

Female dispersal patterns in six groups of ursine colobus (*Colobus vellerosus*): infanticide avoidance is important

Julie A. Teichroeb¹), Eva C. Wikberg & Pascale Sicotte

(Department of Anthropology, University of Calgary, 2500 University Drive N.W., Calgary, Alberta, Canada T2N 1N4)

(Accepted: 21 October 2008)

Summary

Under the dispersal/foraging efficiency model, colobines are predicted to be ‘indifferent mothers’, neither facilitating philopatry for their daughters nor evicting them from the natal home range because food competition is thought to be slight. We observed six groups of *Colobus vellerosus* at the Boabeng-Fiema Monkey Sanctuary in Ghana (2000–2007) and recorded changes in female composition caused by observed ($N = 11$) and inferred ($N = 12$) emigrations and immigrations ($N = 3$). We also observed 14 immigration attempts. Most emigrating females were subadult and nulliparous. Parallel emigration was frequent. Resident females behaved aggressively to immigrating females and immigration attempts were rarely successful. Voluntary female emigration ($N = 10$) occurred mostly when male group membership was unstable or in association with the immigration of all-male bands. Involuntary emigrations ($N = 13$) associated with increased female–female aggression occurred in the two largest groups, where parous females targeted nulliparous maturing females. Larger groups tended to lose females and female immigration was successful only in the study group with the lowest number of females. Females appear to emigrate to reduce infanticide threat although feeding competition is reduced in smaller groups as well. *C. vellerosus* at BFMS are better described as ‘incomplete suppressors’.

Keywords: Colobines, female emigration, female immigration, parallel dispersal, group formation, dispersal/foraging efficiency model.

¹) Corresponding author’s e-mail address: jateichr@ucalgary.ca

Introduction

Dispersal from the natal group (or home-range) is a costly option for either sex in terms of delayed reproduction, reduced access to food resources in unfamiliar areas, loss of allies, as well as increased conspecific aggression and predation risk (Cheney & Seyfarth, 1983; Pusey, & Packer, 1987; Isbell & Van Vuren, 1996; Isbell, 2004). To offset the cost of moving to an unfamiliar area, animals can practice social dispersal without locational dispersal (site desertion) by transferring to a neighbouring social group with an overlapping home-range (Isbell & Van Vuren, 1996; Sterck, 1998). To avoid the loss of allies, individuals may practice parallel dispersal, defined as individuals emigrating with other group members or into groups with familiar individuals (Altmann, 1979; Cheney, 1983; van Hooff, 2000). Parallel dispersal can increase an individual's odds of entering a new group and overcoming the resistance of residents; it has been documented regularly in primates and often involves members of an age-cohort transferring together (e.g., *Macaca fuscata*, Sugiyama, 1976; *M. fascicularis*, van Noordwijk & van Schaik, 1985; *Lemur catta*, Sussman, 1992; *Procolobus badius temminckii*, Starin 1994; *Cebus capucinus*, Jack & Fedigan, 2004a,b; *Gorilla gorilla gorilla*, Bradley et al., 2007). Since individuals from the same group and/or members of an age-cohort may be related, parallel emigration can enable individuals to maintain contact with relatives outside of their natal group (van Hooff, 2000). Therefore, parallel dispersal may not only increase survivorship during the risky period when individuals are not residing in a bisexual group (Jack & Fedigan, 2004a,b) but it can also lead to inclusive fitness benefits (Cheney, 1983).

Though not as common as male dispersal, female dispersal in primates does occur (e.g., *Ptilocolobus spp.*, Struhsaker, 1975; Marsh, 1979; *Gorilla spp.*, Harcourt et al., 1976; Stokes et al., 2003; *Pan troglodytes*, Pusey, 1979; *Alouatta spp.*, Clarke, 1983; Crockett, 1984; *Papio hamadryas hamadryas*, Moore, 1984; *Presbytis thomasi*, Sterck, 1997; *Procolobus verus*, Korstjens & Schippers, 2003; *Colobus polykomos*, Korstjens et al., 2005; *Trachypitecus phayrei*, Borries et al., 2004), and co-occurs with either male philopatry or male dispersal. Many female dispersal species rely on a folivorous diet or live in fission-fusion societies (reviewed by: Moore, 1984), which are two factors that are thought to mitigate levels of direct food competition. Decreased contest competition for food reduces the need to cooperatively defend food resources and may lessen the need to reside with female allies

(Wrangham, 1980). Dispersal costs for females are further decreased if food is not limiting and resistance to female immigration is slight (Isbell & Van Vuren, 1996).

A recent model for the evolution of primate social systems, the 'dispersal/foraging efficiency model' put forth by Isbell (2004), suggests that female dispersal occurs whenever females are unlikely to reproduce in their natal home ranges or groups. Factors such as food competition, risk of infanticide, predation, and the probability of inbreeding can affect the chances of reproduction. Under this model, female primates can be placed into five categories depending on their basal metabolic rate, travelling mode (goal-directed or wandering), diet, behaviour towards other females, and their ability to expand their home range to allow their adult daughters to breed (Isbell, 2004). (1) Stingy mothers, where only one female reproduces in an area with minimal overlap between home ranges and little change in range boundaries (e.g., pottos, aye-ayes, callitrichids, gibbons). (2) Generous mothers, where females forage solitarily but share their home range with their reproductive daughters and home range expansion is possible (e.g., galagos, mouse lemurs). (3) Incomplete suppressors, where females live in home ranges large enough to allow other females to reproduce but only to a point, home ranges have minimal overlap and are constant in size, and targeted female aggression may lead to the emigration of other females (e.g., red howlers, some lemurs and sifakas). (4) Facilitators, where mothers allow and facilitate the reproduction of their daughters with preferential treatment leading to the development of matrilineal groups, home ranges overlap and may grow indeterminately (e.g., baboons, macaques). (5) Indifferent mothers, where females are not limited in their reproduction by food and neither force the dispersal of their daughters nor facilitate philopatry, home ranges overlap substantially and the costs of dispersal are minimal (e.g., many colobines, gorillas) (see Isbell, 2004 for references).

Dispersal allows individuals to rapidly manipulate their social situation. In a given species and population, each sex should have an optimal group composition (size and male/female ratio) to maximize their reproductive success depending on habitat characteristics (e.g., food quality and availability, inter-specific competition, predation, etc.) and the characteristics of the opposite sex group members (e.g., male quality, female reproductive state, etc.) (Pulliam & Caraco, 1984; Ridley, 1986; Strier, 2003). The effects of food competition and the risk of male takeover and infanticide should set the up-

per limit to female group size; while the lower threshold should be set by the predation pressure experienced in the habitat. In the literature, there are four hypotheses regarding the function of female dispersal from the social group that are generally investigated, each of which generates a different set of predictions (Table 1). (1) Inbreeding avoidance (Itani, 1972; Packer, 1979). High levels of inbreeding can be detrimental to lifetime reproductive success (Packer, 1979; Greenwood, 1980) and inbreeding avoidance in some species may result in strongly sex-biased dispersal patterns (Perrin & Mazalov, 1999). (2) Reduction of predation risk (Rasmussen, 1981). Animals may disperse from areas where predators are particularly active, or show net dispersal from smaller to larger groups since the latter groups presumably benefit from increased predator detection (Hamilton, 1971). (3) Reduction of food competition (Howard, 1960; Dobson, 1982). In areas of high population density or in large groups, individuals may experience higher levels of food competition resulting in voluntary emigration or eviction of the individuals with the lowest competitive ability (Dobson, 1982). This could result in net dispersal from larger to smaller groups. (4) Infanticide avoidance (Marsh, 1979; Sterck & Korstjens, 2000; Sterck et al., 2005). Dispersal patterns can reflect infanticide avoidance. For instance, females (i) can disperse with the father of their infant in the case of a male takeover (Rudran, 1973; Hrdy, 1977); (ii) can increase the survival chances of future offspring by transferring to a group with a good protector male (Marsh, 1979); or (iii) can reduce the risk of a male takeover by limiting female group size, either by dispersing themselves or evicting other females (Crockett & Janson, 2000). Bisexual groups with a larger number of females are a greater target for incoming males, showing increased rates of male takeover and infanticide (*Theropithecus gelada*, Dunbar, 1984; *Alouatta seniculus*, Crockett & Janson, 2000; *Presbytis thomasi*, Steenbeek & van Schaik, 2001; *Semnopithecus entellus*, Borries, 1997). As the number of breeding females appears to influence infanticide risk, females are expected to evict maturing, nulliparous females (Crockett, 1984; Sterck & Korstjens, 2000). The last two hypotheses are directly relevant in testing Isbell's model (Isbell, 2004).

We describe observed and inferred female emigrations, immigrations, and immigration attempts in six groups of ursine colobus (*Colobus vellerosus*) at the Boabeng-Fiema Monkey Sanctuary (BFMS) in Ghana during eight years of research. We examine the frequency of female group movements, the identity of emigrants and immigrants (e.g., age, parity, etc.), the factors leading to

Table 1. Hypotheses and predictions for female dispersal.

