Male dispersal patterns in white-faced capuchins, *Cebus capucinus*
Part 1: patterns and causes of natal emigration

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This is the first of two papers examining male dispersal patterns in white-faced capuchins. Our study was based on behavioural and demographic data collected on multiple groups of white-faced capuchins in Santa Rosa National Park, Costa Rica since 1985. Here we examine the patterns and proximate causation of male natal dispersal. Natal dispersal in white-faced capuchins occurred at a median age of 4.5 years, with no males remaining in the natal group past 8 years. Initial departure from the natal group appeared to be in response to an attraction to extragroup males and dispersing groupmates. Rates of parallel dispersal (dispersal with co-resident males and/or into groups containing familiar males) were very high for natal males (71–82%), and this pattern of dispersal may have evolved to increase inclusive fitness benefits in male-dispersed species. Additionally, this pattern of dispersal probably increases survivorship among dispersing males who are not yet physically mature, as is common in white-faced capuchins.

Among both mammalian and avian species, a pattern of sex-biased dispersal is the norm, with the majority of group-living mammals displaying a pattern of male-biased dispersal and female philopatry (Greenwood 1980). The mammalian pattern of dispersal holds to some extent in the order Primates, with the majority of prosimians and Old World cercopithecines being characterized by male dispersal and females remaining in their natal groups for life. The pattern is, however, much less common among New World primates and apes (Strier 1999). Investigations of the costs and benefits of sex-biased dispersal in mammals are numerous (reviewed in Bélichon et al. 1996; Perrin & Mazalov 2000), although the majority of studies are limited to investigations of natal dispersal (e.g. Monard et al. 1996; Byrom & Krebs 1999). Subsequent dispersal (secondary or breeding dispersal) has also been reported for several mammalian taxa (e.g. Greenwood 1980; Waser & Jones 1983; Berger 1986; Pusey & Packer 1987a, b; Mitchell 1994). However, due to the difficult task of tracking dispersing individuals over time and space, our knowledge of their fates is limited to a few well-studied

species (Johnson & Gaines 1990; Waser et al. 1994) and this lack of data is especially pronounced for long-lived taxa such as primates. With the exception of the best-known cercopithecine species (Pusey & Packer 1987a) there remain relatively few reports detailing male life history patterns in free-ranging primates characterized by male dispersal, and the monitoring of known individuals through multiple migrations is especially rare (but see Sussman 1992; Mitchell 1994; Okamoto et al. 2000).

This is the first of two papers summarizing 16 years of behavioural and demographic data collected on male white-faced capuchin monkeys in Santa Rosa National Park, Costa Rica. Together, these two papers provide an extensive life history profile of male white-faced capuchins. Data presented in this first paper provide a detailed description of the timing and circumstances surrounding male natal emigration, whereas the second paper (Jack & Fedigan 2004) details patterns and causes of secondary dispersal, with particular reference to the effects of male age class on these patterns.

Proximate Causes of Natal Dispersal

In most mammals, natal dispersal commonly occurs at, or prior to attaining, sexual maturity and is generally assumed to be an evolutionary mechanism for inbreeding

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avoidance and a means to enhance reproductive success (Itani 1972; Greenwood 1980; Moore & Ali 1984; Clutton-Brock 1989; Moore 1993). Several proximate factors are reported to influence the timing and impetus of natal emigration; those pertinent to male-dispersed primate species usually involve eviction and/or an attraction to extragroup individuals (Pusey & Packer 1987a). The eviction of maturing males from their birth group is most frequently reported in unimale–multifemale langur species. In these cases, dispersal is often the result of aggression from the group's breeding male in response to the increasing maturity of natal males (e.g. grey langur, *Semnopithecus entellus*: Mohnot 1978). Natal eviction is also observed to occur when a new breeding male takes over a group and continually harasses juveniles until they become peripheral and eventually disperse (e.g. grey langur: Sugiyama 1967; Boggess 1980; purple-faced langurs, *Trachypithecus vetulus ventulus*: Rudran 1973). However, natal emigration after a group take-over is not always in response to aggression received from the new breeding male. Mathur & Manohar (1990) observed cases where natal male grey langurs 'voluntarily' left their group along with other members of the all-male band upon arrival of the new breeding male.

