



Social and environmental factors influencing natal dispersal in blue monkeys, *Cercopithecus mitis stuhlmanni*

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We evaluated four factors that may influence the process of male natal dispersal in wild female-philopatric blue monkeys: aggressive eviction by adults, attraction to oestrous females, social integration in the natal group and survivorship risk. Observations of nine males and five females of dispersal age allowed us to compare the social behaviour of males and females and that of dispersing and nondispersing males. We also studied the circumstances of 26 natal dispersals (1997–2006). Aggressive eviction did not appear to be important in most dispersals. We found no significant differences in rates or types of aggression received by juvenile females and males or by dispersing and nondispersing males. Sexual attraction also did not appear to influence dispersal, because males did not disperse more often than expected by chance during conception seasons or during breeding-season influxes of males. Our results confirm low social integration as a correlate of sex-biased dispersal. Juvenile males groomed and sat in contact with groupmates significantly less than females did, although we found few differences between dispersing and nondispersing males. Our results also suggest that males timed dispersals to minimize risks, because dispersal was most likely to occur during months of low rainfall and least likely to occur when fruit was least available. Endogenous factors are probably important in stimulating dispersal, because all males disperse but females never do. Although aggressive eviction may occasionally influence the dispersal process in blue monkeys, given their unimale group structure, our results implicate social integration much more uniformly and strongly.

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Natal dispersal is a fundamental aspect of a species' life history. It may involve dramatic changes for individual animals and has a large impact on the demographic structure, genetics, conservation and management of a population (e.g. Hamilton & May 1977; Melnick 1981; Melnick & Pearl 1987; Van Vuren 1998). A large literature has developed on ultimate reasons for natal dispersal in mammals, which is generally thought to promote inbreeding avoidance and increase access to mates (e.g. Lidicker 1962; Greenwood 1980; Pusey & Packer 1987; Moore 1993). Proximate factors that influence natal dispersal have received less theoretical and empirical attention. For social animals, dispersal is risky: it usually

involves moving through unfamiliar terrain where the location of food sources and predators are unknown and where a temporary decline in access to mates and social partners, increased exposure to potentially aggressive conspecifics and large energy expenditures may result (Cheney & Seyfarth 1983; Dunbar 1987; Crockett & Pope 1993; Alberts & Altmann 1995a; Isbell & Van Vuren 1996; Payne et al. 2003; but see Printes & Strier 1999). Proximate factors driving dispersal must be strong enough to overcome these immediate costs, some of which are probably perceived by dispersers. Proximate factors that have been identified as driving or influencing natal dispersal include attaining sufficient body size or body fat (Belding's ground squirrels, *Spermophilus beldingi*: Holekamp 1986; Nunes et al. 1998), eviction as a result of aggression (lions, *Panthera leo*: Schaller 1972; elephants, *Loxodonta africana*: Douglas-Hamilton & Douglas-Hamilton 1975), food shortage (spotted hyaenas, *Crocuta crocuta*: Frank 1986a, b; snowshoe hares, *Lepus americanus*: Boutin et al.

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1985) and weakening of social bonds (canids: Bekoff 1977; Harris & White 1992).

Primates are particularly well suited for investigating the proximate factors influencing natal dispersal, given the long period of juvenility that characterizes their life history and the diverse social systems in which they live. Among primates, patterns of natal dispersal vary greatly among species. Males disperse in some species, females disperse in others, and in some cases both sexes disperse (Pusey & Packer 1987; Strier 1994). Previous studies on primates have suggested three main proximate factors that stimulate natal dispersal: (1) intragroup aggression (Rudran 1978; Crockett & Pope 1993; Rajpurohit & Sommer 1993; but see Pusey & Packer 1987; Alberts 1992; Smith 1992; Alberts & Altmann 1995a, 2001; Olupot & Waser 2001), (2) sexual attraction to females outside the natal group (Enomoto 1974; Sugiyama 1976; Packer 1979; Pusey 1980; Cheney & Seyfarth 1983; Smith 1992; Kuester & Paul 1999; Olupot & Waser 2001) and (3) a socially disadvantageous situation in the natal group, which may include low dominance rank (Cheney 1978; Colvin 1983; but see Kuester & Paul 1999), weak social relationships with natal group members (Cheney 1978; Henzi & Lucas 1980; Silk et al. 1981; Colvin 1983; Nikolei & Borries 1997), a poor relationship with the mother (Colvin 1983), or the death of the dispersing animal's mother (Cheney et al. 1981; Alberts & Altmann 1995a).

Only one of the above studies (Rajpurohit & Sommer 1993) focused on dispersal in primates living in one-male groups. It appears, however, that for males there is a major difference between natal dispersal in one-male versus multimale social systems. While dispersers from multimale groups usually move directly from the natal group into another heterosexual group, those living in one-male groups usually spend a relatively long period alone or in all-male groups before re-establishing themselves as residents in a group with females (Rudran 1978; Cheney 1983; Cheney & Seyfarth 1983; Pusey & Packer 1987; Alberts & Altmann 1995a, 2001; Kuester & Paul

1999; Cords 2000a; Levréro et al. 2006). This difference in dispersal behaviour could affect the proximate factors influencing natal emigration. Sexual attraction, for example, may be more important in species whose males move directly into new groups. In contrast, aggressive eviction may be more important in species with a one-male group structure, if male–male intolerance maintains this social structure and extends to maturing natal subadults. To evaluate these ideas, further study is needed of factors influencing the dispersal process in species living in one-male groups.