Prediction	Hypotheses				Supported in this study?	
	Inbreeding avoidance ^{1,2}	Predation avoidance ³	Food competition ^{4,5}	Infanticide avoidance ^{6,7,8}		
			Remaining with the father ^{9,10}	Choosing the best male ⁶	Reducing the risk of male take-over ¹¹	
1. Voluntary emigration from natal group when the breeding male(s) remains unchanged	++	-	-	-	-	N
2. No emigration when breeding male(s) change	+	-	-	-	-	N
3. Male philopatry or long male residence	++	-	-	-	-	N
4. No secondary dispersal (unless incoming male related)	++	-	-	-	-	N
5. Voluntary dispersal from smaller to larger groups	-	++	-	-	-	N
6. Female aggression to female immigrants	-	-	++	+	++	Y
7. Forced emigration of females from larger groups	-	-	++	+	++	Y
8. Male infanticide by new resident males	-	-	-	++	++	Y ¹²
9. Infanticide and infanticide attempts during between-group encounters	-	-	-	+	+	Y ¹³

Table 1. (Continued.)

Prediction	Hypotheses				Supported in this study?
	Inbreeding avoidance ^{1,2}	Predation avoidance ³	Food competition ^{4,5}	Infanticide avoidance ^{6,7,8}	
10. No dispersal with dependent infants	-	-	-	++	Y
11. Emigration with ousted sire after a takeover	-	-	-	++	N*
12. Dispersal with a dependent offspring	-	+	+	-	N
13. Movement towards groups with better protector male(s) than current group	-	+	+	++	Y†
14. Voluntary dispersal from larger to smaller groups (potentially after male immigration)	-	-	++	-	Y
15. Eviction of new breeding females from larger groups (potentially after male immigration) ⁷	-	-	+	-	Y‡

Ratings: ++, critical prediction of the hypothesis; +, consistent with the hypothesis under some conditions; -, not predicted by the hypothesis.

* In the five cases where mothers might have transferred with an ousted sire, the infant was not attacked (Teichroeb & Sicotte, 2008a).

† Immigration attempts made by females but not successful due to resident female aggression.

‡ Eviction of new breeding females but not in the context of male immigration.

References: ¹Itani (1972); ²Packer (1979); ³Rasmussen (1981); ⁴Howard (1960); ⁵Dobson (1982); ⁶Marsh (1979); ⁷Sterck & Korstjens (2000); ⁸Sterck et al. (2005); ⁹Rudran (1973); ¹⁰Hrdy (1977); ¹¹Crockett & Janson (2000); ¹²Teichroeb & Sicotte (2008a); ¹³Sicotte & MacIntosh (2004).

emigration (voluntary versus involuntary), the frequency of parallel emigration and immigration, the outcome of immigration, and residents' reactions to immigration attempts. We assess which hypothesis best explains female dispersal patterns for *C. vellerosus* at BFMS. Finally, we evaluate which category this population may correspond to according to the dispersal/foraging efficiency model (Isbell, 2004).

Methods

Study site

Research on *C. vellerosus* has been conducted at BFMS in central Ghana (7°43' N and 1°42' W) under the direction of PS since 2000. This dry semi-deciduous forest is 191.6 ha in size, located 350 m above sea level 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 at BFMS is a mosaic of primary forest, regenerating farmland (secondary forest) and woodland (Fargey, 1991; Saj et al., 2005).

Study species

Colobus vellerosus at BFMS is mainly folivorous (annual diet: 74% leaves, Saj et al., 2005) showing no birth or mating season (Teichroeb & Sicotte, 2008b). The population has been steadily increasing since hunting ceased in 1975 (Fargey, 1991; B.O. Kankam, unpublished data). Group sizes vary considerably (range 9–38, mean 15.0, $N = 15$; Wong & Sicotte, 2006) as does group composition, which is multi-male/multi-female, uni-male/multi-female, or all-male bands (AMBs) (Teichroeb et al., 2003; Saj & Sicotte, 2005). Between-group encounters are usually aggressive, with adult males as the main participants. Group males, solitary males, and males in AMBs attack bisexual groups during male incursions (Sicotte & MacIntosh, 2004). Male incursions involve direct, unprovoked attacks and harassment by male(s) from one group to another; they appear to function in allowing males to assess nearby groups, to perhaps gauge the reproductive state of the females and the resistance they may encounter in immigrating into the group. Targeted aggression towards infants occurs during both between-group encounters and male incursions (Sicotte & MacIntosh, 2004; Saj & Sicotte, 2005). Several infanticides have been observed after new males have immi-

grated, and infanticide accounts for 38.5% of infant mortality. Males that immigrate singly or in pairs usually attack infants when they become high-ranking, whereas males that immigrate as part of an AMB seem to attack infants regardless of rank (Teichroeb & Sicotte, 2008a). Putative sires aid females in infant defence if they are not evicted by incoming males (Saj & Sicotte, 2005; Teichroeb & Sicotte, 2008a,b).

Study groups and data collection

For this study, six groups of *C. vellerosus* were studied for varying amounts of time and were included in this analysis when most or all individuals could be recognized. All individuals in B2 were recognized since 2000, in RT since 2003, in OD and SP since 2006 (note: Group B2 was called B1 before the immigration of an AMB in 2001; Saj & Sicotte, 2005). We have included data from 2004 from the largest groups (DA and WW) even though only some of the females (DA, $N = 5$ of 9; WW, $N = 8$ of 11) were individually recognized because group counts during this period did not show any change in female composition. By 2006, all individuals in DA and WW could be recognized. Study duration is listed in Table 2 and group sizes and compositions are provided in Table 3.

Each study group was followed for at least one day per month (for 7–12 hours) 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 individuals. The observer moved around

Table 2. Study periods for each group.

Group	Years of study ¹	Months of study	Number of follow days
B2	2000–2007	46	290*
SP	2006–2007	6	13
RT	2003–2007	24	89
OD	2006–2007	4	12
DA	2004–2007	22	80
NP ²	2007	4	9
WW	2004–2007	21	79
Total		127	572

* Including follows by J.A.T., E.C.W., T. Saj, A. MacIntosh, S. Marteinson & L. Brent.

¹ Years of study with good individual identification so that dispersals could be recorded.

² NP group contains females that involuntarily emigrated from DA group in 2006, see text.

the group and alternated focal-samples between age-sex classes to insure that no individual was sampled more than once per hour. Ad libitum data collection was employed to record emigration and immigration events as well as other rare behaviours (Altmann, 1974). Group counts were usually obtained at least once per month.

Definitions

We report rates of observed/inferred emigrations and immigrations as number/female per year. Net female dispersal rates were calculated as immigrations–emigrations/female per year. We indicate both the observed and inferred number of emigrants in the following analyses. Observed cases were those where the researcher was present and saw the process of emigration before the individual disappeared or when an individual from one group was seen resident in another group ($N = 11$). The inferred number includes those individuals that disappeared from the study groups and were not observed again ($N = 12$). Although the inclusion of disappearances as dispersals could lead to the overestimations of dispersal events, there are no predators remaining at BFMS that could take a subadult to adult sized colobus monkey and humans do not hunt colobus at this site (Saj et al., 2005). In all of these cases of disappearance, individuals were young and/or appeared in good health.

The age of emigrating and immigrating females was sometimes known from previous contact but in most cases was estimated from the size of the individual relative to those of known age. Juvenile females (1–2 years old) were weaned and smaller than subadult females, subadult females (3–5 years old) were smaller than adult females, and adult females were those that had reached full body size (>5 years old). The parity of adult female emigrants and immigrants was sometimes known and sometimes approximated based on the presence or absence of elongated nipples.

We used the term ‘transfer’ only when we saw individuals leave one group and immigrate into another. We referred to ‘natal emigrations’ only when we knew from previous years of study that individuals were born into the groups they dispersed from. ‘Secondary emigrations’ were defined as individuals leaving a group that they previously immigrated into. We defined ‘female immigration attempts’ as females leaving their own social group and approaching another group outside of their group’s core area without chasing or attacking them. If solicitation and mating occurred with neighbouring

males before a female returned to her original group, the incidence was considered an 'extra-group copulation' and not an immigration attempt (J.A.T., unpublished data, $N = 3$). 'Voluntary emigrations' occurred when individuals dispersed without any observed increase in agonism towards them in their original group. 'Involuntary emigrations' were defined as individuals dispersing after they received increased aggression in their original group. The events that we label as 'involuntary emigrations' in this paper could be interpreted as 'group fissions' or 'female evictions'; we avoided using these terms because of uncertainty in their definitions (see Discussion). We examine all cases of emigration together (voluntary and involuntary) because the end result is the same (e.g., females leave a group) and we wanted to identify the different contexts under which these emigration events occurred (e.g., group size, male quality).

We defined 'high-intensity aggression' as instances with chases, lunges, or contact (e.g., bites, hits, slaps, and wrestling) between subjects. 'Low-intensity aggression' included threatening gestures such as stiff legs, open mouths and jump displays (sensu Oates, 1977). Aggressive events between the same dyads were considered distinct if they were separated by at least 1 h. Each new wound on an individual was counted as a separate event.

'Home range quality' (Table 6) refers to an estimation of food abundance in each home range (low, medium, or high). This was determined by measuring tree species diversity, stem density (number/ha), and the basal area (m^2/ha) of food trees in a quadrat survey covering $\geq 10\%$ of each groups range (see Teichroeb & Sicotte, in press).

