

Dispersal in male ursine colobus monkeys (*Colobus vellerosus*): influence of age, rank and contact with other groups on dispersal decisions

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Summary

Dispersal is male-biased in ursine colobus monkeys (*Colobus vellerosus*), although female dispersal also occurs (Teichroeb et al., 2009). Here we describe the process of male dispersal and its connection with between-group encounters (BGEs, $N = 444$) and male incursions (when males left their group and approached within 50 m of another group; $N = 128$) at the Boabeng-Fiema Monkey Sanctuary in central Ghana. Through BGEs and incursions, particularly those with non-aggressive interactions between individuals in different groups (BGEs, $N = 17$; incursions, $N = 4$), males could probably assess other groups for dispersal opportunities. There was a trend for males to perform incursions more frequently before emigrating voluntarily than involuntarily. Incursions were often performed towards the group that the male eventually transferred to. Incursions by alpha males were temporally shorter and more aggressive than those by non-alpha males. We suggest that non-alpha males used incursions to assess other groups for breeding or dispersal opportunities, whereas alpha males performed incursions mainly to convey information about their quality to neighbouring males and females. Male emigrations/disappearances (natal $N = 20$, secondary $N = 43$, unknown $N = 9$) and immigrations ($N = 62$) were recorded for seven groups during ten years (2000–2010). Alpha males always emigrated involuntarily. Parallel emigration and immigration occurred. Males often immigrated into groups with a more favourable adult male/adult female ratio and improved their rank, both of which likely increased their mating opportunities. The most fitting ultimate explanation for both natal and secondary male dispersal in this population was the intrasexual competition for mates hypothesis, as males of all ages appeared to emigrate to improve their reproductive opportunities.

Keywords: Male emigration, male immigration, male dispersal, parallel dispersal, female group size, between-group encounters, male incursions, male forays, dispersal decisions.

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1. Introduction

Our understanding of dispersal patterns in animals is ever increasing, especially with respect to sex differences in dispersal probability and distance (Clutton-Brock & Sheldon, 2010) and the proximate and ultimate explanations for dispersal (Johnson & Gaines, 1990; Smale et al., 1997). However, for long-lived, social species like primates it is rare to have data on the events before and after dispersal (but see: Gould, 2006; Ekernas & Cords, 2007; Stoinski et al., 2009) or long-term life history information for the dispersing sex throughout more than one transfer (but see Sussman, 1992; Alberts & Altmann, 1995; Okamoto et al., 2000; Jack & Fedigan, 2004a,b).

In mammals, natal and secondary dispersal are male-biased (Greenwood, 1980). Before leaving their resident group, males may assess other groups for dispersal opportunities. They can evaluate other groups during between-group encounters (BGEs, e.g., Steenbeek, 1999; Sicotte & MacIntosh, 2004) or they can use male incursions (sometimes called forays) to 'visit' or 'sample' a group before immigrating. These incursions involve males leaving their resident group, approaching, and sometimes integrating into other groups. Male incursions allow assessment of neighbouring groups for dispersal or breeding opportunities (e.g., mammals: *Otaria byronia*, Campagna et al., 1988; *Suricata suricatta*, Doolan & Macdonald, 1996; Young et al., 2007; *Chlorocebus aethiops*, Cheney & Seyfarth, 1983; *Colobus vellerosus*, Sicotte & MacIntosh, 2004; *C. polykomos*, Korstjens et al., 2005; birds: reviewed in Westneat & Stewart, 2003). Through these interactions males can gauge possible resistance to their immigration and the number of females that may be reproductively active. Incursions may also convey information about male quality (e.g., mammals: *Gorilla beringei beringei*, Watts, 1994; *Presbytis thomasi*, Steenbeek, 1999; *C. vellerosus*, Sicotte & MacIntosh, 2004). Where female dispersal also occurs, males may use incursions to display their strength to entice females to transfer to their group (e.g., *G. b. beringei*, Watts, 1994; *P. thomasi*, Steenbeek, 1999). In species with bisexual dispersal, where both males and females can integrate into existing social units, whether incursions are primarily used to assess other groups for dispersal opportunities or entice female transfer may depend on the rank or life-stage of the male(s) (Steenbeek, 1999).

The competitive ability and/or condition of males may determine the timing of emigration and the strategies used to enter a new group or territory

(e.g., mammals: *Mirounga angustirostris*, Le Boeuf & Reiter, 1988; *Macaca fascicularis*, van Noordwijk & van Schaik, 2004; *Odocoileus virginianus*, McCoy et al., 2005; *Papio hamadryas ursinus*, Clark et al., 2008; *Ctenodactylus gundi*, Nutt, 2008; birds: *Phoenicopterus ruber roseus*, Barbraud et al., 2003; reptiles: *Lacerta vivipara*, Meylan et al., 2002). Male primates can enter groups using relatively little aggression and start at the bottom of the male hierarchy (e.g., *M. mulatta*, Drickamer & Vessey, 1973; *M. fasciata*, Sugiyama & Ohsawa, 1975; *Chlorocebus aethiops*, Henzi & Lucas, 1980) or they can immediately challenge the dominant males and attempt to take over the group, evicting the resident males (e.g., *Presbytis johnii*, Poirier, 1970; *M. fascicularis*, van Noordwijk & van Schaik, 1985; *Alouatta seniculus*, Agoramorthy & Rudran, 1993; *Semnopithecus entellus*, Borries, 2000).

Dispersal is a risky endeavour for animals at any life-stage. For males, the most prominent dangers are greater predation risk while between groups and increased conspecific aggression when attempting to enter new groups (Pusey & Packer, 1987a; Isbell & Van Vuren, 1996; Isbell, 2004). Males may also lose allies when they move between groups. These risks are tolerated because dispersal can improve mating opportunities (Shields, 1987; Pusey, 1992). Males can move to a group or area with more receptive females (e.g., mammals: *Papio anubis*, Packer, 1979; *Lemur catta*, Sussman, 1992; *Ursus arctos*, Krofel et al., 2010), a more favourable adult sex ratio (e.g., mammals: *P. cynocephalus*, Alberts & Altmann, 1995; *Cebus capucinus*, Jack & Fedigan, 2004b; *Meles meles*, Macdonald et al., 2008; *L. catta*, Parga & Lessnau, 2008; birds: *Perisoreus infaustus*, Griesser et al., 2008), or where they can increase their rank relative to their original group (e.g., mammals: *Chlorocebus aethiops*, Cheney & Seyfarth, 1983; *P. cynocephalus*, Smith, 1992; *Cebus capucinus*, Jack & Fedigan, 2004b; birds: *Passer domesticus*, Altwegg et al., 2000; *Melospiza melodia*, Arcese, 1989). However, dispersing males do not always improve their breeding opportunities in the short term (e.g., *Chlorocebus aethiops*, Cheney, 1983; *L. catta*, Sussman, 1992; *S. entellus*, Borries, 2000; *Papio hamadryas ursinus*, Clarke et al., 2008; *G. b. beringei*, Stoinski et al., 2009).