Attraction to extragroup individuals is a more commonly reported factor influencing male emigration and this attraction may take two forms: sexual attraction to extragroup females and an attraction to extragroup males or emigrating male groupmates (Pusey & Packer 1987a). Attraction to potential mates appears to be the driving force behind male mobility in a number of seasonally breeding species where the timing of dispersal coincides with the mating season (vervets, *Chlorocebus aethiops*: Cheney 1983; ringtailed lemurs, *Lemur catta*: Sussman 1992; Japanese macaques, *Macaca fuscata*: Sprague 1992). An attraction to extragroup females may also affect male dispersal in nonseasonally breeding species. Various studies have demonstrated that males are not necessarily attracted to groups containing more females, but to groups containing unfamiliar and unrelated females (for review see Pusey & Packer 1987a).

Furthermore, in several species of Old World monkeys (Pusey & Packer 1987a), young males may leave their natal group and temporarily interact with extragroup males (i.e. members of all-male bands, peripheral males of neighbouring groups, or solitary males). After a series of such interactions, these males will sometimes emigrate together or join the neighbouring group to which they were peripheral (Matsumura 2000). Maturing natal males have also been observed to emigrate with members of their age cohort, older maternal brothers, or into groups containing familiar males (e.g. Japanese macaques: Sugiyama 1976; vervets: Cheney & Seyfarth 1983; longtailed macaques, *M. fascicularis*: van Noordwijk & van Schaik 1985; ringtailed lemurs: Sussman 1992; squirrel monkeys, *Saimiri sciureus*: Mitchell 1994; reviewed in Melnick & Pearl 1987). Often referred to as parallel emigration, this coordinated movement of males from the natal group is thought to be a mechanism by which relatedness between male siblings can be maintained in a male-dispersed species (van Hooff 2000). Parallel emigration may also maintain coalition partners and familiar relationships among males, while reducing the potential costs of dispersing (i.e. increased predation, aggression from conspecifics; reviewed in Cheney 1983).

Capuchins are an anomaly among the New World primates in that they are characterized by a pattern of male-biased dispersal and female philopatry, and thus more closely resemble the Old World cercopithecines (Strier 1999). White-faced capuchins fit this general *Cebus* pattern of dispersal and reside year-round in groups comprised of multiple adult females, their offspring, and multiple immigrant males (Oppenheimer 1968; Fedigan 1993). Changes in adult male membership within groups usually occur in the form of take-overs, with complete replacement of group males occurring every 2–4 years (Fedigan 1993). This frequent replacement of group males indicates that during the course of their lives, most male white-faced capuchins will reside in many different social groups.

Here we examine and describe the conditions under which male natal emigration occurs and elucidate both the proximate causes of natal emigration in white-faced capuchins and the benefits of the observed dispersal pattern. Specifically, we test the following predictions derived from the above review of the literature: (1) if eviction is a primary motivator for male natal emigration, it is expected that male emigration will coincide with group take-overs and involve aggression directed by new resident males towards natal males; (2) if male natal emigration takes place in response to an attraction to extragroup females, emigrations are expected to occur at sexual maturity, and because transfers between groups are direct and immediate, they should be clustered around the 'conception peak' (see below); and (3) if natal emigration is in response to an attraction to extragroup males or departing groupmates, there should be a high frequency of parallel emigration. These predictions are not mutually exclusive. For example, a male may disperse with several groupmates after the take-over of his natal group, indicating both eviction and attraction to dispersing groupmates as proximate factors. However, the relative frequency of the factors and circumstances surrounding natal emigration events will provide insight into the overall dispersal pattern of this species.

METHODS

Study Site

Data were collected on several groups of wild white-faced capuchins residing in the Santa Rosa Sector of the Area de Conservacion Guanacaste. Formerly known as Santa Rosa National Park (SRNP herein), the sector was established as a protected area in 1971 and is located near the Nicaraguan border, 35 km northwest of Liberia in Guanacaste Province of Costa Rica. The original boundaries of SRNP encompass approximately 108 km² of dry deciduous forest and reclaimed pasture in varying stages of regeneration, and this sector is comprised of several stepped plateaus that range from 300 m in altitude to sea level, where the park is bordered by the Pacific Ocean. The

site has been described in detail elsewhere (Fedigan et al. 1996; Fedigan & Jack 2001). The area experiences two distinct seasons: a dry season during December–May, and a rainy season during June–November. Annual rainfall in the park averages between 800 and 2600 mm (mean = 1472 mm) and mean high temperatures range from 21.6°C (September) to 34.4°C (April; D. H. Janzen & W. Hallwachs, unpublished data).