Data analyses

Fisher's exact tests were used to see whether there was an age or parity difference in the proportion of females that were inferred or observed to have emigrated. Fisher's exact tests were run using the interactive tool of Preacher & Briggs (2001). All other tests were done using SPSS 16.0 or by hand. Spearman correlations were used to see whether female immigration rates, emigration rates, or net female dispersal rates correlated with mean female group size. The frequency of observed versus expected rates of female aggression preceding involuntary emigrations were analysed using chi-square tests. Significance was set at $p \leq 0.05$ and tests were two-tailed.

Results

Overall, 572 follow days were conducted for the six study groups over a differing number of study years (range 2–8 years) (Table 2). Twenty-three cases of female emigration (11 observed, 12 inferred) and three cases of immigration were recorded in six dispersal events, some of which involved multiple females (Table 4). Female dispersal in the six groups was less common than male dispersal (50 emigrations: 26 observed, 24 inferred and 40 immigrations) in the same time period. We observed two of nine maturing females breed in their natal group. Average female tenure is unknown in the study population but at least three females have been resident in a single group for more than eight years. In contrast, all males that we have observed from infancy to adulthood ($N = 10$) have emigrated from their natal group and male tenure is short (mean 15.8 months, range from 3 to at least 52 months, $N = 29$).

Female emigration patterns

Of the 23 cases of female emigration reported here, 10 were voluntary (5 observed, 5 inferred) whereas 13 were involuntary (6 observed, 7 inferred). These cases are grouped for analysis; we separate them when we describe the differences between the two types of emigrants below. Table 3 lists the age-classes of females that were observed or inferred to have emigrated and those that joined our groups during the study periods. Emigration for adult females represented 54% of observed cases and 57% including inferred cases whereas emigration for subadult females represented 45% of observed cases and 39% including inferred cases (Table 3). At the time of the emigration events, the study population consisted of 44 adult females and 14 subadult females, so 30% of available adult females and 64% of available subadult females were observed or inferred to have emigrated. Subadult females emigrated significantly more often than adult females (Fisher's exact test: $p = 0.03$). Juvenile female emigration was inferred in only one case (4%) (Table 3).

No adult females had infants when they emigrated. In 12 of 13 cases where the parity of emigrant adult females could be estimated, five appeared parous and seven appeared nulliparous (Table 4). Whether or not adult females were pregnant at the time of their emigration is unknown. At the time

Table 3. Age distribution of observed and inferred, voluntary and involuntary female dispersals at BFMS relative to group size and composition.

Group	Group composition					Female emigrants ¹			Female immigrants			
	Size	AM	AF	SAM	SAF	Juv. + Inf.	Adults	Subadults	Juveniles	Adults	Subadults	Juveniles
B2	7-17	1-6	3-4	0-4	1-2	2-3	1	1	0	2	0	1
SP	9-13	1	4	0	0	4-8	0	0	0	0	0	0
RT	8-15	1-3	5-6	0-4	1	3-5	0	0	0	0	0	0
OD	17-18	1-5	5-8	1-3	3-4	4-6	(3)	(1)	(1)	0	0	0
DA ²	21-31	3-8	9-12	1-5	2-5	4-5	5	4	0	0	0	0
WW ²	28-33	2-10	9-13	2-6	1-5	2-11	(4)	(3)	0	0	0	0
Totals							6 (7)	5 (4)	(1)	2	0	1

Abbreviations: AM, adult males; AF, adult females; SAM, subadult males; SAF, subadult females; Juv., juveniles; Inf., infants.

¹ Observed cases are not in parentheses, inferred cases (disappearances except where the fate of individual was known to be death) are.

² Some emigrations involuntary and precipitated by high-intensity female-female aggression.

of the emigration events, the study population included 38 parous adult females and 20 nulliparous adult and subadult females, of these 13% of parous females and 85% of nulliparous females were observed or inferred to have emigrated. This distribution was significantly skewed with a higher proportion of nulliparous females emigrating than parous females (Fisher's exact test: $p = 0.01$). It is certain that seven of the emigrating subadult and juvenile females were natal but the other females had not been studied long enough to determine whether or not they were emigrating from their natal group. Thus far, we have recorded only one apparent case of female secondary emigration, represented by the adult female that immigrated into B2 before leaving two months later.

Parallel emigration was observed or suspected in four of six emigration events (67%, Table 4) and overall 91% of females were thought to have emigrated with group mates (21 of 23). Of the seven cases of known natal emigration by females, one was individual (14%) while it was known or suspected that parallel emigration occurred in the remaining six cases (86%). Juvenile (100%), subadult (89%), and adult (92%) females participated in parallel emigration. Adult females dispersed with one another and with younger females (Table 4).

Voluntary female emigration

Of these 23 observed and inferred cases of female emigration, 10 cases (43%) were classified as voluntary (5 observed, 5 inferred) (Table 4, Events 1–4). Adult (50%), subadult (40%) and juvenile females (10%) emigrated voluntarily and when parity could be determined ($N = 9$), 67% were nulliparous. Voluntary emigration was known or suspected to be parallel in 80% of cases. All voluntary female emigrations occurred when new adult males were present in the group and 90% took place when the male social situation was unstable and males were challenging and evicting one another (Table 4). In this vein, 80% of voluntary female emigrations occurred in association with take-overs by AMBs (Table 4, Events 2 and 4). The first event involved a parous adult female (E1) and two subadult females (Po and Ce) that voluntarily emigrated from DA group in August 2004 after an AMB of seven males began attacking that group (Teichroeb & Sicotte, 2008a). These females ranged without a permanent male with them for several months before disappearing. In the second event, the adult male in OD group lost his alpha position after the influx of five adult males and one subadult male, which oc-

Table 4. Summary of observed and inferred voluntary and involuntary female emigration events at BFMS.

Event	Group	Age of females	Voluntary	Parallel emigration ²	Parous	Nulliparous (adults and subadults)	Group size	Group comp. ³		After AMB incursion	Male tenure ⁴	Male social situation ⁵	
								AM	AF				
1	B2	1	0	0	Y	N	?	14	6	4	0	LT, N	CH
2	DA	1	2	0	Y	Y	1	31	8	10	3	LT, N	CH
3	B2	0	1	0	Y	N	0	14	3	4	0	LT, N	NC
4	OD	3	1	1	Y	Y	2	18	6	8	5	LT, N	CH
5	WW	4	3	0	N	Y	1	33	3	13	0	LT	NC
6	DA	4	2	0	N	Y	1	25	4	12	0	LT, N	NC
Total		13	9	1			5				8		

Abbreviations: AF, adult female; SAF, subadult female; JF, juvenile female; AM, adult males; LT, long tenure males (>1 year); N, new males (<1 year); CH, challenge period, relationships unstable, male evictions occurring, aggression between males most days; NC, non-challenge, relationships stable, little aggression between males (equivalent to categories in Teichroeb & Sicotte, 2008b).

¹ Observed and suspected parallel emigration.

² Adult group composition at time of emigration event, including emigrating adults.

³ Tenure of within-group males at time of emigration event.

⁴ Within-group male social situation at time of emigration event.

curred in the absence of observers (August 2006–April 2007). When ECW returned to the site, two parous adult females, one nulliparous adult female, one subadult female and one juvenile female had disappeared (Table 4). None of these females have been seen in any of the neighbouring groups encountered in 2007.

Involuntary female emigrations

Emigration was considered involuntary for 57% (13/23) of females in this study (Events 5 and 6, Table 4). Increased female–female agonism in the two largest groups (WW and DA) apparently caused the emigration of eight adult and five subadult females. The females from DA formed a new group (NP) while the fate of the WW females is unknown.

In WW group, females were the main opponents in five out of 15 observed cases of high-intensity aggression during the 2006 observation period. Two of these cases involved three or more females. The rate of high-intensity aggression among females (0.081/h) was elevated during this period (compared with a rate of 0.000/h for the same time period in 2005) and wounds among females were frequent (0.097 wounds/month compared with 0.000 wounds/month in 2005). The identity of aggressors and the victims was not always clear but when ECW returned to the study groups in May 2007, one parous adult female, three nulliparous adult females and three subadult females had disappeared from WW group (two adult males and a subadult male were also missing). These individuals were not found in any of the nine neighbouring groups.

In May 2007, a new group (NP) was found ranging east of DA group containing former DA individuals (4 adult females (1 parous and 3 nulliparous), 2 subadult females (one of them the known daughter of the parous female), and the former alpha male of DA group). DA group remained in the west part of the range and contained the remaining individuals (8 adult females (6 parous), 2 subadult females, 3 subordinate males and the juveniles).