Some of the costs associated with dispersal can be mitigated by parallel dispersal, which involves transferring with other group members or into groups with familiar individuals (van Hooff, 2000). Parallel dispersal has three main benefits: (1) it might reduce predation risk for males while they are between groups; (2) males may avoid the loss of allies; and (3) they may

be able to more easily overcome the resistance of residents with the assistance of allies (Schoof et al., 2009). Some males even continue to reside with kin despite transferring between groups when they disperse with members of their age-cohort (potentially full or half siblings) or their father/son (Altmann, 1979; Cheney, 1983; van Hooff, 2000; Jack & Fedigan, 2004a,b).

The two main ultimate hypotheses for male dispersal are: (1) inbreeding avoidance, which may explain not only natal dispersal (Itani, 1972; Packer, 1979; Pusey, 1987; Clutton-Brock, 1989) but also secondary dispersal if the male resides with maturing daughters (Pusey & Packer, 1987b); and (2) intrasexual competition for mates, which may explain male secondary (or breeding) dispersal (Henzi & Lucas, 1980; Dobson, 1982; Moore & Ali, 1984; Pusey & Packer, 1987a; Alberts & Altmann, 1995; Jack, 2003). Male competitors can come from both inside and outside the group, and losing contests to immigrant males can lead to involuntary emigration from the group or territory (e.g., mammals: *Cebus capucinus*, Jack & Fedigan, 2004b; insects: *Pachydiplax longipennis*, McCauley, 2010). Hence, males are forced to emigrate again and may have to immigrate into a new group (secondary dispersal). Males may also emigrate due to predation risk (Isbell & Van Vuren, 1996) or food competition, though food competition is more likely to cause female dispersal (Trivers, 1972; van Schaik, 1989).

In this paper, we describe male emigrations/disappearances and immigrations in seven groups of ursine colobus (*Colobus vellerosus*) at the Boabeng-Fiema Monkey Sanctuary in Ghana during ten years of research. This is the first detailed study on the process and outcomes of male dispersal for an African colobine species. Previously, we have shown that female dispersal occurs in *C. vellerosus* (Teichroeb et al., 2009), which leaves open the possibility that males could remain in their natal group or emigrate. Here we examine the process of male emigration and the relationship between dispersal, BGEs, and male incursions. We ask the question, does the form and function of male incursions vary with male life-stage and/or temporal proximity to emigration? We also explore the frequency and ways that males moved between groups, the age class of emigrants and immigrants, the factors leading to emigration, the frequency of parallel emigration and immigration, and the outcome of immigration. Finally, we investigate which hypothesis for male dispersal is best supported for *C. vellerosus* at Boabeng-Fiema.

2. Methods

2.1. Study site and species

This research was conducted at the Boabeng-Fiema Monkey Sanctuary (BFMS) in central Ghana (7°43'N and 1°42'W), a dry semi-deciduous forest, 192 ha in size and located at an elevation of 350 m in the Nkoranza district of the Brong-Ahafo Region. BFMS is surrounded by farmland but connects to several smaller forest fragments in the area by a narrow, riparian forest. The vegetation is a mosaic of primary forest, regenerating farmland (secondary forest), and woodland (Fargey, 1991; Saj et al., 2005). Nineteen groups of *C. vellerosus* occupy the Boabeng-Fiema forest fragment, and five of the surrounding fragments (located within a 10 km radius) also present dispersal options as they contain 10 groups of colobus (Figure 1; Kankam et al., 2010).

At BFMS, *C. vellerosus* have been studied under the supervision of P.S. since 2000. They are mainly folivorous (annual diet: 74% leaves, Saj et al., 2005). Groups are multi-male/multi-female, uni-male/multi-female, or all-male bands (AMBs) (Saj et al., 2005). There is no mating or birth season (Teichroeb & Sicotte, 2008b), and females show no external signs of ovulation. Between-group encounters (BGEs) are usually aggressive, with adult males as the main participants, but a small percentage of encounters involve no aggression (17%, Sicotte & MacIntosh, 2004). Group males, solitary males, and males in AMBs also attack and interact with bisexual groups during male incursions (Sicotte & MacIntosh, 2004). Targeted aggression towards infants occurs during both BGEs and male incursions (Sicotte & MacIntosh, 2004; Saj & Sicotte, 2005). Several infanticides have been observed in this population after new males immigrated, and infanticide accounts for 38.5% of infant mortality (Teichroeb & Sicotte, 2008a). Putative sires may aid females in infant defence, if incoming males do not force them to emigrate (Saj & Sicotte, 2005; Teichroeb & Sicotte, 2008a,b).

2.2. Study groups and data collection

We used data from our seven research groups (B2, OD, DA, NP, RT, SP and WW). Groups were followed for varying amounts of time and were only included in this analysis if all adult and subadult males could be recognized (Table 1). Emigrations by juvenile males may be underestimated for two