Species

White-faced capuchins range from as far north as Honduras, throughout Central America, and into northwestern Ecuador (Rowe 1996). The multimale–multifemale groups of white-faced capuchins are comprised of related females, immigrant males and their immature offspring. Female–female relationships within groups of white-faced capuchins are maintained over many years and appear to be based on kinship and stable partner preferences for grooming, proximity and coalitionary support (Perry 1995; Fragaszy et al. 2004). Males, on the other hand, are transient group members and although this makes the formation of durational bonds among them more difficult, there is some evidence of male bonding in this species (Perry 1998; Jack 2003). Males are approximately 25–35% larger than females and are usually individually dominant to them (Fedigan 1993). Annual censuses of the capuchin population in SRNP have yielded a mean group size of 17.2 (range 7–36), with an average of 4.4 adult males and 5.4 adult females per group, and an average adult sex ratio (male:female) of 0.72 (Fedigan & Jack 2001). Female white-faced capuchins do not show any visible signs of oestrus and frequently engage in nonconceptive copulations (Manson et al. 1997). Although they are not strict seasonal breeders, they do display a birth peak between January and April (Fedigan et al. 1996).

Study Groups

We commenced studies of the white-faced capuchins in SRNP with a short demographic survey in 1982, and more intensive censuses in 1983 and 1984 (Fedigan et al. 1985; Fedigan 1986; Chapman et al. 1988). Following the 1984 census, we began habituating two social groups of capuchins, Sendero (SE) and Cerco de Piedra (CP), for intensive research. Individuals residing in these groups were habituated and discrimination of individuals began. In 1985, births, deaths and migrations were recorded (see Fedigan & Rose 1995) and biweekly observations detailing the groups' foraging and social behaviour began, a practice that continues through the present. These groups have been monitored continuously since 1985, with the exception of 21 months spread over 5 years: a 6-month hiatus in 1991, 3 months in 1995, 4 months in 1996, 5 months in 1997 and 3 months in 1999. In 1990, we added a third study group, Los Valles (LV), after several members of the CP and SE groups transferred into it. Observations of the CP and LV groups continue to be the focus of intensive study to this day. The SE group was observed through April 1993, when it dissolved after a series of unsuccessful

male take-overs, loss of range to neighbouring groups, and the death and/or emigration of the majority of group members.

With the exception of the periods specified above, a minimum of 20 h each month were spent observing the study groups. In most years, the study groups were observed on a daily basis during January–August during which intensive behavioural and ecological data were collected. Several studies have focused directly on immature individuals and males residing within our study groups, thereby providing additional detail on the contexts of male migration patterns. Although several members of the original study groups were darted and marked to ease individual identification (Glander et al. 1991), we have since come to rely on natural markings for this purpose (e.g. scars, brow and peak shape, missing/broken digits). When new investigators join the research team, they are trained in the field by prior researchers to identify individual monkeys, ensuring accuracy and continuity of identity assignment. Using this method, individual monkeys have been tracked since 1985 and up to three generations of females have been observed in one of the long-term study groups.

Individuals are also identified according to their age–sex class and the age breakdown used for males in the study groups was as follows: infant: ≤1 year; juvenile: 1–7 years; subadult: 7–10 years; adult: ≥10 years (Fedigan et al. 1996).

Data Analysis

We used SPSS SURVIVAL analysis to determine the median age of natal emigration in the study groups. SURVIVAL analysis allows for the use of both completed/uncensored intervals (i.e. males that have emigrated from their natal group) and incomplete/censored intervals (males that still resided in their natal group as of May 2000; the cutoff point for data used). Analysis based solely on complete intervals can result in shorter intervals; that is, it may underestimate the mean age of natal emigration. As used here, SPSS SURVIVAL generates the median age of male natal emigration while taking into account males who have not yet dispersed from their natal groups. We also used Spearman's rho to test for correlation between the mating peak and the timing of male natal emigration.

