PF, 1 NF	3	4 NF	14	No

TKV=Takeover

<sup>a</sup>Case described in Saj & Sicotte 2005.<sup>b</sup>Cases used in Teichroeb et al., 2009 & 2011 describing immigration and emigration.<sup>c</sup>Cases provided context to describe the process and outcome of infanticides in Teichroeb & Sicotte 2008.<sup>d</sup>Case provided context for infanticides and female loud calling described in Sicotte et al., 2007.<sup>e</sup>AM = adult male, SM = subadult male.<sup>f</sup>Values in parentheses are from the last group count and may have changed preceding the takeover.<sup>g</sup>No = no female dispersal; PF = parous female, NF = nulliparous female.<sup>h</sup>Minimum value.<sup>i</sup>Attempted = Infants were attacked but survived; No = no infant attack or infanticide observed; Yes = confirmed infanticide; N/A = no infant present in the group at time of takeover; Suspected = Death occurred while observers were away; see text for further definition.

multi-female or multi-male/multi-female groups [Sterck, 2012]. *Colobus vellerosus* is one of five species of black and white colobus in Africa [Groves, 2001; Ting, 2008]. Data for this study come from a population of *C. vellerosus* at the Boabeng-Fiema Monkey Sanctuary (BFMS), a small (1.9 km<sup>2</sup>), dry semi-deciduous forest in the forest-savanna transition zone of Ghana (7° 43' N and 1° 42' W). This area is characterized by two rainy seasons and two dry seasons. The mean annual rainfall from 1985 to 1990 was 1,250 mm [SD: 621.1; taken approx. 20 km from BFMS; Fargey, 1991]. The population of *C. vellerosus* at BFMS has been studied under the supervision of PS since the year 2000 and is currently estimated at 275 individuals in 19 groups [Kankam & Sicotte, 2013]. The population density in the core forest has increased during the last three decades [Kankam &

Sicotte, 2013; Saj et al., 2005]. BFMS is connected to several smaller fragments of forests by a narrow riparian forest; colobus are present in some of these fragments and groups or individuals travel between fragments [Kankam & Sicotte, 2013; Saj et al., 2005; Wong & Sicotte, 2006]. *C. vellerosus* females do not have external signs of ovulation and breed all year around. Infants are born with pure white coats and develop the adult black-and-white pelage by the age of 3–4 months [Saj & Sicotte, 2013].

### Age-Sex Class Categories

Our age-sex class categories are based on our knowledge of the range of sizes attained by individuals of known ages [Saj & Sicotte, 2013; Teichroeb et al., 2009, 2013]. In cases where a precise age is not

known, we use an individual's sex and size to determine his or her age category. Subadult males are males between 3 and 6 years old. These males are smaller or the same size as adult females. Adult males are over 6 years old. These males have achieved full body size. Subadult females are females between 3 and 5 years old. These females are smaller than adult females. Adult females are over 5 years old. Females that lacked pendulous nipples are considered nulliparous. Females with pendulous nipples are parous.

### Male Takeovers

The takeover events included in this analysis ( $N = 15$ ) come from nine research groups that were studied for varying periods between 2001 and 2013 (Table II) for a total of 330 months (range per group: 9–64 months). ECW, IB, SAF, JAT, and JV contacted the groups used in this analysis at least one day per month (in most cases between 15 and 20 days per month). These research groups were followed according to a fixed schedule as part of the data collection for a range of projects. We did not change this fixed schedule even if male takeovers occurred, which means that we often did not collect takeover related data on a daily basis during the entire takeover process. To undertake a closer examination of the link between male takeovers and female dispersal, we included only groups (or periods) where all group members were individually recognized. Twelve of 15 takeover cases yielded complete data on the takeover process (number of males and duration), the female dispersal outcome and infanticide events. For the remaining three cases, it was possible to reconstruct female dispersal and infanticide events based on changes that occurred in the group composition between periods when observers were present. We did not include cases of male immigration that did not lead to takeovers.