We focused our study on one such species, the blue monkey, in which adolescent males always disperse but females never do. We used a combination of behavioural data collected over 2.5 months on dispersing individuals and age-matched controls, along with records of dispersals collected over 9 years, to study the dispersal process and identify proximate factors that influence natal emigration. In particular, we considered the influence of received aggression, changing adult male membership, attraction to oestrous females outside the natal group, strength of social ties within the natal group and environmental risk factors related to food abundance, thermoregulation and body mass (Table 1).

METHODS

Study Population

We conducted our study at the Isecheno research site in the Kakamega Forest, Kenya (0°19'N, 34°52'E, elevation 1650 m), the eastern-most remnant (85 km²; Lung 2004) of the Guineo-Congolese rainforest that spans central equatorial Africa. The forest receives about 2000 mm of rain annually, and rain is seasonally variable (Fashing et al. 2004; BIOTA: <http://www.dlr.de/biota-east/biota/data.htm>). The study site supports a high density of primates: blue monkeys live at a density of approximately 170–220 individuals/km² (Fashing & Cords 2000). Up to four

Table 1. Factors influencing the dispersal process in blue monkeys

Factors	Observations supporting a factor's importance
Received aggression, especially from adult males	Juvenile males receive more frequent and/or more severe agonistic behaviour than juvenile females Dispersing males receive more frequent and/or more severe agonistic behaviour than nondispersing males Dispersals are more likely to occur during periods of changing male membership
Attraction to oestrous females	Males disperse more often during the conception season when more females are in oestrous Juvenile males have fewer mating opportunities in the natal group than outside the natal group Juvenile males in smaller natal groups have more sexual stimuli outside the group than males in larger natal groups, motivating males in smaller natal groups to disperse at an earlier age
Strength of social ties within the natal group	Juvenile males spend less time engaged in active social behaviour than females Dispersing males spend less time engaged in active social behaviour than nondispersing males Males with stronger social ties stay in their natal group longer Orphaned males disperse at a younger age than nonorphaned males
Environmental risk factors	Males that stay in their natal group suffer greater risks than males that disperse Males favour dispersing when fruit is most abundant Males disperse only when they are full grown Males favour dispersing when the climate is most favourable

social groups have been studied since 1979 (Cords 2002a). At the time of our study, there were three neighbouring study groups, ranging in size from 33 to 65 individuals (10–23 adult females). The largest group included three adult males during the period of our observations, while the other two groups included only one adult male each, the modal pattern for the species. Close matrilineal kinship relations (mother–offspring, sisters, aunts, cousins) were identified from long-term pedigree records. It is possible that some true aunts and cousins were not included as our subjects' kin because kinship between a few of the older females was unknown.

Subjects

Prior study indicated that male blue monkeys emigrate from their natal group between the ages of 5.9 and 8.1 years (M. Cords, unpublished data; see Results), so this study focused on natal nonreproductive individuals between 5 and 8 years old. There were 14 focal subjects representing all juveniles in this age range in the three study groups. All groups were well habituated to human observers, and individual animals were identified by natural characteristics. Juvenile sex ratios in two of the groups, TW and GS, were even, but in group GN there was a male skew of 5:1, resulting in a subject pool of nine males and five females.

Behavioural Data Collection

Observations were made by L.S.E. from 25 June to 1 September 2004. Data were collected during approximately 0730–1700 hours, with a break at about 1200–1300 hours on most days. We conducted focal animal samples, generally lasting 40 min, with instantaneous activity records at 20-s intervals (Martin & Bateson 1993). Focal samples were aborted if the subject was out of sight for 10 min or if heavy rain affected visibility. Aborted samples were included in the data analysis.

Because of the limited visibility in a forest habitat, we chose focal subjects opportunistically with certain constraints. We avoided sampling any individual that was within 3 m of the previous focal subject unless 10 min had elapsed between samples. We did not sample any individual more than once per day, and we tried to keep total sampling time equal across individuals.

Instantaneous activity records included resting, moving (walking, running or climbing), feeding (reaching for, chewing or holding a food item), or socializing (grooming or being in physical contact). In addition to activity, the focal subject's location within the group was scored as either central, peripheral or uncertain. Peripheral subjects had no more than one groupmate within a 180-degree, two-dimensional arc around their position; otherwise, they were scored as central. In some cases, poor visibility forced us to score the subject's position as uncertain.

To document proximity relations of focal subjects to other group members, we used point samples to record the identities of all animals that were sitting in contact with (but not grooming) the subject, less than 1 m away (but not in contact) and 1–3 m away. As an alternative to the

centre/periphery measure of general social integration, we also recorded the number of groupmates that were within 10 m as more than two or less than two. Individuals that were more than 3 m away were not individually identified. Location within the group is considered to be an important factor in determining food competition and predation risk in other group-living primates (Cheney et al. 1981; Hall & Fedigan 1997; Cowlshaw 1999), although it may be less important for Kakamega blue monkeys, because group members are usually widely dispersed and groups often have no obvious front or back.