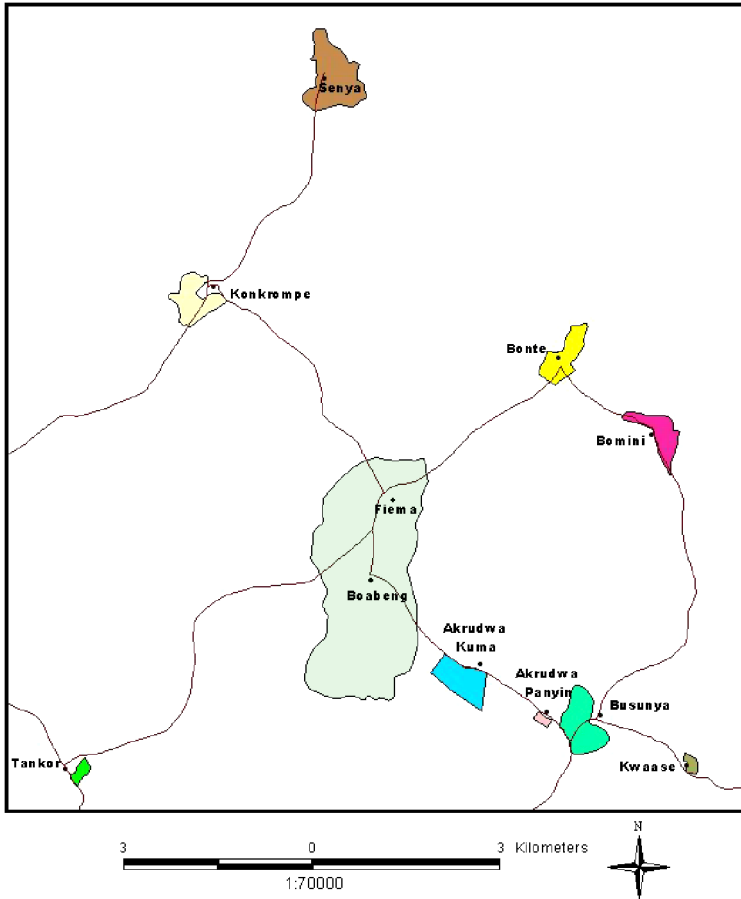


Figure 1. Map of Boabeng-Fiema and surrounding fragments (provided courtesy of Bright Kankam and Woeli Publishers, Accra, Ghana). Ursine colobus populations also exist in Akrukwa Kuma, Busunya, Bonte, Konkrompe and Bomini (Kankam et al., 2010). This figure is published in colour in the online edition of this journal, which can be accessed via <http://www.brill.nl/beh>

larger groups (DA and WW) because juveniles were difficult to individually recognize. Group size varied for each group across study years (Table 1).

Each study group was followed for at least one day per month (range 1–17 days, mean 3.52 days/month, Table 1) during follows lasting 7–12 h when researchers were present at the site. Behavioural 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

Table 1. Study periods and group size.

Group	Years of study ^a	Months of study	Mean No. days followed per month	Number of follow days	Group size range	Number of adult ♂♂	Number of adult ♀♀
B2	2000–2010	47	6	280 ^b	7–17	1–7	2–6
SP	2006–2010	13	2.2	29	9–17	1	3–4
RT	2003–2010	32	3.9	124	8–27	1–3	5–7
OD	2006–2010	9	3	26	15–20	1–6	5–8
DA ^c	2004–2010 ^c	31	3.4	106	17–26	3–8	6–9
NP ^c	2007–2010	11	2.5	27	7–13	1	4–6
WW	2004–2010	27	3.7	101	23–33	2–10	7–11
Total		170		693			

^a Years of study with good individual identification so that dispersal events could be recorded.

^b Including follows by J.A.T., E.C.W., T. Saj, A. MacIntosh, S. Martenson and L. Brent.

^c Between 2006 and 2007 NP group formed from DA individuals (Teichroeb et al., 2009).

per hour. Focal data presented here were collected in 2004–2005 by J.A.T. on four groups, RT, B2, DA and WW (202 follow days, 433.3 focal hours). Emigration and immigration events were recorded using all occurrences data collection, while copulations or male-male aggression occurring outside of focal samples were recorded ad libitum (Altmann, 1974). Group counts were usually obtained at least once per month.

2.3. Definitions

The age of dispersing and immigrating individuals was sometimes known but in most cases was estimated from the size of the individual relative to those of known age. Juvenile males (1–2 years old) were weaned and smaller than young subadult males, young subadult males (3–5 years old) were smaller than adult parous females, older subadult males (5–6 years old) were the same size as adult parous females, and adult males (≥ 7 years old) had achieved full body size (larger than adult females) and regularly participated in loud call bouts with other adult males.

Rates of male emigration/disappearance and immigration were reported as number per male per year. We provided both the observed and inferred number of emigrations when we presented rates of emigration because this may provide a more accurate estimate of the number of males leaving groups.

Observed cases were those where the researcher saw the process of emigration or a male from one group was seen residing in another group ($N = 24$). The inferred number includes those individuals that disappeared from the study groups ($N = 48$) when no observers were present and there was no evidence of death. No predators remain at BFMS that could take a subadult to adult sized colobus monkey and colobus hunting is rare, if it occurs at all (Saj et al., 2005). Adult male mortality caused by intra-specific aggression has been observed infrequently. Only three males have been observed to die from wounds they received in contests with other males (for one such case, see Sicotte et al., 2007). It, thus, seems unlikely that most disappearances are related to death because in all cases, individuals were young and/or appeared in good health, or emigrated involuntarily (see definition below). Thus, we included inferred cases when calculating rates of emigrations, but use only emigrations that were directly observed in all other analyses because the inclusion of disappearances as emigrations could lead to an overestimate of cases.

Natal emigration was defined as instances of departure from the group of birth. Natal emigration could only be determined where a male's group of birth was known. Secondary emigration was defined as males leaving a group into which they were known to have previously immigrated. Voluntary emigration was defined as individuals leaving a group without any observed increase in agonism towards them. Involuntary emigration was defined as emigration following increased aggression (e.g., threats, chasing, contact aggression) between males within a group during the previous days or weeks, observed during focal samples or ad libitum data collection. Depending on the males, aggression could be intense with the losing male(s) emigrating within a few days of its beginning or aggression could be prolonged in the weeks prior to emigration. Takeover events occurred when all the resident males emigrated within a few months of new male(s) immigrating. Between-group encounters (BGEs) occurred when individuals of both sexes from two groups came within 50 m of one another (Oates, 1977), while 'male incursions' occurred when males left their group and approached within 50 m of another group (Sicotte & MacIntosh, 2004). At a distance of 50 m the groups could invariably see one another. Males were defined as forming a separate AMB phase when they left their group of origin and began to sleep and range with other males.

Male dominance relationships were determined from the direction of aggression, displacements, avoidance, and submissive behaviours during focal samples and ad libitum observations. For this analysis, only male dominance interactions from stable periods, without challenges between males, were used. The direction of aggression and submission in each dyad did not differ between focal and ad libitum data. Male dominance relationships within each group were linear and males could be assigned a numerical rank. Bidirectionality in aggression was rare, occurring only in WW group when putative sires defended infants from new males (Teichroeb & Sicotte, 2010). We defined 'high-intensity aggression' as instances with chases or contact aggression between subjects. Low-intensity aggression included threatening gestures such as stiff-legs, open-mouths and jump-displays (*sensu* Oates, 1977).