Observers collected data on group membership and male dominance interactions every time a group was contacted. In the case of a male takeover, we

documented the number of males involved in the takeover, as well as their age-classes. We calculated the duration of takeovers in number of months. “Quick” takeovers were cases in which the transition between alpha males was complete within a month of the initial entry in the group. Although quick takeovers often happened in a matter of days, we did not always have daily contact with the group and are unable to report durations in days for many cases. Cases where incoming male(s) entered the group and challenged the resident male(s) for a period that exceeded the first month following their entry were classified as “slow” takeovers. For each case of takeover, we also noted the number of females, their age-class, and their parity. We also determined whether females had dependent offspring at the onset of the takeover. Nursing cessation occurs around 18 months in *C. vellerosus* [MacDonald, 2011], and in the absence of observational data on nursing, we use this cut off point to distinguish between infants and juveniles. We recorded whether the incoming males attacked infants. Infanticide occurred when we observed males directing aggression towards infants or mother–infant pairs that led to the infant being wounded and subsequently dying. We classified cases as suspected infanticide when seemingly healthy infants disappeared at the same time as a male takeover [Teichroeb & Sicotte, 2008]. We also noted cases of observed or inferred female dispersal during the takeover. Observed cases occurred when researchers witnessed at least part of the dispersal event while inferred cases were recorded when an apparently healthy female disappeared from the study group [Teichroeb et al., 2009]. Large predators able to catch subadult or adult colobus are extirpated from BFMS and monkeys are effectively protected against human hunting [Saj et al., 2005], which suggest that adult female mortality via predation does not make up the bulk of these disappearances. Therefore, including the disappearances of healthy females in our analyses is unlikely to lead to a large overestimation of female dispersal.

**TABLE II. Observation Periods in the Nine Research Groups of *Colobus vellerosus***

Group	Period	# of Months <sup>a</sup>	Takeovers
BO	Oct. 2008–May 2010	9	N
BS	Jan. 2001–May 2012	50	Y
DA	July 2004–May 2011	37	Y
NP	May 2007–May 2012	20	Y
OD	July 2006–May 2012	22	Y
RT	June 2003–October 2013	64	Y
SP	May 2006–October 2013	46	N
WW	July 2004–October 2013	60	Y
WT	June 2012–October 2013	22	N
Total:		330	

<sup>a</sup>Number of months in which a reliable group count was obtained.

## Data Analysis

We analyzed whether the number of observation months with and without takeovers differed between uni-male and multi-male groups. We tested whether takeovers by single males and multiple males differed in: a) the male composition (single or multiple males) of targeted groups, b) the time they took to be completed, or c) frequency of female dispersal post-takeover. We tested whether quick or slow takeovers varied in the degree that they were: a) associated with infanticide, and b) followed by female dispersal. We conducted two analyses to assess whether female dispersal decisions were associated with the immediate risk of infanticide. First, we investigated whether parous and nulliparous females differed in their frequencies of post-takeover dispersal. Second, we examined whether females with dependent infants and other parous females differed in their frequencies of post-takeover dispersal. Because we were unable to distinguish pregnant from cycling females and researchers were not always present at the site to record births, we did not distinguish between these two types of females. For all analyses, we used two-tailed Fisher's exact tests implemented in R [R Core Team, 2014], and the significance level was set to  $P \leq 0.05$ .

## Ethics

Research methods were approved by the University of Calgary Animal Care Committee. This research adhered to the legal requirements of Ghana and was approved by the Ghana Wildlife Division and by the Boabeng-Fiema Monkey Sanctuary Management Committee. This research also adhered to the American Society of Primatologists' Principles for the Ethical Treatment of Non Human Primates.

## RESULTS

Most takeovers occurred in multi-male groups (13/15). However, the number of observation months with and without takeovers in uni-male (2 takeovers during 82 months) and multi-male groups (13 takeovers during 229 months) did not differ (Fisher Exact Test,  $P = 0.37$ ,  $N = 311$ ). Takeovers were achieved by single males ( $N = 5$ ) or by coalitions of males ( $N = 10$ ) (Table I). There was no association between the number of males in the targeted group (one vs. several) and the number of males involved in a takeover (Fisher Exact Test,  $P = 0.49$ ,  $N = 15$ ). Therefore, single males and coalitions of males did not seem to target specifically uni- or multi-male groups in our sample. Per definition, the duration for quick takeovers was one month. In case 11, the male who performed the takeover entered the group on September 14. JAT only returned to the group on October 18, by which time the new male had become

dominant over all the other males in the group. Because the dominance relationships were well established, we assumed that the takeover occurred within one month and we classified it as a quick takeover. Slow takeovers took a mean of 6.9 months ( $N = 8$ ; range: 3–14 mo; median: 5). Single adult males were never involved in slow takeovers, and they performed most quick takeovers (4/5; one takeover by a single male had an unknown duration). Slow takeovers always involved several males immigrating into the group as an all-male band (8/8). There was a significant difference between the frequencies of quick and slow takeovers by single and multiple males (Fisher Exact Test,  $P = 0.02$ ,  $N = 13$  cases with information on the category of takeover).