During the 2006 field season (May–August), intense female–female aggression was observed between the DA females during the 19 observation days that this group was followed (at a rate of 0.211/h). In total, 34 instances of high-intensity aggression were observed and 22 of these cases involved female–female opponents. Most of these aggressions were dyadic, but five cases involved three or more females. The rate of wounding for females during this period was 0.153 wounds/month, compared to 0.000 wounds/month in DA during the same time period in 2005. For cases of high-intensity ag-

gression where the identity of the aggressor versus the recipient was known, the frequency of aggression given by the females who stayed in DA group versus those that emigrated (later NP group females) did not differ from expected values ($N_{DA} = 12$, $N_{NP} = 8$, $\chi^2 = 1.818$, $DF = 1$, $p > 0.05$). In contrast, there was a difference in the number of high-intensity aggressive acts received by the females that emigrated vs. those that stayed in DA group; the former received more high-intensity aggression than expected ($N_{DA} = 4$, $N_{NP} = 12$, $\chi^2 = 6.349$, $DF = 1$, $p = 0.012$).

The females that were aggressed or that eventually emigrated were adult (62%) and subadult (38%); however, the majority was nulliparous (85%, 11/13). Parallel emigration occurred for the DA females and was suspected for the WW females (Table 4).

Emigration and site fidelity

Home range overlap is extensive for *C. vellerosus* at BFMS (Teichroeb & Sicotte, in press). Six emigrating females (NP group) formed a group in the same home range as their former group but none of the other females who were observed or inferred to have emigrated ($N = 17$) could be found in any neighbouring groups, suggesting that they may have dispersed from their entire home range (although not necessarily from their entire social group as the level of parallel emigration indicates). However, in six of these cases (35%) we did not know the surrounding groups or their home ranges well enough to say whether females had indeed dispersed out of their former home range.

Outcome of female immigration and immigration attempts

Only one successful female immigration event has been observed at BFMS, although at least two others have occurred (in Group B2). Saj (2005) observed no female–female aggression when an adult female followed members of an AMB into group B2 and stayed for approximately two months before disappearing. Another adult female (Rx) and juvenile female (Op) immigrated into B2 in the absence of observers sometime between September 2003 and June 2004. Thus, female immigration may have been parallel in 66.6% of cases, although we do not know the origin of females Rx and Op. B2 had the smallest female group size in this study and was the only group to show successful female immigration (Figures 1 and 2).

Nonetheless, several cases of female immigration attempts were observed in 2004–2007 (14 cases, involving at least seven adult females and three subadult females, Table 5). Nine of these cases involved the same subadult female from B2 (female Br) trying to enter two neighbouring groups (Cases 4–12, Table 5). In all but one instance, resident female aggression was observed towards the female(s) attempting the transfer (high-intensity in 71% of attempts and low-intensity in 21%; Table 5). In Cases 1 and 3 (Table 5), when three females were trying to enter a group together, they received high-intensity aggression from resident females.

When we knew the composition of the original group that female(s) attempting immigration came from ($N = 3$, Table 6), there did not seem to be any consistent pattern for targeted groups to have a lower or higher male/female ratio or a smaller group size. Similarly, target groups did not show a larger or better quality home range. However, males in target groups did win a greater proportion of between-group encounters with the original group and perform a greater number of male incursions towards them (Table 6).

Effect of group size on female dispersal patterns

B2 had the smallest female group size in this study and was the only group to show successful female immigration, whereas larger groups lost more females (Figure 1). Despite this, immigration rates ($N = 6$, $r_s = -0.66$, $p = 0.16$) and emigration rates ($N = 6$, $r_s = 0.58$, $p = 0.23$) were not significantly correlated with mean female group size. There was a trend for net female dispersal rate (immigrations–emigrations/female/year) and mean female group size to be negatively correlated however ($N = 6$, $r_s = -0.75$, $p = 0.08$) (Figure 2).

Discussion

Dispersal patterns in *C. vellerosus* appear to be similar to those seen in other black-and-white colobus species, showing mostly male and occasional female dispersal (*C. satanas*, Oates, 1994; Fleury & Gautier-Hion, 1999; *C. guereza*, Fashing, 2001; *C. polykomos*, Dasilva, 1989; Korstjens et al., 2005). Here, we report the process and outcome of female emigration, immigration, and apparent immigration attempts in six groups over several years of research. Observed and inferred emigrations for females occurred more often

Table 5. Description of unsuccessful female immigration attempts observed at BFM5.

Case	Female(s)	Original group	Target group	Level of aggression	Description of events
1	8/04	3 AFs	?	2	9:04 — 3 unknown AFs (with 3 all-male band males) approach DA, a coalition of 4 DA AFs chase and physically attack (slapping and biting) the new females until they leave the group.
2	11/04	AF (El) and SAF (Po)	DA	2	10:09 — Females El and Po (with a SAM) approach WW to 50 m, displaying. 11:07 — An AM from WW approaches them and grooms Po. 11:08 — A WW AF approaches and chases Po but is chased away by El. The WW males stay with El and Po for approx. 3 hours. El and Po do not approach WW again.
3	11/04	AF (El) and 2 SAFs (Po and Ce)	DA	2	6:10 — El, Po, and Ce approach WW to 80 m. 9:00 — WW AF Cr moves to 50 m and displays. 10:31 — WW AF Kw and an AM chase El and Po back. The WW AM stays with El and Po while Kw rests between them and WW for 2.5 hours. 13:10 — El and Po approach WW again. 2 AMs approach displaying, so they flee.
4	2/05	SAF (Br)	B2	2	7:44 — During a BGE, Br leaves B2 and approaches RT, 2 RT AFs (Po and Bl) chase her back to B2.
5	2/05	SAF (Br) and AF (Sf)	B2	1	16:34 — RT approaches and displaces B2 but female Br stays in a tree above RT. 16:59 — Receptive B2 AF Sf moves back to Br and B2 AM Lo follows. 17:05 — Sf approaches RT, Lo follows to 1 m. 17:22 — Sf again approaches RT, but Lo follows to 1 m. 17:24 — The RT AFs and B2 AFs display at one another. RT AM St just stares at the B2 females with an erect penis. 17:41 — Sf and Br move closer to RT, Lo follows to 1 m of Sf. 18:00 — RT AFs and infants move to a sleeping tree. 18:10 — Lo and Sf return to B2. 18:12 — RT AM St moves to the sleeping tree. 18:16 — It is dark and Br had not returned to B2.
6	2/05	SAF (Br)	B2	1	6:50 — Br approaches RT beginning a BGE, 2 RT AFs and AM St approach. 7:12 — RT AF Bl displays at Br. 7:48 — Other individuals are displaying and chasing one another. 7:58 — 2 B2 SAMs (Gi and Li) approach Br and Gi grooms her. 8:32 — The groups move apart.

Table 5. (Continued.)

Case	Date	Female(s)	Original group	Target group	Level of aggression	Description of events
7	2/05	SAF (Br)	B2	RT	2	6:48 — Br approaches RT beginning a BGE, RT AFs Tr and Po display. 6:51 — Tr chases Br back. 6:53 — A B2 SAM approaches and Tr flees. 6:55 — Br approaches RT, Tr chases her back. 7:31 — The groups move apart.
8	3/05	SAF (Br)	B2	RT	2	6:29 — Br approaches RT beginning a BGE, one RT AF chases her back. 6:34 — 2 more RT AFs approach, watching. 6:42 — Br moves back to B2.
9	3/05	SAF (Br)	B2	RT	1	7:00 — Br and 3 other B2 individuals have moved towards RT. RT AFs Po and BI lead the group over towards B2, displaying at them. 7:16 — The B2 females move away.
10	3/05	SAF (Br)	B2	FO	2	7:30 — B2 receives an incursion from 2 AMs from FO group. 9:46 — The 2 FO males are chased by 2 B2 males and Br follows them towards FO. 9:56 — Br is chased back to B2 by 2 FO AFs and an AM.
11	3/05	SAF (Br)	B2	RT	2	6:18 — Br approaches RT beginning a BGE, RT AFs BI and Po chase her back to B2.
12	4/05	SAF (Br)	B2	RT	0	6:40 — Br is found on the edge of B2 with Hu, a SAM from RT. The rest of RT approaches and there is displaying between the males of the two groups. 6:55 — Br moves back to B2.
13	4/05	1 AF	B2	RT	2	8:46 — A B2 AF moves towards RT, 2 RT AFs and SAM Hu chase her back.
14	6/07	2 AF	VG	OD	2	8:20 — 2 VG AFs approach OD group. 9:03 — 2 AF from OD chase the VG females away. 9:13 — The same 2 VG AFs approach the OD AFs again and are chased off again. 9:54 — The VG AFs enter a tree where one OD AF is resting. The females display. 10:25 — At least 2 AF and 2 SAF from OD chase the VG AFs away.

Abbreviations: AF, adult female; SAF, subadult female; SAM, subadult male; AM, adult male; BGE, between-group encounter. Levels of ♀-♀ aggression: 0, no aggression observed; 1, threats (aggressive stiff legs, open mouths and/or jump displays) observed; 2, chases and/or contact aggression observed.

Table 6. Comparison of the original vs. the target group for females during immigration attempts.