Social behaviour was recorded in different ways. We recorded the identity of grooming partners for each point sample and the initiator of each grooming exchange (who either first solicited grooming, or first offered unsolicited grooming) on the first point sample for that exchange. We recorded all occurrences of approaches to within 1 m (defined here as distinct from approach–retreat interactions, below) and agonistic behaviour. Agonistic behaviour included both aggressive forms, such as attacks, chases and threats, and nonaggressive forms, such as spontaneous submissive vocalizations and approach–retreat interactions (when one animal moved away within 5 s of its partner moving closer).

Definitions

Of the nine male focal subjects, three dispersed (all from one group, GN) within 1 month after our study ended: one dispersed directly and one dispersed gradually into a neighbouring multimale study group (TW), and the third initially dispersed to an unknown location (although he also joined the TW group 3 months after leaving his natal group). These males were defined as dispersing males. We collected behavioural data on these males during the 2.5–3 months preceding their dispersal, so our definition of dispersing males corresponds closely to the 100-day cutoff used by Smuts (1985) and Alberts (1992) in their studies of baboons. The other six juvenile male subjects were classified as nondispersing males. Two of these males disappeared gradually (presumably dispersed, see below) from their natal group in January 2005, 4 months after our behavioural sampling had ended, both to unknown locations.

Periods of change in adult male membership in a group occurred for up to 2 months after a new male established residence in a group and during influxes of nonresident males, usually during the conception season or during group take-overs (Cords 2000b, 2002b). Influxes were defined as periods when nonresident males were observed in the group on more than 50% of observation days (Cords 2002b).

The gestation period for blue monkeys averages 176 days, with 95% of pregnancies lasting 162–190 days (Pazol et al. 2002). We therefore defined the conception season for each group in a given year as taking place during the fifth and sixth months before each birth within the group. If there were births in consecutive months, we defined the conception season as lasting from 6 months before the first birth to 5 months before the last birth.

Data from Past Dispersals

M.C. and assistants monitored the three study groups almost daily during 1997–2006. These records provided the input data for dispersals and the circumstances in which they occurred. During this period, 26 juvenile males disappeared from their natal group. We considered all of these disappearances to be dispersal events, for several reasons. First, we had no directly contradictory evidence. Second, mortality in juvenile female peers is very low (Chowdhury 2004; M. Cords, unpublished data), and there was no reason to expect higher intrinsic mortality among juvenile males. In addition, no juvenile had injuries or signs of illness immediately before disappearing. Thirteen of the 26 individuals that disappeared from their natal groups were resighted by our team in subsequent months and years. Of the remaining 13 individuals in our sample, seven were observed to be present in the group intermittently for weeks or months (typically 1–5 weeks) before their disappearance: such intermittent presence was never observed among females, although it did occur in seven of nine young males whose dispersal was confirmed by resighting, and for whom attendance records were sufficiently dense prior to disappearance to evaluate a potential change. Thus, intermittent presence prior to disappearance provides indirect evidence that males dispersed, even though they were not resighted outside the natal group. To be conservative, we repeated our analysis of all 26 males for the subset of 13 verified plus seven supported dispersals. We refer to these 20 cases as the subset of most-confident dispersals.

We used records of all observed agonistic behaviour to create annual dominance hierarchies with the program Matman (Noldus Information Technology, Wageningen, The Netherlands; de Vries 1998). Only dyadic agonistic behaviour with a single individual giving submissive signals was included in the construction of hierarchies, all of which were statistically linear. Each juvenile was assigned a numerical rank signifying the proportion of older juveniles (at least 6 years old) and adult females that ranked lower. This ranking system standardizes for group size and gives a fairly even distribution of ranks between 0 and 1.

Fruit Availability

To assess seasonal variation in fruit availability, we used data from an earlier study by Pazol (2001) of the same study groups. Pazol used vegetation plots (to measure basal area density) and monthly plant phenology samples to construct a food availability index for each home range that included all tree species comprising at least 1.5% of the annual diet (Pazol 2001). While year-to-year variation in plant production is well known in Afro-tropical forests, making extrapolation from one year to the next potentially problematical, three other studies that examined seasonal variation in plant food abundance for Kakamega primates found similar seasonal patterns (Cords 1986; Fashing 1999; Gathua 2000).

Data Analysis

For behavioural elements recorded on each point (activity, location within the group and all measures of proximity to other animals), we report percentages of total point samples. For types of behaviour scored with all occurrences (approaches and agonistic behaviour), we report rates.

In comparing observed versus expected rates of behaviour for particular partner combinations, we calculated expected rates as the probability of the specific behaviour category times the fraction of natal group members in the specific partner class.

Our analysis of agonistic behaviour separated the rate of winning from the rate of losing. For decided agonistic interactions, where one and only one animal showed a submissive response such as fleeing, cowering or vocalizing submissively, we designated that animal as the loser, and its partner as winner.

Our comparisons of males and females always involved nine male subjects and five females. We also compared three dispersing and six nondispersing males. All statistical tests were two tailed.