2.4. Data analyses

We present the mean duration of incursions for alpha versus non-alpha males. A mean duration per male was calculated and then used to compute an overall mean for duration, so that no single male with unusual durations skewed the results. Mann–Whitney *U*-tests were employed to examine differences in incursion duration and the proportion of incursions where the male initiated high-intensity aggression between alpha and non-alpha males, as well as to investigate rates of aggression received by immigrant adult males versus subadult males. Fisher's exact tests were used to establish: (1) whether males that emigrated voluntarily performed more incursions before emigrating compared to males that emigrated involuntarily; (2) the association between male age (adult or subadult) and the context surrounding emigration; (3) the relationship between male age and tendency to challenge dominants and become high-ranking in the new group; and (4) whether males that immigrated with others were more likely to challenge dominants than those that immigrated alone. Wilcoxon signed-rank tests were used to compare a male's rank before and after transferring to a new group, the sex ratios of original groups (including transferring males) with new groups (not including transferring males), and the percentage of males ranking higher than transferring males in new groups versus original groups. When examining the number of males in the new and original groups, transferring males were included in both counts. The duration of male tenure in a group was sometimes known exactly because the entrance (birth or immigration) of that male and the exit

(death or emigration) were both observed. Whenever the entrance or the exit of a male was not observed, the duration of his tenure was truncated. Truncated tenure durations occurred either because the male was still in the group at the end of our data collection period, or the male entered and/or exited when observers were not present at the site. Since it is difficult to estimate the effect that truncated observations will have on tenure durations, we provide mean male tenure for both truncated and non-truncated observations. Tests were two-tailed and significance was set at $p \leq 0.05$. SPSS 16.0 was used for all tests except Fisher's exact tests, which were done using Preacher & Briggs (2001) interactive calculation tool.

3. Results

3.1. *Male movement between groups*

Overall, 693 follow days were conducted for the seven study groups over differing numbers of study years (Table 1). Seventy-two male emigrations (24 observed, 48 inferred, $N = 65$ males) and 62 male immigrations ($N = 55$ males) occurred in the seven groups during the study periods. Forty-two males in the sample were involved in both emigration and immigration. In comparison, during the same time period in the same groups, 25 female emigrations (5 observed, 20 inferred, $N = 25$ females) and four female immigrations ($N = 4$ females) occurred.

3.2. *Assessment of other groups during between-group encounters and male incursions*

Males could have assessed other groups for dispersal opportunities whenever groups met (e.g., aggressive and non-aggressive BGEs and male incursions). However, non-aggressive BGEs and incursions may allow males to gather more information about individuals from other groups through mingling and affiliative interactions. We, thus, analyzed non-aggressive BGEs and incursions separately. In this sample, 12.4% of all encounters were not aggressive (71/572, 14.2% of BGEs (63/444) and 6.3% of male incursions (8/128)). More specifically, non-aggressive interactions involving individual males were recorded during 3.8% of BGEs (17/444). In eleven of these interactions (11/17, 65%), males engaged in sexual behaviours such as presents,

mounts, and copulations with females in the other group; playing (2/17, 11.8%), grooming (2/17, 11.8%), and touching were also observed (2/17, 11.8%). During incursions, non-alpha intruders sometimes mingled with individuals from the other group (21.7%, 10/46) while alpha male intruders never did so (0/26). Six non-aggressive interactions between intruding males and resident individuals were recorded during incursions (4/46 or 8.7% of incursions by non-alpha males). Half of these were sexual behaviour with females 50% (3/6), 33.3% was grooming (2/6), and 16.7% was playing (1/6). We also observed males residing in different groups present to one another during three BGEs and one male incursion.

Male incursions ($N = 128$) varied in duration and aggression level depending on the intruder's status. Incursions by non-alpha males were characterized by a slow and calm approach, which often involved males simply moving close to and watching the other group (28.9% (13/45) compared to 7.1% (2/28) for alpha incursions). Incursions by alpha males were short (mean = 17.3 min., SD = 11.0, $N = 8$ males) compared to non-alpha males (mean = 109.4 min., SD = 180.5, $N = 16$ males) ($N_{\text{alpha}} = 8$, $N_{\text{non-alpha}} = 16$, $Z = -2.05$, $p = 0.04$). We observed high-level aggression in most incursions by alpha males (88.9%, 24/27 incursions) and this aggression was initiated by the intruding alpha male in 77.3% of cases (17/22). Although 63.6% (28/44) of incursions initiated by non-alpha males also showed high-level aggression, the non-alpha intruder(s) initiated the aggression in only 31.6% (6/19) of incursions (when it could be determined who initiated aggression). Alpha male intruders initiated high-level aggression during a greater proportion of incursions compared to non-alpha male intruders ($N_{\text{alpha}} = 8$, $N_{\text{non-alpha}} = 12$, $Z = 2.01$, $p = 0.04$). Indeed, since non-alpha male intruders did not always create agitation in the group, the frequency of incursions by non-alpha males may be underestimated.

In cases of voluntary emigration where a male's destination group was known ($N = 10$ males), 78.2% of the observed male incursions (18/23) prior to immigration were directed towards the group the male transferred to (Table 2). There was a trend for males that emigrated voluntarily to show an increased frequency of incursions two months before leaving their group compared to males that emigrated involuntarily (6/11 voluntary dispersers versus 1/10 involuntarily dispersers, Fisher's exact test: $p = 0.06$).

Table 2. Number of male incursions and to which group they were performed before emigration.

Case	Original group	$\sigma^7\sigma$	Rank in original group/total No. $\sigma^7\sigma$	Voluntary (V) or involuntary (I) emigration?	No. of σ^7 incursions per month and target group						Date of emigration	Destination group
					Months prior to dispersal*							
					6	5	4	3	2	1		
1	WW/AMB	Mo	7/9	V	-	-	-	-	3-DA	6-DA	Sept. 2004	DA
		Ma	8/9	V	-	-	-	-	3-DA	6-DA	Sept. 2004	DA
		Sh	9/9	V	-	-	-	-	3-DA	6-DA	Sept. 2004	DA
2	WW	Be	4/7	V	0	0	0	0	0	1-DA	Mar. 2005	?
3	DA	Cy	2/6	V	0	0	0	-	1-BO	0	Mar. 2005	BO
		Jp	6/6	V	0	1-BO	1-WW	-	0	0	Mar. 2005	BO
		Jf	5/6	V	0	1-BO	0	-	1-WW	0	Mar. 2005	BO
4	B2	Wo	2/6	V	0	0	0	1-WW	2-RT	2-RT	Sept. 2005	RT
		Li	4/6	V	0	0	0	1-WW	1-WW, 1-RT	1-RT	Sept. 2005	RT
		Gi	5/6	V	0	0	0	0	0	0	Sept. 2005	RT
		Go	6/6	V	0	0	0	0	0	0	Sept. 2005	RT
5	B2	T	2/4	I	-	-	-	-	0	1-SP?	Sept. 2004	?
		Lx	1/4	I	-	-	-	-	0	0	Sept. 2004	?
		Le	3/4	I	-	-	-	-	0	0	Sept. 2004	?
		Lo	4/4	I	-	-	-	-	0	0	Sept. 2004	Solitary
6	WW	Pc	1/6	I	-	-	-	0	0	0	Oct. 2004	?
7	DA	Ry	1/3	I	-	-	-	0	0	0	Oct. 2004	?
		Td	2/3	I	-	-	-	0	0	0	Oct. 2004	?
8	DA	Ca	4/9	I	-	-	0	0	0	0	Nov. 2004	?
9	DA	Mo	4/8	I	-	0	0	0	0	0	Jan. 2005	?
10	DA	Mc	3/7	I	0	0	0	0	-	0	Feb. 2005	?

