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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.

Keywords: age-related behaviour; blue monkey; *Cercopithecus mitis stuhlmanni*; development; dispersal; emigration; environmental risk; primates; sex differences

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 km^2; Lung 2004) of the Guineo-Congolean 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/km^2 (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