RESULTS

Our 207 focal samples spanned 105.6 h, with a mean \pm SE total sampling time per individual of 6.6 ± 0.6 h. From January 1998 to February 2006, 26 natal dispersals were recorded in the study population. The mean \pm SE age of the 26 dispersing animals was 7.25 ± 0.59 years (range 5.92–8.08, median = 7.1; subset of 20 most-confident dispersals: 7.37 ± 0.57 years, range 6.08–8.08, median = 7.45). When dispersals occurred gradually over the course of several weeks or months, we defined dispersal age as the age when the animal was last seen in the natal group. Gradual dispersal, with intermittent presence in the natal group for a period of typically 1–5 weeks before final departure, was a common pattern: 14 of 16 males in our total sample dispersed gradually (for 10 males, observations were not sufficiently dense for us to judge).

Agonistic Behaviour

In encounters with all opponents, there were no differences between juvenile males and females in rates of agonistic or aggressive interactions (attacks, chases and threats) that were won or lost, although rates of interaction were more variable among males than among females (Table 2). In encounters with adult males, who would be most likely to evict juvenile males, there were also no differences between juvenile males and females in rates of agonistic or aggressive interactions that were won or lost. Only two of the nine juvenile males were observed receiving aggression from an adult male, and they received aggression only after harassing an adult male that was copulating.

Dispersing and nondispersing males did not differ in any type of agonistic interaction with all group members

Table 2. Agonistic behaviour of dispersal-age males ($N = 9$) and age-matched females ($N = 5$)

Behaviour*	Males (mean, range)	Females (mean, range)	Mann–Whitney U	
			U	P
Agonistic encounters won against				
All opponents	0.64 (0–1.63)	0.23 (0–0.54)	29	≤ 0.44
Adult males	0.16 (0–1.14)	0.00 (0–0)	27.5	≤ 0.52
Agonistic encounters lost against				
All opponents	1.20 (0.13–2.94)	0.49 (0–1.22)	32	≤ 0.24
Adult males	0.43 (0–0.98)	0.11 (0–0.54)	35	≤ 0.11
Aggression won against				
All opponents	0.31 (0–1.14)	0.07 (0–0.36)	30	≤ 0.36
Adult males	0.16 (0–1.14)	0.00 (0–0)	27.5	≤ 0.52
Aggression lost against				
All opponents	0.16 (0–0.98)	0.13 (0–0.36)	23.5	≤ 0.90
Adult males	0.09 (0–0.65)	0.00 (0–0)	27.5	≤ 0.52

*Number per hour.

or with adult males. Compared to nondispersing males, however, dispersing males spent significantly less time within 1–3 m of adult males ($\bar{X} \pm \text{SE}$ percentage of time: dispersing males: $0 \pm 0\%$; nondispersing males: $2.3 \pm 1.0\%$; Mann–Whitney U test: $U = 16.5$, $N_1 = 3$, $N_2 = 6$, $P \leq 0.05$). In fact, none of the three dispersing males was ever observed within 3 m of an adult male. These results suggest that dispersing males may have been avoiding adult males, although dispersing males also spent significantly less time than nondispersing males within 1–3 m of any group member ($\bar{X} \pm \text{SE}$ percentage of time: dispersing males: $15.0 \pm 1.2\%$; nondispersing males: $25.5 \pm 5.1\%$, Mann–Whitney U test: $U = 18$, $N_1 = 3$, $N_2 = 6$, $P \leq 0.02$).

Juvenile male rank also did not appear to influence age at dispersal. For the 23 dispersing males for whom data on agonistic behaviour were available, there was no significant correlation between dominance rank and age at dispersal (Spearman rank correlation: $r_s = 0.31$, $P \leq 0.14$). We obtained the same results for the 18 individuals in the most-confident subset for whom data on agonistic behaviour were available ($r_s = 0.24$, $P \leq 0.33$).

Change in Adult Male Membership

Dispersal records indicated that group members did not disperse during periods of change in adult male membership more often than expected by chance (5 of 26 dispersals: binomial probability = 0.27, $P \leq 0.74$; 4 of 20 most-confident dispersals: binomial probability = 0.27, $P \leq 0.66$). Notably, however, three of the five dispersals that took place during such a period occurred within 1 month of a particular male, PH, establishing residence (in GN). This male actually entered the group twice, first for one month in December 2003 (after which he was deposed by the former resident male, who made a temporary comeback), and again for a period of more than 2 years, starting in late March 2004. The three young males who dispersed did so within the first month of one residence period or the other. Overall, juvenile dispersal was

more likely to occur during the three initial months of this male's residence (one in December 2003, two in April–May 2004) than expected by chance, given that males disperse in a 26-month window between the ages of 5.92 and 8.08 years (3 of 7 dispersals: binomial probability = 0.12, $P \leq 0.005$). Furthermore, juvenile males of dispersal age were more likely to disperse when PH became resident (3 of 7 juvenile males dispersed) than during periods when other males became resident (2 of 37 juvenile males dispersed; Fisher's exact test: $P \leq 0.051$). The difference was also significant when we limited our analysis to the most-confident subset (3 of 7 juvenile males dispersed when PH became resident versus 1 of 30 juvenile males dispersed when all other males became resident; Fisher's exact test: $P \leq 0.04$). Ad libitum observations suggested that PH's arrival in the group coincided with high levels of aggression directed towards older juvenile males.

Sexual Attraction to Oestrous Females

Males did not disperse during the conception season more often than expected by chance (7 of 26 dispersals: binomial probability = 0.42; $P \leq 0.92$; 4 of 18 most-confident dispersals: binomial probability = 0.42, $P \leq 0.93$; Fig. 1a). Group size, which should relate to reproductive opportunity in the natal group, was not related to age at dispersal (Spearman rank correlation: $r_s = -0.15$, $N = 26$, $P \leq 0.46$).