-, researchers were not present at the site.

3.3. Process of male emigration

Adult males and subadult males showed similar rates of emigration/disappearance. Each year a mean of 31.4% of all adult males studied emigrated/disappeared (rate 0.04, $N = 10$ years, range 0–71.4%), while 33.4% of subadult males emigrated/disappeared (rate 0.04, $N = 8$ years, range 0–100%). The rate of juvenile male emigration/disappearance was 0.002 and the mean percentage of juvenile males that emigrated was 4.2% ($N = 8$ years, range: 0–33.3%). In 63 cases of male emigration/disappearance, it was possible to discern whether males were natal or immigrants. Natal emigration/disappearance was made up of adult males (7.3%, 3/41), subadult males (80%, 16/20), and juvenile males (50%, 1/2). Natal males emigrated at an estimated mean age of five years ($N = 18$, range: 2.5–7.5 years) and no males remained in their natal group after eight years of age.

Using only directly observed cases of emigration, the above results are similar, though rates of emigration were lower (adult males 0.008, range 0–31.8%, subadult males 0.017, range 0–60%, juvenile males 0) and all natal emigrations were by subadult males ($N = 7$). The following analyses include only directly observed cases of emigration.

Emigration was involuntary in 52.6% of cases (10/19) and voluntary in 47.4% of cases (9/19). Eight of 10 cases of involuntary emigration (80%) involved adult males and six of nine cases of voluntary emigration involved subadult males (66.7%). However, this distribution was not significantly skewed (Fisher's exact test, $p = 0.07$). Alpha males always left involuntarily ($N = 3$) while only 43.8% of non-alpha adult males (7/16) emigrated involuntarily. Aggression towards adult males before involuntary emigration was by new males in 70% of cases (7/10) and by resident males in 30% of cases (3/10).

Males emigrated singly and showed parallel emigration in 35.3% and 64.7% of cases, respectively ($N = 17$). For these cases of parallel emigration (three transfers of groups of three to four males), males were observed leaving their groups together and were later seen together in another group, with and without an AMB phase ($N = 11$ males). Observed natal male emigration was parallel in all cases ($N = 7$). It follows then that observed instances of parallel emigration involved mostly subadult males (72.7%, 8/11). Males emigrated with members of their age-cohort and with males that had entered the group previously, in a wide age range (young subadults to adults). In one

case, two transferring males in 2006 were known to be maternal half-siblings and possibly full-siblings that stayed together in their new group until 2008. In another case, a father-son dyad (E.C.W., unpubl. genetic data) transferred together in 2008 from OD to DA and remained until the end of the study in 2010.

In eight emigration events, the fate of 17 emigrating males was known. For these males, 70.6% (12/17, Figure 2) transferred to a group with a more favourable AM/AF sex ratio than the one they left, that is, to a group with more adult females to adult males. When independent cases (i.e., taking into account the occurrence of parallel immigration) are compared, this was not significant ($N = 8$, $Z = -1.68$, $p = 0.093$; Figure 2). For nine transferring males, rank was known for both the original group and the new group. Three months after entering a new group, all immigrating males had improved their rank, compared to their rank in their original group, by forcing the emigration of resident males and males with whom they transferred ($N = 9$,

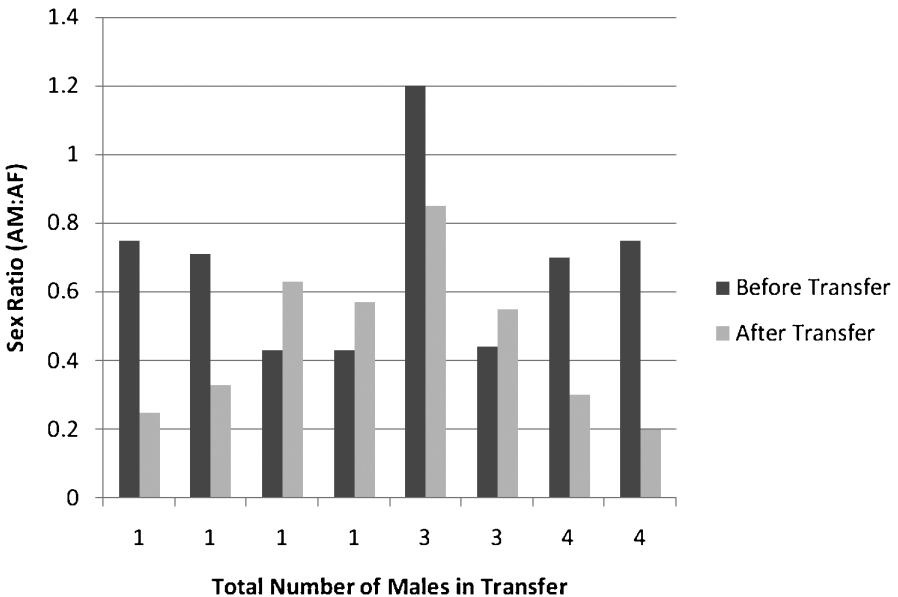


Figure 2. The AM/AF ratio in the original group and the new group for transferring males in eight cases, some involving multiple males. In five of the eight cases, the males transferred into a group with more adult females to adult males than their original group. When cases with parallel transferring males are treated independently, the tendency to move towards groups containing more adult females to adult males than the original group was not significant ($N = 8$, $Z = -1.68$, $p = 0.093$).