Case	Group	Group size	AM:AF	HR size (ha)	HR quality	Rate of MIs performed against one another (number/day) ¹	Rate of BGEs won against one another (%) ²
1	? DA	? 26	? 3:10	? 12.8	? Low	? ?	? ?
2–3	<i>DA</i> WW	<i>30</i> 31	<i>4:10</i> 7:10	<i>15.8</i> 14	<i>Low</i> Medium	<i>0.02 (N = 1)</i> 0.15 (N = 9)	<i>29 (N = 7)</i> 71 (N = 7)
4–12	<i>B2</i> RT	<i>16</i> 13	<i>3:4</i> 1:5	<i>12.8</i> 6.8	<i>Medium</i> Medium	<i>0.06 (N = 6)</i> 0.13 (N = 12)	<i>0 (N = 8)</i> 100 (N = 8)
13	<i>B2</i> RT	<i>16</i> 13	<i>3:4</i> 1:5	<i>12.8</i> 6.8	<i>Medium</i> Medium	<i>0.06 (N = 6)</i> 0.13 (N = 12)	<i>0 (N = 8)</i> 100 (N = 8)
14	<i>VG</i> OD	? 18	? 5:5	? ?	? ?	? ?	? ?

Case numbers refer to those in Table 5. Data for the original group are in italics, data for the target group are in boldface. Home range (HR) quality measurements are based on tree species diversity, stem density and basal area (see Teichroeb & Sicotte, in press).

¹The number of male incursions (MIs) (where male(s) from one group approach the other group and direct aggression and/or displays at them) performed per day against the other group that year.

²The percentage of decided between-group encounters (BGEs) that were won when the two groups met that year. WW and DA had 30 BGEs but only 7 were decided. RT and B2 had 23 BGEs but only 8 were decided.

than immigration in the study groups and females sometimes resisted female immigration. Parallel dispersal was relatively common for females of all age ranges. This indicates that even when dispersing, females can maintain contact with familiar and/or related females (van Hooff, 2000; Bradley et al., 2007). It is unknown at this time whether relatedness affected the occurrence of parallel dispersal for females. Female entry into new groups may be facilitated if they have established allies (Cheney, 1983). However, resistance to potential immigrants appeared more intense when greater numbers of females were trying to enter a new group (Table 5, Cases 1–3). It is, thus, likely that when large groups of females emigrate together, they must form their own group in order to remain together. For example, several days after the first event listed in Table 5, where three adult females failed to enter DA group due to female resistance, a new group (SP) with three adult females

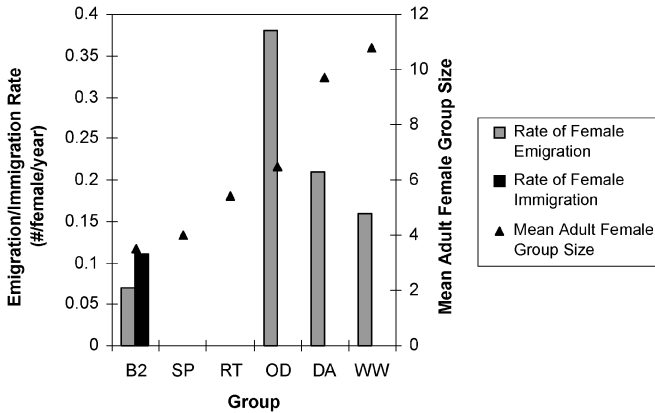


Figure 1. Female emigration and immigration rates (#/female/year) according to mean adult female group size. For this figure observed and inferred emigrations are displayed together. Immigration rates ($N = 6$, $r_s = -0.66$, $p = 0.16$) and emigration rates ($N = 6$, $r_s = 0.58$, $p = 0.23$) were not significantly correlated with mean female group size.

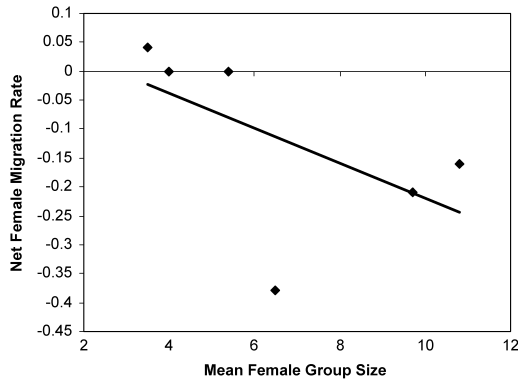


Figure 2. Scatter plot with trend-line for the net female dispersal rate (immigrations–emigrations/female/year) in relation to mean adult female group size. For this figure observed and inferred dispersals are displayed together. The net female dispersal rate was not significantly negatively correlated with mean female group size ($N = 6$, $r_s = -0.75$, $p = 0.08$).

and two adult males was noticed immediately east of DA’s range (J.A.T., personal obs.). These may have been the same females from the immigration attempt. SP group has remained in that range since then and the females have given birth. Thus, new *C. vellerosus* groups may form quickly when several females emigrate together and attract males to reside with them. This process makes it likely that females in newly formed groups are related or at least familiar with each other.

Involuntary female dispersal for C. vellerosus: group fissions or female evictions?

Struhsaker & Leland (1988) defined group fission as the permanent separation of members of a social group into two or more new social groups. However, much more is known about the group fissions of female resident cercopithecines, which tend to split along matriline, than is known for female dispersal species (Nsubuga et al., 2008). In female resident species, fission events involve a progressive increase in the frequency of subgroup formation before these subgroups discontinue coalescing (e.g., *Macaca sinica*, Dittus, 1988; *Papio cynocephalus*, Van Horn et al., 2007). Sometimes the frequency of aggression between females increases before fissions (e.g., *M. fuscata*, Oi, 1988; *M. sylvanus*, Prud'Homme, 1991; *Lemur catta*, Hood & Jolly, 1995; Ichino, 2006) and other times it does not (e.g., *M. fuscata*, Sugiyama, 1960; *M. mulatta*, Malik et al., 1985). Many group fission events take months or up to several years to be finalized. There are fewer fission events described for female dispersal species. In the Asian colobines, the two fission events observed have been interpreted as being induced by male–male rather than female–female aggression (*Presbytis johnii*, Hohmann, 1987; *P. rubicunda*, Davies, 1987). The only group fission in the literature for a black-and-white colobus species (*C. guereza*) reports subgrouping but does not provide information on the level of aggression prior to the fission or which sex was involved (Dunbar & Dunbar, 1974). On the other hand, female eviction in primates is relatively rare but has been reported mostly for female dispersal species (*Eulemur rubriventer*, *Lemur catta*, *Propithecus verreauxi*, *P. tattersalli*, *Alouatta palliata*, *A. seniculus*, reviewed in Sterck & Korstjens, 2000; *Hylobates muelleri*, *H. klossii*, reviewed in Leighton, 1987). It usually involves increased female aggression against a single female before she leaves the group, but targeted aggression towards dyads and small cohorts of females has been seen in lemurs. Targeted attacks were interpreted as a way to alleviate resource competition, either by evicting the female(s) and/or interrupting their reproduction (Vick & Pereira, 1989).

Researchers have labelled events as either 'group fission' or 'female eviction' in the literature but rarely provide definitive definitions of these two processes. As this study on a female dispersal species with parallel dispersal shows, the number of females emigrating cannot be used to differentiate between these two categories, as we observed up to five females voluntarily emigrate in one group and six involuntarily emigrate in another. The cri-

teria defining 'group fission' and 'female eviction' need to be thought out, for instance: (1) the role of female aggression towards the female(s) that are leaving (necessary for eviction but perhaps not fission); (2) males emigrating with the female(s) (necessary for fission but perhaps not eviction); (3) relatedness of the females that leave (common in fission but not necessarily with eviction); (4) formation of a new group by the emigrating females (necessary for fission but perhaps not eviction). All of these criteria show grey zones where either female eviction or group fission could apply. The results that we present for *C. vellerosus* at BFMS, showing varying numbers of females leaving groups (voluntarily and involuntarily) challenge the notion that we are dealing with a simple dichotomy (female eviction versus group fission). Thus, for the moment, we think it best to use strictly descriptive terms ('voluntary' and 'involuntary' emigration) to define these events.

Why do C. vellerosus females disperse?

Inbreeding avoidance is not sufficient to explain natal female dispersal patterns for *C. vellerosus* at BFMS (Table 1) because male immigration and emigrations are common and male tenure is relatively short in this population. In fact, the seven confirmed cases of natal female emigration at BFMS occurred after the resident males had recently changed in these groups (Table 4, Events 2–6).

The predation risk hypothesis is not supported by this data either (Table 1). Predation risk is usually assumed to be decreased in larger groups (Alexander, 1974), so if females were dispersing to avoid predation we should see a higher rate of emigration from smaller groups compared with larger groups. This is the opposite trend to what was observed for *C. vellerosus* females at BFMS. Female emigration occurred primarily from large groups, while the only group where females successfully immigrated had the smallest number of females (B2, Figure 1). This is similar to data from gorillas (*Gorilla beringei beringei*: Watts, 1990; *G. g. gorilla*: Stokes et al., 2003) showing that females tend to transfer towards smaller groups. The predation pressure at BFMS has been low in recent decades. It may, thus, not be necessary for females to live in large groups for predation defence. However, it is unclear how flexible anti-predator strategies such as living in large groups are and how rapidly they respond to a changing environment (but see Bshary, 2001).