Social Integration

Males and females did not differ in the time that they spent in the centre of the group or within 10 m of at least two group members (Table 3). However, time spent in social activities was eight times greater in juvenile females than in juvenile males, while males spent more time resting. Specifically, compared to males, juvenile females spent more time sitting in contact with groupmates

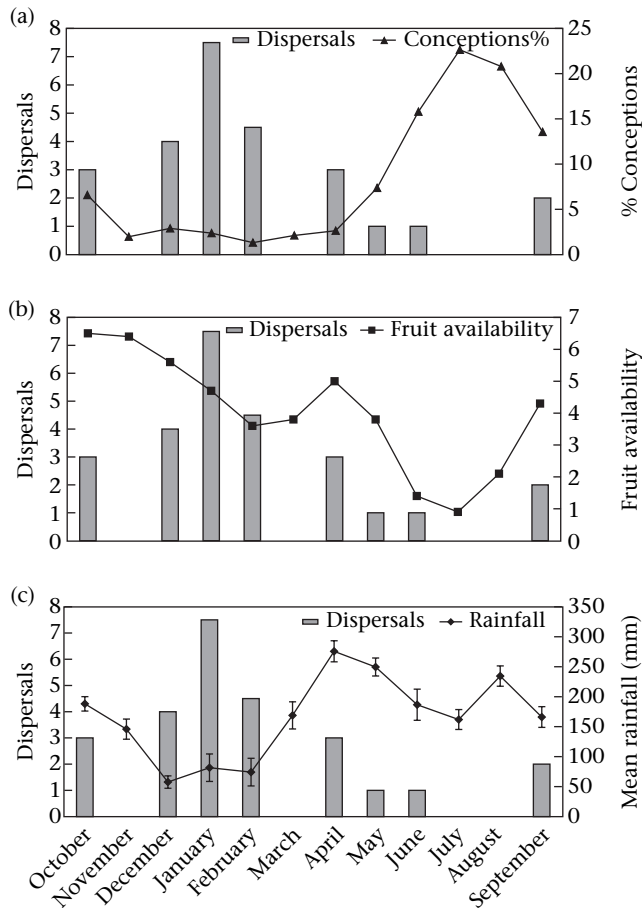


Figure 1. Monthly distribution of dispersals and (a) percentage of conceptions (from M. Cords, unpublished data), (b) fruit availability (for TW, from K. A. Pazol, unpublished data) and (c) rainfall (mean \pm SE; BIOTA: <http://www.dlr.de/biota-east/biota/data.htm>). For one animal, dispersal could be dated only to a 2-month period (January and February), so those months were both given a score of 0.5. In (a), cumulative conceptions are shown for all groups and all years (for 1997–2006 births), although statistical tests were based on group-year-specific conception records.

(Mann–Whitney U test: $U = 38$, $N_1 = 5$, $N_2 = 9$, $P \leq 0.04$), and were approached more often ($U = 45$, $P \leq 0.001$), groomed other animals more often ($U = 45$, $P \leq 0.001$) and received grooming more often ($U = 40$, $P \leq 0.02$). Although females groomed with other animals at higher rates than males, males and females were responsible for initiating a similar proportion of the grooming interactions ($\bar{X} \pm \text{SE}$ percentage: males = $53 \pm 14\%$; females: $65 \pm 15\%$; U test: $U = 24$, $N_1 = 8$, $N_2 = 5$, $P \leq 0.62$).

Juvenile females spent significantly more time than juvenile males grooming adult females ($\bar{X} \pm \text{SE}$ percentage of time: females: $2.4 \pm 0.8\%$; males: $0.3 \pm 0.1\%$; Mann–Whitney U test: $U = 38$, $N_1 = 5$, $N_2 = 9$, $P \leq 0.04$), but there was no significant difference in the percentage of time that adult females groomed juvenile males and females (females: $1.6 \pm 0.8\%$; males: $0.8 \pm 0.4\%$; $U = 31$, $N_1 = 5$, $N_2 = 9$, $P \leq 0.30$). The difference in the time that juvenile males and females spent grooming was almost entirely driven by interactions with related adult females

(including mothers): on average, juvenile females groomed related adult females 10 times more than males did (Mann–Whitney U test: $U = 39$, $N_1 = 5$, $N_2 = 9$, $P \leq 0.03$), while there was no significant difference in time spent grooming unrelated adult females ($U = 23$, $P \leq 1.0$). We found no other significant sex differences in juveniles' interactions with related or unrelated adult females.

There were few differences in social behaviour between dispersing and nondispersing males. Activity budgets and time spent in the centre of the group or within 10 m of two group members did not differ for these two classes of animal. While dispersing and nondispersing males also did not differ in the percentage of time spent within 1 m of other group members (dispersing males: $1.8 \pm 1.0\%$, $N = 3$; nondispersing males: $3.6 \pm 0.7\%$, $N = 6$; Mann–Whitney U test: $U = 14$, $P \leq 0.26$), dispersing males spent significantly less time within 1–3 m of any group member (as reported above), and significantly less time within 1–3 m of adult females (dispersing males: $4.9 \pm 0.4\%$; nondispersing males: $9.0 \pm 1.5\%$; Mann–Whitney U test: $U = 18$, $P \leq 0.02$), and adult males (as reported above), in particular.