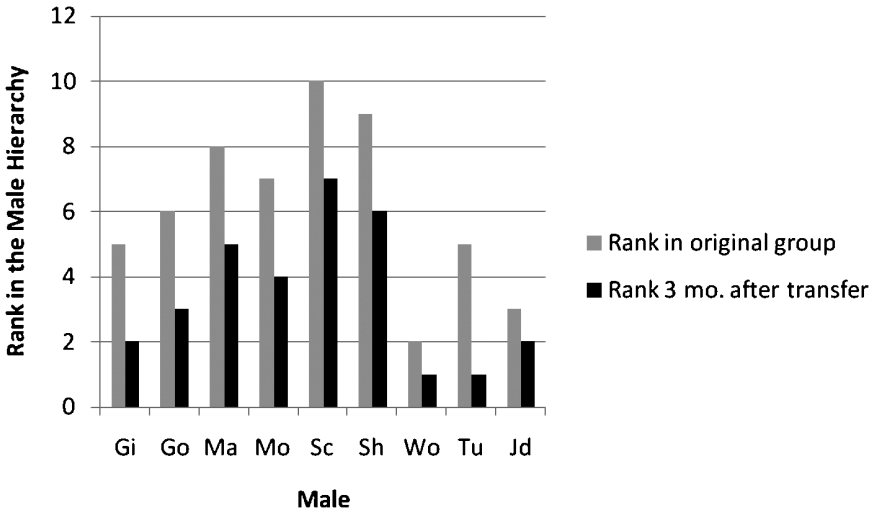


Figure 3. Dispersing males' rank in their original group compared to their new group, three months after transferring. All males improved their rank by transferring ($N = 9$, $Z = -2.754$, $p = 0.006$). All represented males transferred voluntarily, except Tu and Jd for whom data are not available.

$Z = -2.754$, $p = 0.006$; Figure 3). This improvement in rank was largely a function of there being fewer males in the new group compared to the original group. All transferring males resided with a smaller percentage of males ranking higher than themselves three months after transfer, compared to the original group ($N = 9$, $Z = 2.78$, $p = 0.005$).

3.4. Outcome of male immigration

Immigration by adult males (69.4% of cases (43/62), rate 0.03) was more common than by subadults (29.0% of cases (18/62), rate 0.03) and juveniles (1.6% (1/62), rate 0.002). Male immigrations had a range of outcomes. Most often, a resident male(s) remained in the group and new males either challenged residents and became high-ranking (15/47 cases), or did not challenge and stayed low-ranking (15/47) (Table 3). Slow takeovers after male immigration(s) also occurred frequently (14/47) whereby all the resident male(s) emigrated within several months, involuntarily or voluntarily. However, when examining the participation of a single male in a slow takeover, he could (1) challenge dominants and become high-ranking, and be actively involved in the aggression directed at resident male(s), leading to their involuntary emigration (6/47); or (2) be one of several males immigrating into

Table 3. Occurrence of different outcomes for male immigrations.

Outcome ($N = 47$)	No. of cases	Occurrence (%)	Adults (%)	Subadults/ juveniles (%)	Parallel immigration (%)
1. Immediate takeover	3	6.4	66.7	33.3*	66.7
2. Slow takeover: residents gradually emigrate, immigrant challenges and becomes high-ranking	6	12.8	50	50	100
3. Slow takeover: residents gradually emigrate, immigrant does not challenge and stays low-ranking, another immigrant male becomes alpha	8	17	62.5	37.5	100
4. Resident male(s) stay but immigrant challenges (becomes high-ranking)	15	31.9	100	0	33.3
5. Resident male(s) stay and immigrant does not challenge (stays low-ranking)	15	31.9	46.1	53.8	71.4

* Represents one older subadult male who was with an adult male that took-over a group.

the group, leading to a takeover, but not challenge dominants and stay low-ranking (8/47). Quick takeovers, where all resident male(s) emigrated within a few days, were infrequent (3/47) (Table 3). A significantly greater proportion of adult males than subadults challenged dominants and became high ranking after immigration (Fisher's exact test: $p = 0.05$) (Table 3). When the outcome was known ($N = 40$), young subadult males ($N = 4$) never challenged dominants, while 57.1% of the older subadult males (4/7) and 82.8% of adult males (24/29) challenged dominants.

For 41 males it was possible to discern whether they had entered groups alone or with other males. Parallel immigration was more frequent (70.7% of males (29/41)) than males entering groups alone (29.3% of males (12/41)). The entire process of immigration was observed for five of 12 males that entered groups alone. In two of these five cases, the single male was aided in his initial attacks on the group by male(s) that disappeared before he immigrated. Parallel immigration was more frequent for adult males (62.1% of cases, 18/29) than parallel emigration (27.3% of cases, 3/11) suggesting that males gathered allies while between groups, potentially during an AMB

phase. The opposite pattern was seen for subadult males who left groups in the company of others 72.7% of the time (8/11) but entered a new group with other males in only 34.5% of cases (10/29). There was no relationship between the tendency to challenge dominants and whether a male had entered the group alone or with others (Fisher's exact test: $p = 0.39$) (Table 3).

3.5. Resident male reactions to male immigration

Resident males resisted male immigration in all but one of the observed cases ($N = 21$ immigrations), and the frequency and intensity of aggression that a male received upon entering a group was dependent upon his age. In the first three months after immigration, juveniles and young subadult males received little aggression (none recorded in focal-samples), while older subadult males received more (low and high-intensity aggression combined: mean = 0.017/min), and adult males received the most (low and high-intensity aggression: mean = 0.044/min). This difference in aggression received between adult and subadult males was significant ($N_{\text{Adults}} = 6$, $N_{\text{Subadults}} = 5$, $Z = 2.28$, $p = 0.02$).

Of the 62 instances of male immigration in this study, at least 24 were into multi-male groups. The events surrounding these immigrations were well documented in 16 cases. When the interacting males could be recognized, chases and fights with the new male(s) were by single resident males in 88% of cases (15 of 17 encounters) and by coalitions of two resident males in 12% of cases (2/17). The alpha male was not always the primary aggressor. In WW group in 2004–2005, the 1st to 4th ranking adult males (out of 7 adult males) directed aggression at new males and the primary aggressor would often change during the days following a male immigration. In DA group, threats (stiff-legs and jump displays) between resident males and immigrants occurred at a rate of 0.45/h in the first three months after new males entered the group ($N = 9$ males) compared to 0.04/h in the absence of new males. The rate of high-intensity aggression also increased from 0.05/h to 0.11/h. In all groups (having roughly the same number of males), we observed more fresh wounds among males in the first three months after a male immigration (0.29/month), compared to times with no male immigration (0.12/month).

3.6. Male tenure

Observations of male tenure were often truncated either because observers were not present during the month when the male immigrated or emigrated

($N = 40$) or because the male(s) were still present in the study groups ($N = 9$). Mean male tenure in groups, including truncated observations, was 18.9 months ($N = 57$, range 1–>71 months, $SD = 19.1$). When only male tenures that were completely observed are included, the mean was 22.3 months ($N = 8$, range 1–58 months, $SD = 25.1$).