There are several lines of evidence in this study that support the infanticide avoidance hypothesis for female dispersal. First, parous females dis-

persed. In several species, parous female dispersal, particularly secondary female dispersal, has been thought to indicate mate choice (*G. b. beringei*, Harcourt et al., 1976; Watts, 1989; Sicotte, 2001; *Procolobus rufomitratu*s, Marsh, 1979; *Presbytis thomasi*, Sterck, 1997; Steenbeek, 2000; Sterck et al., 2005). In addition, female *C. vellerosus* were never seen to disperse when they had a dependent infant. Females trying to avoid infanticide should time their dispersals so that they do not have dependent offspring (Sicotte, 1993) and they should choose to move to a group where the chances of producing surviving offspring are greater (Sterck et al., 2005). The risk of infanticide is high in this population and male defence of infants has been observed (Saj & Sicotte, 2005; Teichroeb & Sicotte, 2008a). As such, females should choose groups that are not a target for new males (e.g., smaller female groups), or choose groups with high-quality resident males that have the potential to protect their infants. Females in this study did emigrate more often from larger female groups (whether voluntarily or involuntarily) and only the smallest female group showed female immigration.

Strong males in their prime are likely to reduce the level of male immigration, which directly decreases the rate of infanticide in *C. vellerosus* (Teichroeb & Sicotte, 2008a). High-quality resident males may also contribute to food defence in black-and-white colobus (Emlin & Oring, 1977; Fashing, 2001; Sicotte & MacIntosh, 2004; Harris, 2006), which would be an added benefit for females. The evidence for females attempting to choose certain males in our data comes from the female immigration attempts (Table 5). Although the data are limited, attraction to these groups did not seem to be due to the size or quality of the home range, a smaller group size, or a certain male/female ratio (Table 6). This is unlike female mountain gorillas (*G. b. beringei*), which prefer multi-male groups and along with red howlers (*A. seniculus*), prefer groups with a small number of females because both these features decrease the threat of infanticide (Robbins, 1995; Watts, 2000; Crockett & Janson, 2000). Infanticide in *C. vellerosus* groups occurs relatively equally in multi-male and single-male groups and while larger female groups may be a bigger target for incoming males, good quality resident males can resist the immigration of new males (Teichroeb & Sicotte, 2008a). For *C. vellerosus*, it appears that the overall quality of the male(s) is important to females, rather than the absolute number of males. As is shown in Table 6, groups that females targeted for immigration were those where the males won more intergroup encounters against the females' original group and performed more male incursions towards them. Thus, the attraction to

these groups seems to rely on the quality of the male(s) and their success in these contests in comparison with the male(s) in the original group. The fact that these immigration attempts were unsuccessful due to female resistance suggests that free female choice of groups and/or males in this population is limited.

Further support for the infanticide avoidance hypothesis comes from that fact that most voluntary female emigration in this study (90%) was seen when the current male membership of the group was unstable and male–male aggression was frequent (Table 4, Events 1–4). In two of these cases (Events 2 and 4) eight females emigrated in association with the incursion of AMBs. These observations suggest that females leave groups that are a target for new male immigration or where male dominance relations are undecided. Perhaps quick takeovers with a decided alpha male inform females of male quality immediately (e.g., the takeover described in Sicotte et al., 2007), whereas long drawn-out takeovers by an AMB which may continue for months with many rank changes and male aggression, inform females that the males are low-quality or not yet fully mature (J.A.T., personal obs.). It may be risky from an infanticide standpoint to stay and breed in a group with weak males.

In the cases of involuntary female emigration reported here, the parous adult females seemed to be targeting the nulliparous adult and subadult females. According to the infanticide avoidance hypothesis, adult females are predicted to evict maturing females (Table 1) when there is competition for breeding positions within the group (Crockett, 1984; Sterck & Korstjens, 2000).

There is weaker and overlapping evidence in this study for the food competition hypothesis (Table 1). *Colobus vellerosus* at BFMS are predominantly folivorous and do not show contest competition for food (Saj & Sicotte, 2007). They do however show scramble competition for food (Saj & Sicotte, 2007; Teichroeb & Sicotte, in press). Larger groups show greater home range size, day range length and percent of time spent feeding (Teichroeb & Sicotte, in press). Thus, females may benefit by residing in smaller groups because they travel less and devote less time to feeding. Food competition is, therefore, a potential explanation for female *C. vellerosus* attempting to keep group size small by emigrating from larger groups, forcing the dispersal of other females from these groups, and resisting female immigration. The groups that showed involuntary emigrations in this study (DA and WW) were the largest of our study groups and DA occupied the lowest quality home range of four study groups for which this information is

known (RT, B2, DA and WW) (Teichroeb & Sicotte, in press). It is, therefore, possible that females are forced to emigrate when levels of within-group scramble competition became too costly (e.g., van Schaik, 1989; Sterck et al., 1997) and females can no longer increase day range or time spent feeding to compensate. The food competition hypothesis could also explain why parous adult females tended to target nulliparous maturing females in the cases of involuntary emigration. If females want to decrease group size due to increasing scramble competition, younger, smaller females may simply be easier targets for larger, older females. Indeed, the maturation of daughters has been suggested as mechanism increasing food competition in toque macaques (Dittus, 1988).

The evidence in this study lends more support to the infanticide avoidance rather than the food competition hypothesis for female dispersal. It makes sense that infanticide would be a more immediate and pressing threat to females' reproductive success than the effects of scramble competition. However, since several of the predictions for these two hypotheses overlap (Table 1), females would benefit in both ways from keeping female group size small.

Isbell's dispersal/foraging efficiency model

Within the dispersal/foraging efficiency model for primate social organization (Isbell, 2004), colobines are suggested to be 'indifferent mothers' when they have no contest competition for food. This means that mothers should neither force the dispersal of their daughters nor facilitate philopatry because food abundance should not be as limiting for highly folivorous primates as other factors such as time, predation, or infanticide. *Colobus vellerosus* females at BFMS are rather behaving like the 'incomplete suppressors' described by Isbell (2004). First, females disperse when their chances of reproducing are poor (e.g., due to infanticide threat). Second, females show targeted aggression towards mostly nulliparous females, thereby decreasing female group size. Korstjens et al. (2005) suggested that the closely related *C. polykomos* in the Tai Forest should also be categorized as 'incomplete suppressors' partly due to increased aggression observed towards three young females before they emigrated. Third, females cannot transfer readily between groups because of female resistance to new female immigrants. Finally, it may be impossible for some *C. vellerosus* groups to increase their home ranges sufficiently to allow the reproduction of additional females. Home range size increases with group size in this population (Teichroeb &

Sicotte, in press) but there is probably an upper limit for home range expansion due to the presence of neighbouring groups. Each of our study groups has four or five neighbouring groups and intrusion in other groups' home ranges often leads to aggressive between-group encounters (Sicotte & MacIntosh, 2004; J.A.T. and E.C.W., unpublished data). The population at BFMS has increased rapidly during the last two decades (Wong & Sicotte, 2006; B.O. Kankam, unpublished data), and a higher population density may lead to a lack of available habitat for home range expansion.

There are however, two ways that *C. vellerosus* differs from the predictions for 'incomplete suppressors' (Isbell, 2004). First, their home ranges overlap significantly (Teichroeb & Sicotte, in press) and second, females do not compete aggressively over food but rather they are subject to scramble competition (Saj & Sicotte, 2007; Teichroeb & Sicotte, in press). Perhaps in its next inception, the dispersal/foraging efficiency model will have to consider female–female aggression over breeding positions in the group rather than just aggression over food as an additional characteristic of 'incomplete suppressors'.

Conclusions

Female *C. vellerosus* at BFMS appear to be showing competition-conditional dispersal patterns (Isbell & Van Vuren, 1996). The infanticide avoidance hypothesis is well supported by their dispersal patterns. However, the food competition hypothesis also cannot be ruled out. Females appear to utilize different strategies to reduce infanticide risk and food competition. First, they attempt to keep female group size small through forced female emigration and resistance to female immigration. This strategy likely reduces the risk of male takeovers and the effects of scramble competition. Second, females voluntarily emigrate from groups with unstable male dominance hierarchies or those that are a target for new males. Finally, females attempt to immigrate into groups with higher-quality male(s) than their own. However, free mate choice is limited because female resistance to female immigration often counters these attempts. Female *C. vellerosus* at BFMS conform to the predictions for 'incomplete suppressors' rather than 'indifferent mothers' (Isbell, 2004), as they appear to disperse when their chances of successfully reproducing in their current group are low, they show targeted aggression to other females, and the opportunities for home range expansion are likely limited.

Acknowledgements

We would like to thank Kathy Jack and Lynne Isbell for inviting our submission to this special issue of *Behaviour*. Permission to conduct this research was given by the Ghana Wildlife Division and the management committee of the Boabeng-Fiema Monkey Sanctuary. NSERC, the University of Calgary, Alberta Ingenuity, and the Province of Alberta granted funding. Lauren Brent, Rachel Boratto, Robert Koranteng, Kwame Duodo, Kwaku Amponsah, Johanna Hedlund, Danica Stark, and Lucy Anderson provided research assistance. Tania Saj, Andrew MacIntosh, Sarah Marteinson and Lauren Brent provided contributions to the database on dispersals and immigrations at BFMS. Comments from Kathy Jack, Lynne Isbell and one anonymous reviewer improved the quality of this manuscript. Data collection methods complied with the rules of the University of Calgary's Animal Care Committee and with the laws of Ghana.