Amonged the five focal subjects that dispersed subsequent to our study, there was no correlation between the age at dispersal and the percentage of time that each male was engaged in social activity (namely grooming or sitting in contact with a partner; Spearman rank correlation: $r_s = 0.65$, $P \leq 0.19$).

Two males in the study groups were orphaned during the study period. They dispersed 21 and 37 months after the deaths of their mother, at the ages of 7.5 and 7.0 years, respectively. These values are very close to the average dispersal age of 7.25 years, suggesting that being orphaned, although it means losing an important grooming partner, does not strongly affect dispersal age.

Climate, Food Availability and Body Mass

Male dispersal was most likely to occur during dry months. Males dispersed more often than expected by chance during the 3-month period of lowest average rainfall (16 of 26 dispersals in December–February: binomial probability = 0.25, $P \leq 0.0001$; 12 of 20 most-confident dispersals in December–February: binomial probability = 0.25, $P \leq 0.0002$; Fig. 1c). This same pattern held when we considered only the three driest months in the year of dispersal instead of multiyear norms (9 of 20 dispersals with rainfall data available: binomial probability = 0.25, $P \leq 0.02$; 6 of 14 in most-confident subset with rainfall data available, binomial probability = 0.25, $P \leq 0.04$).

Dispersals were not especially likely during the 3-month peak in fruit availability in October–December (7 of 26 dispersals: binomial probability = 0.25, $P \leq 0.69$; 6 of 20 in most-confident subset: binomial probability = 0.25, $P \leq 0.21$; Fig. 1b). However, males dispersed less frequently than expected by chance during the 3 months with the lowest fruit availability (June–August; 1 of 26 dispersals: binomial probability = 0.25, $P \leq 0.006$; 0 of

Table 3. Mean \pm SE activity budgets, spatial location within the group and presence of neighbours of male and female subjects (medians in parentheses)

	Females (N=5)	Males (N=9)	Mann–Whitney U	
			U	P
Behaviour*				
Social	0.16 \pm 0.03 (0.16)	0.02 \pm 0.005 (0.03)	45	\leq 0.001
Rest	0.28 \pm 0.02 (0.29)	0.37 \pm 0.02 (0.35)	40	\leq 0.02
Move	0.12 \pm 0.01 (0.11)	0.12 \pm 0.01 (0.13)	23	\leq 1.0
Feed	0.43 \pm 0.04 (0.42)	0.48 \pm 0.01 (0.48)	30	\leq 0.36
Location				
Centre	0.67 \pm 0.07 (0.64)	0.58 \pm 0.05 (0.54)	34	\leq 0.15
Neighbours				
2+ animals within 10 m	0.53 \pm 0.08 (0.59)	0.51 \pm 0.03 (0.52)	26	\leq 0.70

*Proportion of total point samples.

20 in most-confident subset: binomial probability = 0.25, $P \leq 0.004$).

Data on body mass and growth rates for immature blue monkeys were unavailable, so we could not evaluate the prediction that juveniles disperse after they are full grown. One study (Gautier-Hion & Gautier 1976) investigated growth rates in eight species of closely related cercopithecines in captivity (seven species of *Cercopithecus* and *Miopithecus talapoin*) and reported that none had reached full body mass by 7 years of age. Our long-term observations of animals of known age suggest that male blue monkeys do not reach full body size before they are 8–10 years old. All animals that dispersed appeared obviously smaller than fully grown adult males.

DISCUSSION

Are Juvenile Males Evicted from the Natal Group?

Our data suggest that males are usually not evicted from the natal group. Juvenile males were not especially likely to disperse during periods of change in male membership. Males and females did not differ significantly in the amount of aggression received. Dispersing males did not receive higher rates of aggression than nondispersing males, and lower-ranking males did not disperse at an earlier age than higher-ranking males.

We did not observe an actual dispersal, so we were unable to determine whether dispersals were triggered by a brief spike in aggression received or a general increase in aggression received over a period of months. An acute increase in aggression is unlikely, however. Most dispersals since 1998 occurred gradually over periods of up to 5 weeks, and occasionally over months. Such a gradual transition would be unexpected if intense, limited aggression were driving dispersal; furthermore, in the 16 cases when group observations were frequent before the dispersal, no heightened aggression towards the young male was ever noted.

Although eviction did not appear to be a causal factor in most dispersals, we found some anecdotal evidence that

aggression from adult males may occasionally drive young males to emigrate. The arrival of a new and exceptionally aggressive resident male in GN group was followed within a month by the dispersal of three of the seven juvenile males in the group at that time. These three dispersals accounted for only 12% of the total, however.

Does Sexual Attraction to Nongroup Females Motivate Dispersal?

Although juvenile males have never been observed to copulate with females in their natal group (Cords 2000a), every female in the study population who reproduced did so in her natal group. This disparity in access to mates in the natal group should motivate males to search elsewhere and should cause males to experience much stronger sexual stimuli outside than inside the natal group. Despite these asymmetries, sexual attraction appears not to influence the natal dispersal process in this species.