4. Discussion

4.1. Rank and age effects on male dispersal patterns

For *Colobus vellerosus* at BFMS, dispersal was male-biased although female dispersal also occurred (Teichroeb et al., 2009). Indeed, all males eventually left their natal group, while some females remained in their natal groups to breed (Teichroeb et al., 2009). Males transferred between groups frequently and appeared to assess other groups during BGEs and incursions before emigrating. Males often performed incursions towards a group before transferring into that group. Subadult males had more options for examining other groups and received less aggression upon entering groups than did adult males. Indeed, the function of male incursions in *C. vellerosus* appeared to vary depending on the life-stage and situation of the male(s). Incursions by non-alpha males seemed to be important in dispersal decisions. These males often approached other groups slowly, sometimes mingling with them. High-intensity aggression during incursions was usually initiated by the resident males towards the non-alpha male intruders. Younger, non-alpha males sometimes played with young individuals in the group and copulated with females during incursions. For several males, incursions increased in frequency before voluntary emigration, while this increase was not seen for males that emigrated involuntarily. These types of incursions allow non-alpha males to gauge the resistance they could encounter by immigrating to specific groups as well as the number of reproductively active females these groups include. Incursions to assess neighbours for dispersal or breeding opportunities have also been seen in many other animal species (e.g., mammals: *Otaria byronia*, Campagna et al., 1988; *Suricata suricatta*, Doolan & Macdonald, 1996; Young et al., 2007; *Colobus polykomos*, Korstjens et al., 2005; birds: reviewed in Westneat & Stewart, 2003).

Incursions by alpha males showed a different pattern. Alpha males often left their group to briefly and aggressively attack neighbouring groups,

chasing resident males and sometimes females and infants (Sicotte & MacIntosh, 2004), though a successful between-group infanticide has never been observed (Teichroeb & Sicotte, 2008a). Incursions by alpha males are consistent with the idea that these interactions work to convey information about the quality of the male, which has also been reported in mountain gorillas (*Gorilla beringei beringei*, Watts, 1994) and Thomas langurs (*Presbytis thomasi*, Steenbeek, 1999). Alpha males appear to be displaying their strength, testing the competitiveness of resident male(s), and perhaps trying to entice females to transfer to their group (Watts, 1994; Steenbeek, 1999). Indeed, in some species, males of greater quality perform more and suffer fewer incursions (e.g., mammals: *P. thomasi*, Steenbeek, 1999; birds: *Luscinia megarhychos*, Naguib et al., 2001; *Geothlypis trichas*, Pedersen et al., 2006). These encounters must necessarily be brief however, as alpha males could lose the females in their own group and put their own infants in danger if they are gone long from their group.

Rank was also an important determinant of the way in which males emigrated. Alpha males always emigrated involuntarily. Being alpha and being able to mate guard females (Teichroeb & Sicotte, 2010) gives males many reproductive opportunities and, thus, alpha males resisted leaving their group. Whether or not males have (or perceived that they have) sired infants in their group, may also affect whether alpha males stayed in their group after being deposed. When new males were successful in taking over a group, but not able to force the resident males to emigrate, former high ranking males often stayed in their resident group (e.g., *Theropithecus gelada*, Dunbar, 1984). These formerly high-ranked males frequently defended infants against intruding male(s) (Saj & Sicotte, 2005; Teichroeb & Sicotte, 2008a), although paternity is currently unknown. In Hanuman langurs (*Semnopithecus entellus*) at Ramnagar, Borries et al. (1999) found that males that were alpha when infants were sired stayed to defend those infants after new male(s) immigrated. These males defended their genetic offspring exclusively. Males that had not been present in the group during the previous mating season did not remain in the group.

Parallel emigration and immigration were frequent for *C. vellerosus* males. As with most primate species in which it has been reported (reviewed in Pusey & Packer, 1987a; Schoof et al., 2009), parallel emigration was more common for subadult males than for adult males. However, adult male *C. vellerosus* showed higher levels of parallel immigration than did subadult

males. This indicates that adult males were joining other males while between groups and that the benefits of entering groups with allies must be substantial for adult males, who receive more aggression upon entering new groups than do subadult males. Maintaining allies between transfers and creating new coalitions before immigrating probably gives males better odds of successfully entering and/or taking over a group (Pusey & Packer, 1987a; Schoof et al., 2009). Since subadult males received less aggression after entering groups compared to adult males, they may not need allies to the same extent in that context. When the process of joining other males takes time, a distinct AMB phase may be seen by researchers. For *C. vellerosus* however, AMBs do not appear to last very long or be very stable in comparison with some other primate species (e.g., *S. entellus*, Hrdy, 1977; *T. gelada*, Dunbar, 1984) because full-count censuses performed intensively for a few weeks every few years at BFMS have yet to report AMBs (Saj et al., 2005; Wong & Sicotte, 2006; Kankam et al., 2010). When AMBs have been observed ($N = 2$), their composition was quite fluid. They selected a bisexual group to attack and integrate into within the first couple of months of their existence (J.A.T., unpubl. data).

Parallel dispersal for male *C. vellerosus* often occurred with members of their age-cohort, who may have been sired by the same male. Thus, these males may have been related up to the level of half-siblings and may have gained inclusive fitness benefits by aiding one another (van Hooft, 2000). It is still unknown whether *C. vellerosus* males can maintain alliances over several migrations as has been seen in squirrel monkeys (*Saimiri sciureus*, Mitchell, 1994) and white-faced capuchins (*Cebus capucinus*, Jack & Fedigan, 2004b). Males that form coalitions in AMBs do not seem to maintain their alliances once they enter a new group and they often attempt to force one another to emigrate. Nonetheless, males that come from the same group do seem to form longer-term coalitions. Four males from the same age cohort in WW that transferred together to DA in 2004 did not direct aggression at one another and two of them were still together until 2009. In addition, the maternal brothers that transferred from B2 to RT in 2006 and the father/son dyad that transferred to DA in 2008 were not seen to direct aggression at one another and remained together for several years.

The outcome of male immigration at BFMS showed that males usually immigrated into a group and either stayed low-ranking or gained high-rank without the former resident males leaving. Slow takeovers, where all of the

resident male(s) emigrated within a few months, also occurred frequently and were always accomplished by males that transferred in parallel (Table 3). Quick takeovers, where the resident male(s) was ousted within a few days, did not occur often. Immigrant males challenged dominant males and attempted to rise in rank more often when they were adult. Whether or not males challenge dominants probably depends on an assessment of their strength relative to other males and their odds of a rise in rank. Previous research has shown that male *C. vellerosus* use display behaviours to assess one another's strength (Teichroeb & Sicotte, 2010) and new males who challenge dominants and rise in rank are also those most likely to attack infants (Teichroeb & Sicotte, 2008a).