RESULTS

Mortality and Age of Natal Emigration

Table 1 presents data on the 36 individual males born into each of the study groups and their subsequent fates (e.g. died, transferred, etc.) and these data are summarized in Table 2. Only those males who were positively identified as natal are included in the sample. In total, 36 males were born during the specified periods, 33% (N = 12) of whom were later confirmed (N = 7) or presumed dead (N = 5). The five cases in which we presumed individuals to be dead concerned young males who disappeared

Table 1. Natal males, age (months), and details of their natal emigration, disappearance, or death (N=36)

Male (mother; birth year)	Emigration age	Natal group*	Outcome†
BB1984	60	SE	Transfer
BB1986	39	SE	Transfer
BB1988	51	SE	Transfer
CH1987	19−26	SE	Transfer
CH1989	48	SE	Transfer
BB1990	13	SE	Dead
PI1989	5	SE	Dead
BB1992	14	SE	Dead
?PA1987	48−56	CP	Unknown
PA1989	96	CP	Unknown
BE1989	80	CP	Unknown
BE1993	25	CP	Unknown
LI1991	26	CP	Unknown
LI1996	>48	CP	Natal
LI2000	4	CP	Dead
NY1999	5	CP	Dead
BE1992	3	CP	Dead
TU1992	7	CP	Dead
CH1992	9	CP	Dead
BO1989	90	LV	Transfer
BL1989	86	LV	Transfer
SP1991	68	LV	Transfer
BO1992	56	LV	Transfer
MY1992	54	LV	Transfer
BL1994	64−68	LV	Transfer
BO1994	48	LV	Unknown
SP1994	18−22	LV	Unknown
GR1994	17−21	LV	Unknown
BO1996	24	LV	Unknown
KL1996	35	LV	Unknown
CA1996	>53	LV	Natal
DL1999	>12	LV	Natal
KL2000	4	LV	Dead
FE1999	5	LV	Dead
FE1998	1 day	LV	Dead
BL1998	5	LV	Dead

*Sendero (SE), Cerco de Piedra (CP), Los Valles (LV).
†Transfer: male was observed in a new group following natal dispersal; unknown: male was not seen again after natal dispersal; dead: male was confirmed to have died rather than dispersed; natal: male was still residing in his natal troop as of May 2000.

before the age of 14 months (mean: 7 months; range 1 day−14 months). Although it is possible that some of these males survived and entered into new groups, the youngest confirmed age for successful natal emigration on record for this study site is 20 months. This young male transferred into a neighbouring group where an older maternal male sibling and a natal-group agemate had immigrated approximately one month before his own transfer.

Three of the males in the sample (8%) were still alive and residing in their natal groups as of May 2000. Their mean age was approximately 3 years (or 37.7 months; range 12−53 months). Eleven natal males (31%) were confirmed to transfer directly into neighbouring groups and their mean age of emigration was 58 months. The remaining 10 males (28%) who disappeared from the study area but were not presumed dead dispersed at a mean age of 42.5 months. The mean age of natal emigration/disappearance for these 21 dispersing/disappearing males was 50 months (4 years, 2 months; range 20−96 months). When the three males that were still residing in their natal groups were included, and censored (incomplete) intervals were assigned to them, SURVIVAL analysis indicated that the median age at natal emigration was approximately 4.5 years, or 54.6 months (N = 24).