Infant attacks and infanticide by males may have occurred in up to 10 of 13 takeovers when infants were present: We observed infanticide in six cases, suspected in three, and observed attacks on infants in one additional case. Infant attacks and infanticide occurred during four of five quick takeovers and five of eight slow takeovers. The type of takeover (quick or slow) was not associated with presence or absence of infanticide (including suspected infanticide) and infant attacks (Fisher Exact Test,  $P = 0.65$ ,  $N = 12$  with known type of takeover and for which infants were present in the group at time of takeover).

Female dispersal never occurred during the five quick takeovers, while it occurred in five of eight slow takeovers (Table I). The number of females that dispersed differed significantly between quick ( $N = 0$  of 34 females present) and slow takeovers ( $N = 15$  of 72 females present) (Fisher Exact Test,  $P = 0.002$ ,  $N = 106$ ). Females remained in the group during the four takeovers by single males with complete information on female dispersal ( $N = 28$  females present). Females dispersed during four of ten takeovers by multiple males ( $N = 15$  of 84 females present). There was a significant difference in the total number of dispersing females during takeovers that involved one male versus multiple males, with more females dispersing after a multi-male takeover (Fisher Exact Test,  $P = 0.02$ ,  $N = 112$ ).

A greater proportion of nulliparous females ( $N = 11/31$ ) than parous females ( $N = 5/83$ ) dispersed during takeovers, and the frequencies of dispersal during takeovers differed significantly between these two categories of females (Fisher Exact Test,  $P = 0.0002$ ,  $N = 114$ ). During the takeovers, five of 49 parous females without dependent infants at the onset of the takeover dispersed. None of the 34 females with dependent infants dispersed permanently with the ousted alpha male. In only one case (case 7), did a parous female disperse with her juvenile offspring. However, there was no difference in dispersal frequencies of parous females with vs. without a dependent infant (Fisher Exact Test,  $P = 0.08$ ,  $N = 83$ ). The 14 females whose infants

died from infanticide (observed or suspected) during or shortly after the takeover remained in the group, regardless of the type of takeover that had occurred in their group.

## DISCUSSION

Takeovers in *C. vellerosus* vary in duration and are regularly associated with infanticide and with female dispersal [Saj et al., 2005; Teichroeb & Sicotte, 2008; Teichroeb et al., 2009, 2011; this study]. When a single male was involved in a quick takeover, females usually stayed in their group with the new resident male. The social upheaval associated with single male takeovers was shorter than that observed in multi-male takeovers because there was no struggle over alpha status once the takeover was completed. Takeovers performed by several males took longer to complete, partly because males in the takeover coalition jointly attempted to evict the resident male(s) who sometimes resisted for a long time, and partly because members of the coalition often tried to evict one another over a period of several months before dominance ranks were settled [Poirier, 1969; Sterck & van Hooff, 2000; Teichroeb et al., 2011; Ridley, 2012].

Because slow takeovers involved prolonged male aggression, they may have led to longer periods of elevated stress levels and lowered female reproductive output even in the absence of infanticide [Dunbar, 1987; Steenbeek et al., 2000; Sterck & van Hooff, 2000]. Perhaps because of these costs, females were more likely to disperse during a slow takeover [this study; Dunbar, 1987; Poirier, 1969; Sterck, 2012]. Female dispersal in Thomas langurs also occurred during elevated extra-group male harassment of bisexual groups [Sterck, 1997]. Thus, female dispersal in several primate populations is associated with actual or potential upheaval in male group membership.

The number of males involved in the takeover and the duration of the takeover may also relate to the quality of the invading males. The capacity of males to acquire and retain a group of females is probably related to dominance, size, and stamina (McElligott & Hayden 2000; McElligott et al., 2001). These qualities should also influence a male's ability to take over a group. In some species however, success in takeovers is influenced less by the quality of the male himself, and more by demographic conditions such as the number of males involved in the coalition to expel the resident male(s) [Fedigan & Jack, 2004; Ridley, 2012]. In *C. vellerosus*, males living in one-male groups engage in more costly displays and emit longer loud calls than males in multi-male groups, and they also displace multi-male groups in intergroup encounters [Teichroeb & Sicotte, 2010; Teichroeb et al., 2012]. Thus, single invading males may be of higher quality than males in all-male bands, allowing them to take

over the group more quickly than several lower-quality males. If this is the case, females in our study may have dispersed after takeovers by multiple males more often than after takeovers by single males because they were seeking a group with a higher-quality male. A mate with better competitive ability could provide good genes to females' offspring, protect these offspring more effectively, and/or potentially defend a larger or better quality home range [Fashing, 2001; Harris, 2006; Harris et al., 2006].