References

- Alexander, R.D. (1974). The evolution of social behaviour. — *Annu. Rev. Ecol. Syst.* 5: 352-382.
- Altmann, J. (1974). Observational study of behaviour: sampling methods. — *Behaviour* 49: 227-267.
- Altmann, J. (1979). Age cohorts as paternal sibships. — *Behav. Ecol. Sociobiol.* 6: 161-164.
- Borries, C. (1997). Infanticide in seasonally breeding multilex groups of Hanuman langurs (*Presbytis entellus*) in Ramnagar (South Nepal). — *Behav. Ecol. Sociobiol.* 41: 139-150.
- Borries, C., Larney, E., Derby, A.M. & Koenig, A. (2004). Temporary absence and dispersal in Phayre's leaf monkeys (*Trachypithecus phayrei*). — *Folia Primatol.* 75: 27-30.
- Bradley, B.J., Doran-Sheehy, D.M. & Vigilant, L. (2007). Potential for female kin associations in wild western gorillas despite female dispersal. — *Proc. Roy. Soc. Lond. B Biol.* 274: 2179-2185.
- Bshary, R. (2001). Diana monkeys, *Cercopithecus diana*, adjust their anti-predator behaviour to human hunting strategies. — *Behav. Ecol. Sociobiol.* 50: 251-256.
- Cheney, D.L. (1983). Proximate and ultimate factors related to the distribution of male migration. — In: *Primate social relationships* (Hinde, R.A., ed.). Blackwell Scientific, Oxford, p. 241-249.
- Cheney, D.L. & Seyfarth, R.M. (1983). Nonrandom dispersal in free-ranging vervet monkeys: social and genetic consequences. — *Am. Nat.* 122: 392-412.
- Clarke, M.R. (1983). Infant-killing and infant disappearance following male takeovers in a group of free-ranging howling monkeys (*Alouatta palliata*). — *Am. J. Primatol.* 5: 241-247.
- Crockett, C.M. (1984). Emigration by female red howler monkeys and the case for female competition. — In: *Female primates: studies by women primatologists* (Small, M.F., ed.). Alan R. Liss, New York, NY, p. 159-173.
- Crockett, C.M. & Janson, C.H. (2000). Infanticide in red howlers: female group size, group composition, and a possible link to folivory. — In: *Infanticide by males and its implications* (van Schaik, C.P. & Janson, C.H., eds). Cambridge University Press, Cambridge, p. 75-89.
- Dasilva, G.L. (1989). The ecology of the western black-and-white colobus (*Colobus polykomos polykomos* Zimmerman 1780) on a riverine island in southeastern Sierra Leone. — PhD Dissertation, University of Oxford, Oxford.

- Davies, A.G. (1987). Adult male replacement and group formation in *Presbytis rubicunda*. — *Folia Primatol.* 49: 111-114.
- Dittus, W.P.J. (1988). Group fission among wild toque macaques as a consequence of female resource competition and environmental stress. — *Anim. Behav.* 36: 1626-1645.
- Dobson, F.S. (1982). Competition for mates and predominant juvenile dispersal in mammals. — *Anim. Behav.* 30: 1183-1192.
- Dunbar, R.I.M. (1984). Reproductive decisions: an economic analysis of gelada baboon social strategies. Princeton University Press, Princeton, NJ.
- Dunbar, R.I.M. & Dunbar, E.P. (1974). Ecology and population density of *Colobus guereza* in Ethiopia. — *Folia Primatol.* 21: 188-208.
- Emlen, S.T. & Oring, L.W. (1977). Ecology, sexual selection, and the evolution of mating systems. — *Science* 197: 215-223.
- Fargey, P.J. (1991). Assessment of the conservation status of the Boabeng-Fiema Monkey sanctuary. — Final report to the flora and fauna preservation society. University of Science and Technology, Kumasi.
- Fashing, P.J. (2001). Male and female strategies during intergroup encounters in guerezas (*Colobus guereza*): evidence for resource defense mediated through males and a comparison with other primates. — *Behav. Ecol. Sociobiol.* 50: 219-230.
- Fleury, M.C. & Gautier-Hion, A. (1999). Seminomadic ranging in a population of black colobus (*Colobus satanas*) in Gabon and its ecological correlates. — *Int. J. Primatol.* 20: 491-509.
- Greenwood, P.J. (1980). Mating systems, philopatry and dispersal in birds and mammals. — *Anim. Behav.* 28: 1140-1162.
- Hamilton, W.D. (1971). Geometry of the selfish herd. — *J. Theor. Biol.* 31: 295-311.
- Harcourt, A., Stewart, H.K.S. & Fossey, D. (1976). Male emigration and female transfer in wild mountain gorilla. — *Nature* 263: 226-227.
- Harris, T.R. (2006). Between-group contest competition for food in a highly folivorous population of black and white colobus monkeys (*Colobus guereza*). — *Behav. Ecol. Sociobiol.* 61: 317-329.
- Hohmann, G. (1989). Group fission in Nilgiri langurs (*Presbytis johnii*). — *Int. J. Primatol.* 10: 441-454.
- Hood, L.C. & Jolly, A. (1995). Troop fission in female *Lemur catta* at Berenty Reserve, Madagascar. — *Int. J. Primatol.* 16: 997-1015.
- van Hooff, J.A.R.A.M. (2000). Relationships among non-human primate males: a deductive framework. — In: *Primate males: causes and consequences of variation in group composition* (Kappeler, P.M., ed.). Cambridge University Press, Cambridge, p. 183-191.
- Howard, W.E. (1960). Innate and environmental dispersal of individual vertebrates. — *Am. Mid. Nat.* 63: 152-161.
- Hrdy, S.B. (1977). The langurs of Abu — Female and male strategies of reproduction. — Harvard University Press, Cambridge, MA.
- Ichino, S. (2006). Troop fission in wild ring-tailed lemurs (*Lemur catta*) at Berenty, Madagascar. — *Am. J. Primatol.* 68: 97-102.
- Isbell, L.A. (2004). Is there no place like home? Ecological bases of female dispersal and philopatry and their consequences for the formation of kin groups. — In: *Kinship and behavior in primates* (Chapais, B. & Berman, C.M., eds). Oxford University Press, New York, NY, p. 71-108.
- Isbell, L.A. & Van Vuren, D. (1996). Differential costs of locational and social dispersal and their consequences for female group-living primates. — *Behaviour* 133: 1-36.

- Itani, J. (1972). A preliminary essay on the relationship between social organization and incest avoidance in nonhuman primates. — In: Primate socialization (Poirier, F.E., ed.). Random House, New York, NY, p. 165-171.
- Jack, K.M. & Fedigan, L.M. (2004a). Male dispersal patterns in white-faced capuchins (*Cebus capucinus*). Part 1: patterns and causes of natal emigration. — *Anim. Behav.* 67: 761-769.
- Jack, K.M. & Fedigan, L.M. (2004b). Male dispersal in white-faced capuchins, *Cebus capucinus*. Part 2: patterns and causes of secondary dispersal. — *Anim. Behav.* 67: 771-782.
- Korstjens, A.H., Nijssen, E.C. & Noë, R. (2005). Intergroup relationships in western black-and-white colobus, *Colobus polykomos polykomos*. — *Int. J. Primatol.* 26: 1267-1289.
- Korstjens, A.H. & Schippers, E.P. (2003). Dispersal patterns among olive colobus in Tai National Park. — *Int. J. Primatol.* 24: 515-539.
- Leighton, D.R. (1987). Gibbons: territoriality and monogamy. — In: Primate societies (Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W. & Struhsaker, T.T., eds). University of Chicago Press, Chicago, IL, p. 135-145.
- Malik, I., Seth, P.K. & Southwick, C.H. (1985). Group fission in free-ranging rhesus monkeys of Tughlaqabad, Northern India. — *Int. J. Primatol.* 6: 411-422.
- Marsh, C.W. (1979). Female transference and mate choice among Tana River red colobus. — *Nature* 281: 568-569.
- Moore, J. (1984). Female transfer in primates. — *Int. J. Primatol.* 5: 537-589.
- van Noordwijk, M.A. & van Schaik, C.P. (1985). Male migration and rank acquisition in wild long-tailed macaques (*Macaca fascicularis*). — *Anim. Behav.* 33: 849-861.
- Nsubuga, A.M., Robbins, M.M., Boesch, C. & Vigilant, L. (2008). Patterns of paternity and group fission in wild multimale mountain gorilla groups. — *Am. J. Phys. Anth.* 135: 263-274.
- Oates, J.F. (1977). The social life of a black-and-white colobus monkey, *Colobus guereza*. — *Z. Tierpsychol.* 45: 1-60.
- Oates, J.F. (1994). The natural history of African colobines. — In: Colobine monkeys: their ecology, behaviour and evolution (Davies, A.G. & Oates, J.F., eds). Cambridge University Press, Cambridge, p. 75-128.
- Oi, T. (1988). Socioecological study on the troop fission of wild Japanese monkeys (*Macaca fuscata yakui*) on Yakushima Island. — *Primates* 29: 1-19.
- Packer, C. (1979). Intertroop transfer and inbreeding avoidance in *Papio anubis*. — *Anim. Behav.* 27: 1-36.
- Perrin, N. & Mazalov, V. (1999). Dispersal and inbreeding avoidance. — *Am. Nat.* 154: 282-292.
- Preacher, K.J. & Briggs, N.E. (2001). Calculation for Fisher's exact test: an interactive calculation tool for Fisher's exact probability test for 2 × 2 tables [computer software]. — Available online at <http://www.quantpsy.org>
- Prud'Homme, J. (1991). Group fission in a semi-free ranging population of Barbary macaques (*Macaca sylvanus*). — *Primates* 32: 9-22.
- Pulliam, H.R. & Caraco, T. (1984). Living in groups: is there an optimal group size? — In: Behavioural ecology (Krebs, J.R. & Davies, N., eds). Sinauer, Sunderland, MA, p. 122-147.
- Pusey, A.E. (1979). Intercommunity transfer of chimpanzees in Gombe National Park. — In: The great apes (Hamburg, D.A. & McCown, E.R., eds). Benjamin/Cummings, Menlo Park, CA, p. 465-479.