Timing of Natal Disappearance Compared to Annual Distribution of Conceptions

The month of departure was noted for each of the 21 natal males who emigrated/disappeared from the three main study groups. The males for whom the exact month of departure was unknown (N = 5) were divided across the range of possible months. That is, if two males dispersed during a period of researcher absence between 31 August and 31 December, 0.5 dispersals were recorded for each of those months. These males were included in the sample because the majority of periods during which monthly observations were not taken coincided with the rainy season, and we did not want to bias the sample by excluding them. Figure 1 plots emigration month, for both total emigrations (including disappearances) and confirmed emigrations, against conception month. We extrapolated month of conception by counting back 164 days (5.4 months; estimated gestation in white-faced capuchins; see Fedigan et al. 1996) from 72 known births that occurred in the study population between 1985 and May 2000 (Fedigan 2003). The conception peak clearly fell in July, although there was a second peak in November and December (Fig. 1). This second peak corresponded with the December peak in natal emigrations (both total and confirmed); however, these variables were not significantly correlated (total emigrations: Spearman rank correlation: $r_S = -0.244$, $N = 12$, $P = 0.444$; confirmed emigrations: $r_S = 0.196$, $N = 12$, $P = 0.541$). The December peak in natal emigration also did not coincide with the birth peak, which fell between January and April (Fedigan et al. 1996).

Table 2. Summary of number of males born into study groups and their fates

Study group	Dead	Transferred	Disappeared	Not dispersed	Total
Sendero (1986−1992)	3	5	0	0	8
Cerco de Piedra (1989−2000)	5	0	5	1	11
Los Valles (1990−2000)	4	6	5	2	17
Total	12	11	10	3	36
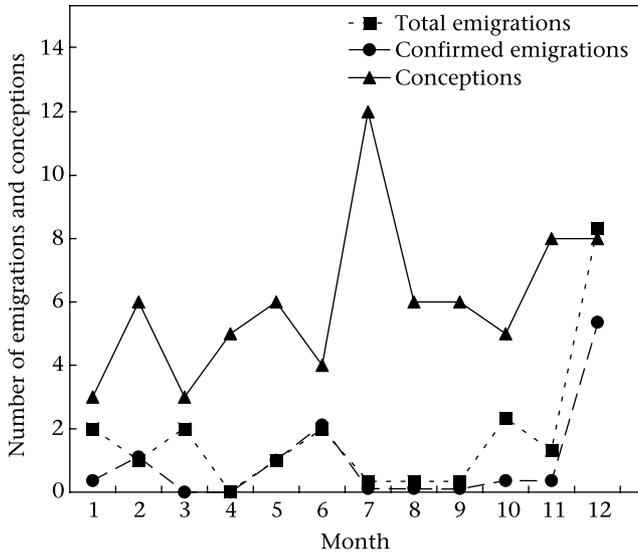
Figure 1. Timing of conceptions and natal dispersal by male white-faced capuchins. Conceptions were extrapolated by counting back 164 days from 72 births to individually known mothers based on data presented by Fedigan (2003).

Proximate Conditions of Natal Dispersal

Table 3 summarizes the immediate circumstances surrounding the emigration of the males born into the study groups ($N = 21$, excluding the 12 young males confirmed or suspected to be dead and the three that were still resident in their natal groups as of May 2000). Examination of the data set and the ad libitum notes recorded by the Santa Rosa research team since 1986 indicated three key circumstances surrounding male natal emigration: (1) a breakdown of relationships among group males (adults and subadults), (2) a series of intergroup interactions and (3) suspected fissioning of the natal group. We also added a fourth 'unknown' category representing disappearances that took place during several periods when the groups were not under biweekly observation.

None of the natal emigrations that occurred while the study groups were under daily observation (intensive focal animal sampling) were the direct result of eviction following a take-over of the group by invading males. Three of the natal males in our sample did disperse from their groups shortly after a change-over in the resident males of their group; however, their emigration did not

Table 3. Frequency of proximate conditions of natal emigration (confirmed emigrations)

Proximate condition	Sendero	Cerco de Piedra	Los Valles	Total
Breakdown in group dynamics	1 (1)	2	5 (5)	8 (6)
Intergroup interactions	4 (4)	0	2 (1)	6 (5)
Group fission suspected	0	2	2	4
Unknown	0	1	2	3
Total	5	5 (5)	11 (6)	21 (11)

appear to involve any aggression or harassment from the new resident males. Two of these young natal males dispersed together 2 months after a male from a neighbouring group ousted the single resident adult male of their group. Following this take-over, there were frequent interactions with the new male's former group, and the two natal males eventually stayed behind and joined that group. The new resident male was never observed to behave aggressively towards these natal males and these two natal emigrations were, therefore, classified as occurring in the context of intergroup interactions. In the third case associated with a change-over in resident males, a young natal male emigrated one month after an adult male nonaggressively joined his natal group (all adult males had left before the arrival of this male). Again, no aggression was ever observed between the natal male and the new resident male. This dispersal event has been classified as occurring in the context of a breakdown in the relationships among group males, because the natal male followed several of his former co-resident males in joining a neighbouring group. None of these three cases of male transfer following a change-over in resident males can be described as an eviction, because they involved no overt harassment or aggression between the new residents and the natal males.