Where sexual attraction is implicated as a cause of dispersal, males are expected to disperse more frequently during the conception season (Sugiyama 1976; Cheney & Seyfarth 1983; Olupot & Waser 2001; Jack & Fedigan 2004). In blue monkeys, multimale influxes are more likely to occur during the conception season (Cords 1987b, 2002b; Henzi & Lawes 1987), which confirms that adult males are most attracted to females during this period (Cords 2002b). Males in our study population, however, did not favour dispersing during the conception season.

If sexual attraction triggers male dispersal, males should favour dispersing into larger groups with more available mates (Pusey & Packer 1987; Smith 1992; Sprague 1992; Olupot & Waser 2001). This prediction is problematic for blue monkeys because males seldom move directly from their natal group into another heterosexual group (Rudran 1978; Cords 2000a). Between December 2003 and September 2004, however, five of the six males that dispersed from group GN, the smallest study group, immigrated into group TW, the largest study group. They might have favoured TW because it contained a large number of adult females, but there are alternative explanations.

TW contained multiple resident males at the time, so dispersing males might have chosen a group where additional males were tolerated. Also, the first two males that moved from GN into TW did so together, and subsequent GN males might have chosen TW because it contained familiar individuals, a pattern found in several other primate species (Sugiyama 1976; Cheney & Seyfarth 1977; Melnick 1981; Kuester & Paul 1999; Korstjens & Schippers 2003). Without more information about the groups that dispersing males eventually join, we cannot evaluate definitively the prediction that males disperse into larger groups. It is clear, however, that males in smaller groups do not disperse at an earlier age.

Do Dispersers Have Weak Social Bonds in the Group?

Our results indicate that dispersing animals have relatively weak social ties with group members. In particular, juvenile males have weaker social bonds with other group members than female peers do, and therefore perhaps less reason to stay in the natal group (Colvin 1983). Our data confirmed that males spent significantly less time grooming and sitting in contact with others than did females. The sex difference remained when grooming was separated into grooming given and received.

Weak social ties could result from a lack of social motivation in the dispersing animals themselves, or in their groupmates (Henzi & Lucas 1980; Alberts 1992). If group members avoid social interaction with dispersers, the potential for better social relations outside the group would presumably drive emigration. If dispersing animals avoid social interactions, it would seem that some endogenous factor affects the degree to which they value social relationships with current group members or, more generally, with anyone (Colvin 1983; Alberts 1992; Alberts & Altmann 2001). We found that juvenile females groomed related adult females at a higher rate than juvenile males did, even though both received grooming from these partners at similar rates. This asymmetry may indicate that males did not value social relationships with related adult females to the same extent that females did, supporting the idea that there are intrinsic sex differences in social motivation in these young animals. Juvenile male blue monkeys apparently begin to take an interest in extragroup male peers at the age of 3–4 years: during aggressive intergroup confrontations between adult females, natal males older than 3–4 years often play with male peers in the neighbouring group (Cords 2002a). We have never observed juvenile females play with peers in other groups. This behavioural difference may also reflect intrinsic sex differences in social motivation.

We found few differences in social integration among males, however. Social integration was not correlated with age at dispersal in the five focal subjects that eventually dispersed. Furthermore, two orphaned males that lacked the usual close relationship with a mother dispersed at ages close to the mean. Finally, if dispersal is stimulated by a lack of social ties, dispersing males should have less

frequent social interactions than nondispersing males. Evidence for such a difference was rather limited in our study, although proximity relations suggested that dispersing males spent less time in dense clusters of individuals than did nondispersing males. Studies of baboons have documented extensive predispersal social changes (Smuts 1985; Alberts 1992).

If social integration is an important proximate stimulus of dispersal, it is puzzling that differences between dispersing and nondispersing males do not mirror the sex differences that we observed. Four hypotheses may explain this discrepancy: (1) lack of social integration is necessary but not sufficient for stimulating dispersal; (2) lack of social integration operates over a different time-scale (either shorter or longer) than the 3 months before dispersal; (3) the effects of weak social integration are cumulative, such that dispersal occurs once a threshold has been reached; or (4) lack of social integration is not a causal factor for dispersal, and sex differences in social integration are unrelated to dispersal. Our data are unable to refute any of these hypotheses, but we note that the first three hypotheses seem more likely than the fourth, given the magnitude of sex differences in social integration that we observed. It is plausible that a lack of social integration works over the course of several years to lessen the bonds that tie males to their natal group. If so, lack of social integration would not be the immediate, or a sufficient (unless effects are cumulative), causal factor for dispersal, but it would be a necessary condition.

Is Dispersal Timed to Minimize Reproductive and Survivorship Risks?

Although the minimization of risks can be considered an ultimate explanation for dispersal, risk minimization can also influence the dispersal process itself on a proximate level. Environmental and social conditions that signify safe dispersal conditions can function as cues for dispersal events. Costs associated with remaining in the natal group, such as inadequate access to food (e.g. Boutin et al. 1985), can also trigger dispersal, although it seems that this ecological factor seldom drives dispersal in mammals (Smale et al. 1997). It does appear, however, that dispersing animals often minimize the risks inherent to the dispersal process, for example, by trying to move into groups where they have the greatest chance of being accepted (Cheney & Seyfarth 1983; Waser 1988; Smith 1992; Isbell et al. 1993; Kuester & Paul 1999), or by dispersing when sufficient body size or body fat has been attained (Holekamp 1986; Smale et al. 1997; Nunes et al. 1998).