- Pusey, A.E. & Packer, C. (1987). Dispersal and philopatry. — In: Primate societies (Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W. & Struhsaker, T.T., eds). University of Chicago Press, Chicago, IL, p. 250-266.
- Rasmussen, D.R. (1981). Communities of baboon troops (*Papio cynocephalus*) in Mikumi National Park, Tanzania. — *Folia Primatol.* 36: 232-242.
- Ridley, M. (1986). The number of males in a primate troop. — *Anim. Behav.* 34: 1848-1858.
- Robbins, M. (1995). A demographic analysis of male life history and social structure of mountain gorillas. — *Behaviour* 132: 21-47.
- Rudran, R. (1973). Adult male replacement in one-male troops of purple-faced langurs (*Presbytis senex senex*) and its effect on population structure. — *Folia Primatol.* 19: 166-192.
- Saj, T.L. (2005). Ecological influences on the social organization of *Colobus vellerosus* at Boabeng-Fiema, Ghana. — PhD thesis, University of Calgary, Calgary, AB.
- Saj, T.L. & Sicotte, P. (2005). Male takeover in *Colobus vellerosus* at Boabeng-Fiema Monkey sanctuary, central Ghana. — *Primates* 46: 211-214.
- Saj, T.L. & Sicotte, P. (2007). Scramble competition among *Colobus vellerosus* at Boabeng-Fiema, Ghana. — *Int. J. Primatol.* 28: 337-355.
- Saj, T.L., Teichroeb, J.A. & Sicotte, P. (2005). The population status of the ursine colobus (*Colobus vellerosus*) at Boabeng-Fiema, Ghana. — In: Special topics in primatology, Vol. 4: Commensalism and conflict: the human primate interface (Paterson, J.D. & Wallis, J., eds). American Society of Primatologists, Norman, OK, p. 350-375.
- van Schaik, C.P. (1989). The ecology of social relationships amongst female primates. — In: Comparative socioecology: the behavioural ecology of humans and other mammals (Standen, V. & Foley, R.A., eds). Blackwell Scientific, Oxford, p. 195-218.
- Sicotte, P. (1993). Inter-group encounters and female transfer in mountain gorillas: influence of group composition and male behaviour. — *Am. J. Primatol.* 30: 21-36.
- Sicotte P. (2001). Female mate choice in mountain gorillas. — In: Mountain gorillas: three decades of research at Karisoke (Robbins, M.M., Sicotte, P. & Stewart, K.J., eds). Cambridge University Press, New York, NY, p. 59-87.
- Sicotte, P. & MacIntosh, A.J. (2004). Inter-group encounters and male incursions in *Colobus vellerosus* in central Ghana. — *Behaviour* 141: 533-553.
- Sicotte, P., Teichroeb, J.A. & Saj, T.L. (2007). Aspects of male competition in *Colobus vellerosus*: preliminary data on male and female loud-calling and infant deaths following a take-over. — *Int. J. Primatol.* 28: 627-636.
- Starin, E.D. (1994). Philopatry and affiliation among red colobus. — *Behaviour* 130: 253-270.
- Steenbeek, R. (2000). Infanticide by males and female choice in wild Thomas langurs. — In: Infanticide by males and its implications (van Schaik, C.P. & Janson, C.H., eds). Cambridge University Press, Cambridge, p. 153-177.
- Steenbeek, R. & van Schaik, C.P. (2001). Competition and group size in Thomas's langurs (*Presbytis thomasi*): the folivore paradox revisited. — *Behav. Ecol. Sociobiol.* 49: 100-110.
- Sterck, E.H.M. (1997). Determinants of female dispersal in Thomas langurs. — *Am. J. Primatol.* 42: 179-198.
- Sterck, E.H.M. (1998). Female dispersal, social organization, and infanticide in langurs: are they linked to human disturbance? — *Am. J. Primatol.* 44: 235-254.
- Sterck, E.H.M. & Korstjens, A.H. (2000). Female dispersal and infanticide avoidance in primates. — In: Infanticide by males and its implications (van Schaik, C.P. & Janson, C.H., eds). Cambridge University Press, Cambridge, p. 293-321.

- Sterck, E.H.M., Watts, D.P. & van Schaik, C.P. (1997). The evolution of female social relationships in nonhuman primates. — *Behav. Ecol. Sociobiol.* 41: 291-309.
- Sterck, E.H.M., Willems, E.P., van Hooff, J.A.R.A.M. & Wich, S.A. (2005). Female dispersal, inbreeding avoidance and mate choice in Thomas langurs (*Presbytis thomasi*). — *Behaviour* 142: 854-868.
- Stokes, E.J., Parnell, R.J. & Olejniczak, C. (2003). Female dispersal and reproductive success in wild western lowland gorillas (*Gorilla gorilla gorilla*). — *Behav. Ecol. Sociobiol.* 54: 329-339.
- Strier, K.B. (2003). Demography and the temporal scale of sexual selection. — In: *Sexual selection and reproductive competition in primates: new perspectives and directions* (Jones, C.B., ed.). American Society of Primatologists, Norman, OK, p. 45-64.
- Struhsaker, T.T. (1975). The red colobus monkey. — Chicago University Press, Chicago, IL.
- Struhsaker, T.T. & Leland, L. (1988). Group fission in red-tailed monkeys (*Cercopithecus ascanius*) in the Kibale forest, Uganda. — In: *A primate radiation: evolutionary biology of the African guenons* (Gautier-Hion, A., Bourliere, F., Gautier, J.P. & Kingdon, J., eds). Cambridge University Press, Cambridge, p. 363-388.
- Sugiyama, Y. (1960). On the division of a natural troop of Japanese monkeys at Takasakiyama. — *Primates* 2: 109-148.
- Sugiyama, Y. (1976). Life history of male Japanese monkeys. — *Adv. St. Behav.* 7: 255-284.
- Sussman, R.W. (1992). Male life history and intergroup mobility among ring-tailed lemurs (*Lemur catta*). — *Int. J. Primatol.* 13: 395-413.
- Teichroeb, J.A., Saj, T.L., Paterson, J.D. & Sicotte, P. (2003). Effect of group size on activity budgets in ursine colobus (*Colobus vellerosus*) in Ghana. — *Int. J. Primatol.* 24: 743-758.
- Teichroeb, J.A. & Sicotte, P. (2008a). Infanticide in ursine colobus monkeys (*Colobus vellerosus*): new cases and a test of the existing hypotheses. — *Behaviour* 145: 727-755.
- Teichroeb, J.A. & Sicotte, P. (2008b). Social correlates of fecal testosterone in male ursine colobus monkeys (*Colobus vellerosus*): the effect of male reproductive competition in aseasonal breeders. — *Horm. Behav.* 54: 417-423.
- Teichroeb, J.A. & Sicotte, P. (in press). Test of the ecological constraints model in ursine colobus monkeys (*Colobus vellerosus*) in Ghana. — *Am. J. Primatol.*
- Van Horn, R.C., Buchan, J.C., Altmann, J. & Alberts, S.C. (2007). Divided destinies: group choice by female savannah baboons during social group fission. — *Behav. Ecol. Sociobiol.* 61: 1823-1837.
- Vick, L.G. & Pereira, M.E. (1989). Episodic targeting aggression and the histories of Lemur social groups. — *Behav. Ecol. Sociobiol.* 25: 3-12.
- Watts, D.P. (1989). Infanticide in mountain gorillas: new cases and a reconsideration of the evidence. — *Ethology* 81: 1-18.
- Watts, D.P. (1990). Ecology of gorillas and its relation to female transfer in mountain gorillas. — *Int. J. Primatol.* 11: 21-45.
- Watts, D.P. (2000). Causes and consequences of variation in male mountain gorilla life histories and group membership. — In: *Primate males* (Kappeler, P.M., ed.). Cambridge University Press, Cambridge, p. 169-179.
- Wong, S.N.P. & Sicotte, P. (2006). Population size and density of *Colobus vellerosus* at the Boabeng-Fiema Monkey Sanctuary and surrounding forest fragments in Ghana. — *Am. J. Primatol.* 68: 465-476.
- Wrangham, R.W. (1980). An ecological model of female-bonded primate groups. — *Behaviour* 75: 262-299.