The most frequently observed circumstance surrounding the disappearance of natal males was a breakdown in the relationships between group males. Such breakdowns involved either a loss in the cohesiveness of group males, which often occurred when some of the group's adult males would disappear for days at a time while 'visiting' neighbouring groups prior to immigration, or the actual emigration (death in one case) of older co-resident males. In the majority of these cases, all co-resident males, with the exception of the alpha male, emigrated from the group. Eight of the natal males in the study groups (38%) dispersed under these conditions. For example, in December 1996, two of the three LV co-resident adult males dispersed from the group and four juvenile and two subadult males (five of which were natal males) accompanied them into neighbouring groups, leaving the LV alpha male to defend the group on his own (Rose 1998).

Another condition for male natal emigration was to transfer groups following encounters with a neighbouring group ($N = 6$; 29% of the natal male sample). The home ranges of two or more groups of capuchins usually overlap (Freese & Oppenheimer 1981; Rose & Fedigan 1995; Jack 2001; Fragaszy et al. 2004). Although intergroup encounters do not occur on a daily, or often even a weekly, basis, they are a major component of this species' behavioural ecology and social organization (Perry 1996). Such encounters among adult members of neighbouring groups are usually hostile, but young males have been observed to stay behind and interact affiliatively with similarly aged individuals of neighbouring groups, and sometimes remain as members of these neighbouring groups (group transfer). Four of the natal males in the sample (19%) were suspected to have dispersed as a result of a fissioning of their group (two cases of fission). In these two cases, several group members, including adult males, adult females and immatures, disappeared at the same time.

The three remaining natal males in the sample (14%) disappeared during periods when monthly observations were not being conducted and the factors surrounding their departures were unknown. Of these three males, the two youngest (ages 24 and 35 months) disappeared with a low-ranking adult male during a 3-week period when researchers were absent from the park in December 1998. Another natal male disappeared from CP with an adult female who was probably his mother (they affiliated regularly and she was part of his natal group since the study began in 1985). The latter two animals went missing during the 6-month period in 1991 during which no observations were made on the groups.

In summary, 38% ($N = 8$; six confirmed emigrations) of the natal males emigrated when relationships between co-resident males began to break down; 29% ($N = 6$; five confirmed emigrations) transferred into neighbouring groups following a series of intergroup encounters; 19% ($N = 4$) were suspected to have left their natal groups as part of a group fission; and the remaining 14% ($N = 3$) disappeared for unknown reasons during a period of observer absence (Table 2).

Frequency of Parallel Emigration

Of the 21 natal male emigrants, 16 emigrated in the company of at least one other groupmate and a 17th male joined a group containing familiar individuals. Table 4 summarizes the frequency of the observed dispersal patterns: 13 males emigrated/disappeared (eight confirmed emigrations/immigrations) with one or more adult/subadult co-resident males; two brothers (ages 6.7 and 2 years) disappeared at the same time as their mother and another adult female; one male was confirmed to join a previously transferred older brother and male agemate in a neighbouring group; and one male disappeared with an adult female who was probably his mother. The remaining four natal emigrants (19%) dispersed from their birth groups on their own and two of these were confirmed emigrations/immigrations.