It therefore seems that female dispersal in colobines—and probably in most species where females have the option of dispersing—is an important form of mate choice for high quality males. Dispersal also allows these females to reduce the costs associated with long periods of social upheaval. Strictly philopatric females are more constrained, in comparison. However, female colobus do not always disperse during takeovers by multiple males with prolonged periods of social upheaval, even when they do not have a dependent infant. This may be because dispersal is associated with certain costs. Not only do dispersing females face the costs of delayed reproduction, potential loss of allies, reduced access to food resources, and predation risk while between groups [Cheney & Seyfarth, 1983; Isbell & Van Vuren, 1996; Isbell, 2004; Pusey & Packer, 1987], females in our study population also aggressively resist female immigration, and the majority of immigration attempts fail [Teichroeb et al., 2009]. After two of the takeover events presented in this paper (case 5 and 13), the dispersing females failed to immigrate to another study group and eventually disappeared from the study area [Teichroeb et al., 2009; EW, unpublished data]. Presumably, dispersing females who fail to enter a neighbouring study group and who fail to establish a new group within the densely populated study area are forced to disperse further to an unstudied group or to one of the surrounding forest fragments. These females are then dispersing to unfamiliar areas and to forest fragments that consist of potentially lower-quality habitats than the study area [Wong et al., 2006]. Thus, female dispersal is likely a trade-off between the benefits of exerting mate choice and the costs associated with dispersal.

In our study, only females without infants dispersed, which is similar to the pattern reported in a review of female dispersal in primates by Sterck and Korstjens [2000]. Our prediction that females with infants might disperse with the ousted alpha male (the putative sire of their offspring) was thus not supported. These females stayed in their group with the new male(s). This was surprising because these females faced an extremely high risk of losing their infants to infanticide by remaining with male(s) that presumably did not sire their infants [Watts, 1989; Teichroeb & Sicotte, 2008]. Female dispersal with the ousted alpha male is sometimes reported in other colobine populations [Hrdy, 1974; Sterck &

Korstjens, 2000: 309; Zhao et al., 2011]. This behavior may be a counter-strategy to infanticide, the “remaining with the father hypothesis” [Sterck & Korstjens, 2000], as females may return and join the new alpha male once their infants are weaned [Hrdy, 1974; Zhao et al., 2011]. In the case reported by Sterck and Korstjens [2000], the association with the father was temporary. In the six cases reported by Zhao et al. [2011], three females stayed to breed with their former resident male and three females stayed with their former male only until their infants were weaned, after which they rejoined the new male. We have observed a similar situation in our study population (case 4). During a slow takeover, two females with dependent infants temporarily ranged away from their group with the severely injured former alpha male. They stayed away during the day for several days in a row but slept in visual contact of their group. These females eventually returned to their group and lost their infants to infanticide (IB, unpublished data). This strategy of splitting away with the former alpha may be risky because this male has already been outcompeted by other males. He is thus potentially not a strong defender of infants. Therefore, females are likely to lose their infant to infanticide during future takeovers by stronger males. Furthermore, females that choose to leave with an ousted alpha male would need to establish a new home range area, which may not be possible because of intergroup competition.

We did not find support for our hypothesis that, after losing their infants to infanticide, females may disperse more often after takeovers by all-male bands than after takeovers by single males. Females whose infants were killed by invading males in this study ( $N = 14$ ) always remained in the group afterwards. Remaining in the group after infant loss may not be associated with significant additional fitness costs for a female if the group is already socially stable at that point.

In conclusion, female *C. vellerosus* at BFMS tended to stay with single males that quickly ousted their competitors; these males were presumably of higher competitive ability. We suggest that female dispersal post-takeover is a form of mate choice and a way to reduce the costs associated with prolonged social upheaval, that strictly philopatric females lack. However, dispersal did not seem to be an option for lactating females. As a result, weaker or younger males may gain access to groups of females if they cooperate with other males during the initial phase of a takeover. This study thus highlights the conflicting reproductive strategies of males and females and how these strategies vary for individuals in different life stages.

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