4.2. Why do *C. vellerosus* males disperse?

All natal male *C. vellerosus* at BFMS dispersed eventually and voluntarily. The mean age of natal emigration was five years, generally occurring before males were fully adult as estimated by their body size (approx. 7 years of age). Dispersing natal males avoid mating with natal females and older females who may be related to the male. However, the inbreeding avoidance hypothesis may not be the best explanation for natal male dispersal in this population. Males lose little by mating with a relative, while female fitness can be highly affected by the costs of inbreeding depression (Parker, 1979; Waser et al., 1986). Thus, females are expected to be choosy and avoid mating with related males. The number of available mates is, therefore, likely to be lower than overall female group size within a male's natal group, and males may disperse to find more mates (Lehmann & Perrin, 2003). Natal males may also have increased their mating opportunities by dispersing since they gained higher dominance rank in their new group and tended to transfer to groups with a more beneficial sex ratio. Indeed, if *C. vellerosus* avoid breeding with their relatives, our analyses of adult male/adult female ratios in original versus new groups for transferring males would have more accurately reflected available mates if we had used adult male/unrelated adult female ratios. Nevertheless, genetic data is not yet available for this entire population. These results suggest that inbreeding avoidance might not be the main cause of natal dispersal and that the best ultimate explanation for male natal dispersal in this population is the intrasexual competition for mates hypothesis. However, since natal males always emigrated voluntarily,

intrasexual competition between males may not fully explain natal dispersal; rather female mate choice may limit a natal male's access to mates and these males may disperse to increase reproductive opportunities.

Dispersal for inbreeding avoidance may sometimes apply to adult male *C. vellerosus*, who, in certain circumstances, may emigrate to avoid mating with their maturing daughters (Cheney, 1983; Pusey & Packer, 1987a; Clutton-Brock, 1989). These situations seem rare, however. Females normally begin mating between 3 and 5 years of age in this species (J.A.T. & E.C.W., unpubl. data) and relatively few males at BFMS have tenures approaching this length (range >51–>71 months, $N = 7/58$ males, or 12.1%). Females also have the possibility of emigrating from their natal group if their father is still resident (Teichroeb et al., 2009) and approx. 77% of groups at BFMS are multi-male (Saj et al., 2005). Therefore, daughters in all likelihood have the option of mating with males other than their father, even if he is resident.

The intrasexual competition for mates hypothesis is the best explanation for secondary male dispersal at BFMS. In the majority of cases (and in all cases for alpha males), emigration was involuntary and caused by aggression from other males. Adult males received a high level of aggression upon entering new groups. Involuntary emigrations were most commonly caused by new male immigration; thus, intrasexual competition appeared to be stronger from extra-group males than from intra-group males. When the fate of males was known, many moved towards groups with a more favourable adult male/adult female ratio than their original group. They also improved their rank by transferring because there were fewer males in the new group, which likely led to an increase in breeding opportunities. These results are congruent with most primate studies which have found that male transfer can be best explained by male reproductive competition (e.g., Packer, 1979; Packer & Pusey, 1987a; Sussman, 1992; Alberts & Altmann, 1995; Borries, 2000; Korstjens, 2001; Jack, 2003; Jack & Fedigan, 2004a,b; Clarke et al., 2008). Several males in this study transferred at least three times and for most males, tenure was relatively short, indicating that *C. vellerosus* males continue to move between groups for their entire lives. This pattern has been seen in several primate species and in lions (reviewed in Jack, 2003) and is thought to be due to males continually trying to increase their reproductive success by voluntarily transferring between groups or trying to immigrate into another group after involuntary emigration.

4.3. Dispersal in a fragmented landscape

In fragmented landscapes, research has shown that dispersal may be inhibited (e.g., amphibians: Gibbs, 1998; reptiles: *Egernia cunninghami*, Stow et al., 2001; marsupials: *Lasiorhinus latifrons*, Walker et al., 2008) or dispersal distances may be longer but a smaller proportion of animals will migrate (e.g., mammals: Diffendorfer et al., 1995; birds: *Sitta europaea*, Matthysen et al., 1995). Census data of BFMS and the surrounding fragments has demonstrated that though the colobus population in the Boabeng-Fiema fragment has increased over time, in both the number of individuals and groups, the population size of the smaller fragments has remained relatively similar since 1997 (Wong & Sicotte, 2006), though some additional fragments have become populated (Kankam et al., 2010). This suggests that the Boabeng-Fiema fragment probably acts as the source population and the smaller surrounding fragments are sinks. However, we cannot rule out that some individuals born in the smaller fragments may disperse to BFMS (Wong & Sicotte, 2006), possibly due to a higher number of available mates or superior habitat quality. BFMS may consist of better habitat since it has a more complex forest structure (Kankam et al., 2010) and is less disturbed than the smaller fragments (Wong et al., 2006). Although colobus move between fragments, BFMS provides more dispersal opportunities since it contains 19 groups. Therefore, we think it is likely that the majority of the individuals in our study groups transferred to other groups in this fragment. When we knew the location of transferring males in this study, they had usually joined a neighbouring group; however this data is skewed because we did not monitor groups outside of the study area. The probability of identifying a dispersing male in a neighbouring group is, thus, higher than in a group located further away from the original group.

4.4. What do the male dispersal patterns in *C. vellerosus* tell us about their group formation?

Data from BFMS seem to indicate that group formation in *C. vellerosus* is often a function of parallel dispersal by several females (Teichroeb et al., 2009) who establish a home range and attract males. Female residency then appears to remain relatively stable (E.C.W., unpubl. data), while male residency is more fluid and changes more frequently. Solitary males or AMBs attracting females to them, a process which occurs in some primate species

(e.g., *Gorilla beringei beringei*, Sicotte, 1993; Watts, 2000; Stoinski et al., 2009; *Presbytis thomasi*, Sterck, 1997; *Trachypithecus phayrei*, Koenig & Borries, submitted) and in many bird species (Greenwood, 1980; Dobson, 1982) has never been observed in *C. vellerosus*. This lends support to the notion that male *C. vellerosus* are not responsible for establishing home ranges, though their behaviour in BGEs after a group is established can be compatible with resource defence (Sicotte & MacIntosh, 2004), as has been shown for *C. guereza* (Fashing, 2001; Harris, 2010). Once groups are established, female *C. vellerosus* show longer tenures and greater allegiance than males to their group and their range (Teichroeb et al., 2009).

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