Parallel emigration can occur in two main ways: first, when maternal siblings or members of the same age cohort (possible paternal siblings) emigrate together or, second, when migrating males enter groups containing familiar, previously dispersed, males from their natal group (Altmann 1979; van Hooff 2000). Fifteen (71%) of

Table 4. Frequency of observed dispersal patterns (confirmed emigration/immigration)

Dispersal pattern	Number of observations
With co-resident males*	15 (8)
Joins familiar male(s)†	1 (1)
With female co-residents	1
Alone	4 (2)
Total	21 (11)

*Includes two young brothers who disappeared at the same time as their mother and another adult female.
†Dispersing male transferred into a group containing a familiar male.

the natal emigrations were thought, or known, to be parallel. Note that this total excludes one natal male who disappeared with two recent immigrants into his natal group, because it was unlikely that the three males were related and the occurrence did not fit with the traditional definition of parallel dispersal as followed here. Eleven of the dispersing natal males were observed following their transfer into their next group. Of these confirmed transfers ($N = 11$), nine (82%) were parallel.

DISCUSSION

The emigration of male white-faced capuchins from their birth group appears to be in response to three main circumstances: frequent interactions between neighbouring groups, the breakdown in group dynamics (particularly in the relationships among resident males) and a fission of the natal group. To elucidate the proximate cause of natal emigration in this species, we examine these circumstances in light of the predictions set forth in the Introduction. Our review of the long-term behavioural and demographic data collected on the capuchins in SRNP indicates that eviction, in the context of a group take-over, was not a direct cause of natal emigration in the study population. None of the natal emigrations summarized herein were classified as an eviction from the natal group following a take-over by extragroup males. Furthermore, there were no observed cases of natal males being evicted during non-take-over times and male–male aggression within groups was very low. Indeed, we observed many occasions where co-resident males and females, particularly alpha males, actively searched and called for the missing natal males. In these cases, the alpha male became extremely vigilant and produced a special vocalization, known as a 'lost call', which is only produced when an individual is either lost or missing from the group. These calls travel over long distances and function as location calls (see Perry 1998).

We predicted that if males emigrate from their natal group because of an attraction to extragroup females, emigration should occur at or near the age of sexual maturity. Male natal emigration in the Santa Rosa study groups was confirmed to occur as early as 20 months and as late as 96 months, with a median of 54.6 months (~ 4.5 years). Male white-faced capuchins are not estimated to attain sexual maturity until approximately 8 years of age (Freese & Oppenheimer 1981), which coincides with the upper age limit of natal emigration observed in the Santa Rosa study groups but is well above the sample mean of 4.5 years. However, data on captive representatives of this species are needed for confirmation of this estimate, as great variation in age at sexual maturity has been reported for captive males of the closely related tufted capuchin, *C. apella*. For example, Fragaszy & Adams-Curtis (1998) found that males in their captive study population were reproducing for the first time by 4.4 years, whereas Patino et al. (1996) and Nagle & Denari (1982) reported that males in their colonies were not capable of reproduction before 7 years of age. No comparable captive data are currently available for male white-faced capuchins;

however, in general, the Santa Rosa population appears to display a slower life history than captive tufted capuchins (cf. Fedigan et al. 1996; Fragaszy & Adams-Curtis 1998). The youngest male confirmed to mate within our study groups (i.e. ejaculation was confirmed) was a 6- or 7-year-old immigrant male (L. M. Rose, personal communication). It is possible that 4.5 years represents the lower limit of reproductive ability for male white-faced capuchins and therefore, that this age of natal emigration evolved in response to breeding potential and as a mechanism of inbreeding avoidance. However, it seems more likely that these males typically emigrate from their natal groups 2–3 years before becoming sexually active.

Regardless of the timing of sexual maturity in white-faced capuchins, males emigrate many years prior to attaining full body size, a common occurrence in many male-dispersed species (Greenwood 1980; Pusey & Packer 1987a). The upper age limit for natal emigration that we observed in the SRNP population was 8 years. At 8 years, male white-faced capuchins are classified as subadults and it is at this age that they begin to undergo noticeable changes in their social interactions and physical appearance. During the subadult phase, young males begin to spend more time interacting with adult females in their groups (nonkin, as all males have emigrated from their natal groups by this age), less time playing, and generally behave in a way more on par with adult males (K. Jack, unpublished data). Between the ages of 8 and 10 years, male capuchins also begin to fill out, changing from the long and lanky physique of a juvenile, and approximating the more robust frame of an adult male. Observations of known natal males in SRNP confirm that they do not attain full adult male body size until approximately 10 years of age.