While male mammals generally do not disperse to avoid low food availability (review in Smale et al. 1997), few studies have evaluated the influence that food availability has on timing of dispersals (Efford 1998). Our results, while not conclusive, suggest that blue monkey males at Kakamega are more likely to disperse when climate and food availability are most favourable (Alberts & Altmann 1995b). Dispersals were concentrated in the three driest

months. Although dispersing blue monkeys are unlikely to suffer severe consequences from variation in the tropical climate at Kakamega, dispersal means forsaking the huddles that are common during rainstorms and in the cooler temperatures at night, and may therefore impose energetic costs.

Males are also expected to disperse when food is readily available, to compensate for their travel through unfamiliar terrain where food sources are unknown (Waser & Jones 1983; Pusey & Packer 1987; Isbell et al. 1993; Isbell & Van Vuren 1996). Fruits are the most important high-quality food item in the blue monkey diet (Rudran 1978; Cords 1986, 1987b, 2002a), and we found that dispersals were less likely to occur than expected when fruit availability was lowest. That dispersals were not concentrated in the 3 months with the highest fruit availability suggests further that the availability of high-energy foods might be a necessary but not a sufficient condition for dispersal to occur.

Many of the risks associated with dispersal, such as increased exposure to predators, inclement weather and reduced food availability, can be partly mitigated by being full grown (Smale et al. 1997; Bronikowski et al. 2002). All of our subjects dispersed before they were full grown, suggesting that climate and food availability serve as short-term cues for the timing of dispersals rather than as long-term, or overwhelmingly large, risks to be avoided.

Endogenous Factors

Hormonal or biochemical changes associated with puberty may also influence natal dispersal in blue monkeys. Serotonin activity has been positively correlated with dispersal age in one population of rhesus macaques, *Macaca mulatta*, for example (Kaplan et al. 1995; Mehlman et al. 1995; Trefilov et al. 2000). Although very little is known about the physiological development of blue monkeys, the age range of dispersing animals in this population was small compared to that of other wild primates (baboons, *Papio* spp.: 4–9 years, Packer 1979; 6.8–13.4 years, Alberts & Altmann 1995a; vervets, *Chlorocebus aethiops*: 2.5–7 years, Cheney 1983) and that of provisioned primates (rhesus macaques: 2.5–12 years, Colvin 1983; Barbary macaques, *Macaca sylvanus*: 1.75–11.75 years, Kuester & Paul 1999; Japanese macaques, *Macaca fuscata*: 2–12 years, Sugiyama 1976), suggesting that endogenous developmental cues may be important. Endogenous factors are likely to be important cues for natal dispersal in species where all members of one sex emigrate (Smale et al. 1997), as is the case for our study population.

Conclusion

We originally suggested that the proximate factors stimulating natal emigration might differ in species with one-male versus multimale groups. Our results provide some support for this idea, but they also suggest some commonalities across species, regardless of their social

organization. We are aware of only one other study that focused explicitly on dispersal mechanisms in a primate species with a modally single-male group social organization where only one sex disperses. As in our study, attraction to sexual partners was unimportant as a proximate cue in grey langurs, *Semnopithecus entellus*, at Jodhpur, but in contrast to our study, aggressive eviction, often associated with adult male membership change, was associated with the majority of natal transfers in the langur population (Rajpurohit & Sommer 1993). In contrast, our results indicate that eviction and changes in adult male membership are generally not important in stimulating natal dispersal in blue monkeys. Lack of social integration in the group, however, seems to predispose males (rather than females) to leave their natal group, and the timing of their departure reflects favourable climatic and feeding conditions. Similar results have been found in several primate species living in multimale groups (social integration: Cheney 1978; Henzi & Lucas 1980; Silk et al. 1981; Colvin 1983; Nikolei & Borries 1997; minimized risks: Sugiyama 1976; Cheney & Seyfarth 1983; Waser 1988; Smith 1992; Isbell et al. 1993; Kuester & Paul 1999; Alberts & Altmann 1995a). Rajpurohit & Sommer (1993) did not examine these factors in their study of langurs.

Overall, the available evidence suggests that weakening social bonds and environmental cues are widespread and perhaps fundamental proximate factors stimulating male dispersal in group-living primates (Cheney 1978; Henzi & Lucas 1980; Silk et al. 1981; Colvin 1983; Nikolei & Borries 1997). Weak social bonds in dispersing individuals also appear to be important in canids (Bekoff 1977; Harris & White 1992) but not in horses (Monard et al. 1996) or ground squirrels (Holekamp 1983; Wiggett & Boag 1993). Eviction occurs in many taxonomic groups, but it is differentially important across species (review in Smale et al. 1997) and it is not closely tied to social organization. The one proximate factor that may align with social organization is sexual attraction by the emigrants. In species whose males move directly into new groups, sexual attraction appears to be important in stimulating dispersal (Enomoto 1974; Packer 1979; Pusey 1980; Cheney & Seyfarth 1983; Smith 1992; Wiggett & Boag 1993; Waser 1996; Kuester & Paul 1999; Olupot & Waser 2001). In species living in one-male groups, however, sexual attraction does not appear to explain variation in the process of natal emigration, even though the search for suitable mates is probably important as an ultimate reason for natal dispersal.

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