We also predicted that if natal dispersal occurs in response to an attraction to extragroup mates, the timing should coincide with the mating/conception season. Such coordination in the timing of dispersal has been observed for a number of seasonally breeding primate species (Pusey & Packer 1987a; Sprague 1992; Sussman 1992). Although white-faced capuchins are not considered seasonal breeders, they do display a significant birth peak between January and April (Fedigan et al. 1996) and, therefore, there must also be a peak in the timing of conception. Gestation in this species is estimated at approximately 6 months (Fedigan et al. 1996), and the long-term data indicate that the majority of conceptions occur during the rainy season (June–November). Natal emigrations in the SRNP study groups occurred during the dry season. This observation, together with the finding that natal males probably disperse prior to sexual maturity, and many years prior to attaining physical maturity, suggests that mating opportunities, and an attraction to extragroup females, may not be an initial trigger for natal emigration.

Instead, the data point to an attraction to extragroup males or dispersing groupmates. Twenty-nine per cent of the natal males dispersed following intergroup encounters (direct transfers), and observations of natal males emigrating together and/or into groups containing individuals familiar to them, were common. In fact, the data collected on the SRNP capuchins demonstrate that male natal emigration is rarely a solitary event. Among the 21 emigrating males in the natal sample, 17 dispersed in the company of at least one other groupmate (male or female in the case of suspected group fissions) or into a group containing a familiar male. These 17 males represented 81% of the surviving natal male sample, and all but two of the 11 confirmed natal transfers (observed together in new group) were parallel. That is, 82% of confirmed male transfers were in the company of maternal siblings, members of their age cohort, and/or into groups containing familiar males.

Although the benefits of dispersal, in terms of inbreeding avoidance, may be high, dispersal also comes with risks. Dispersing individuals are probably at a higher risk of predation, aggression from unfamiliar conspecifics, or even starvation once they leave their familiar natal area in search of a new social group (e.g. Gartlan 1975; Dittus 1977; van Schaik 1983; Johnson & Gaines 1990; Isbell et al. 1993). The high frequency of parallel emigration and immigration observed among male white-faced capuchins indicates that the benefits of this dispersal pattern must be high. Familiarity and predictability in relationships may be an important benefit of parallel dispersal (van Hooff 2000), and dispersing in the company of other individuals provides added protection from predation and attacks by extragroup individuals (Rood 1987; Sussman 1992; reviewed in Isbell & van Vuren 1996). This pattern of dispersal has also been suggested to assist young, physically immature males, in their initial entry into another group (Cheney 1983; Cheney & Seyfarth 1983; van Noordwijk & van Schaik 1985).

Furthermore, one of the most important benefits of parallel dispersal may be increased inclusive fitness. Given the observations of male cooperation within groups, particularly in the context of group defence during intergroup aggression (Perry 1996; K. Jack, unpublished data), and the open mating system of this species (Manson et al. 1997), it may be in a male's best interest to reside in groups with related males. Relatedness among males residing in the LV and CP study groups from 1993 to 2000 is currently being analysed through the amplification of microsatellite markers obtained from follicular and faecal DNA. Given the high frequency of parallel emigration reported here, it is reasonable to assume a high degree of relatedness among group males even in the absence of these genetic data. Moore (1992) suggested that when natal individuals disperse together and subsequently join the same group, as has been observed among white-faced capuchins, this pattern may result in a level of relatedness within the new group that is comparable to that found in groups comprised of philopatric individuals. In her discussion of age cohorts, Altmann (1979) stressed the importance of considering the relatedness not only between maternal siblings (usually half-siblings when male tenure in groups is short), but also between members of an age cohort. Members of an age cohort are likely to be closely related, either as half-siblings if there is only one breeding male, or to a slightly lesser degree when several males are siring a cohort (Altmann 1979), as appears to be the case for white-faced capuchins.

In summary, our examination of natal dispersal of male white-faced capuchins indicates that their dispersal occurs primarily in response to an attraction to extragroup males or dispersing groupmates, rather than as the result of eviction by resident males, or an attraction to extragroup females. These findings are supported by the observed frequency of parallel dispersal, a dispersal pattern that may confer inclusive fitness benefits and provide added protection for these young, vulnerable males.

Acknowledgments

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