



Male dispersal patterns in white-faced capuchins, *Cebus capucinus*

Part 2: patterns and causes of secondary dispersal

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(Received 23 April 2002; initial acceptance 20 November 2002;
final acceptance 18 June 2003; MS. number: A9338R)

Male dispersal from the birth group is common in the majority of social mammals, and in many species, males also engage in secondary or breeding dispersal following natal emigration. However, the patterns and causes of secondary dispersal are poorly understood due to the difficulty in following emigrants. Here, we detail the patterns and causation of male secondary dispersal in several groups of white-faced capuchins observed between 1985 and 2000 in Santa Rosa National Park, Costa Rica. Subsequent to natal emigration, which occurs between 2 and 8 years of age (median 4.5 years), male white-faced capuchins embark on a life of continual movement. Although males of all age classes engage in voluntary secondary dispersal, the ways by which males enter groups varies according to their age class. Adult males (≥ 10 years old) are more likely to enter groups aggressively, and they display longer tenure than either subadult males (7–10 years of age) or juvenile males (1–7 years of age). Given our finding that adult males face the highest risks in terms of aggressive interactions with conspecifics, we examined several explanations as to why they continue to disperse throughout their lives. Our data best support the intragroup mating competition hypothesis for secondary dispersal, whereby males move frequently between groups as a means of increasing their reproductive opportunities. Males may also engage in frequent secondary dispersal to avoid mating with their maturing daughters, although this hypothesis was not strongly supported by the current data. Males of all age classes displayed very high levels of parallel dispersal, which probably serves to offset the high costs of dispersal (predation, starvation and/or aggression from conspecifics) and it may also serve as a means of retaining kinship among group males.

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Most mammals residing in multimale–multifemale social groups are characterized by a pattern of female philopatry and male emigration from the breeding site before attaining full maturity (Packer 1979; Greenwood 1980; Dobson 1982; Waser & Jones 1983; Cockburn et al. 1985; Pusey & Packer 1987a; but see Moore 1984; Strier 1994). Movement between groups does not, however, always end with natal dispersal. In many species, males engage in subsequent immigration into new breeding groups and several species are characterized by life-long movement of males between groups, which may be interspersed with periods of living alone or in all-male groups (e.g. lions, *Panthera leo*: Pusey & Packer 1987b; Japanese macaque,

Macaca fuscata: Sprague et al. 1998; longtailed macaques, *M. fascicularis*: van Noordwijk & van Schaik 1985; lion-tailed macaques, *M. silenus*: Kumar et al. 2001; moor macaques, *M. maurus*: Okamoto et al. 2000; rhesus macaques, *M. mulatta*: Drickamer & Vessey 1973; yellow baboons, *Papio anubis*: Packer 1979; olive baboons, *P. cynocephalus*: Alberts & Altmann 1995; vervets, *Chlorocebus aethiops*: Cheney 1983; South American squirrel monkeys, *Saimiri sciureus*: Mitchell 1994; ringtailed lemurs, *Lemur catta*: Sussman 1992). While natal dispersal has received much attention from behavioural ecologists, the patterns and causes of subsequent dispersal between breeding or social groups (Clobert et al. 2001), known as secondary or breeding dispersal, remain relatively unknown (Berteaux & Boutin 2000). Danchin et al. (2001) state that, in most animal species, the proximate mechanisms involved in natal and secondary dispersal are very different and they should therefore be studied independently (see also Suzuki et al. 1998; van Noordwijk &

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van Schaik 2001). Béchichon et al. (1996), in their review of the vertebrate literature addressing differential fitness of philopatric and dispersing individuals, found that studies focusing on secondary dispersal are primarily limited to birds. Few studies, particularly those focusing on long-lived social mammals such as primates, have followed the fates of individual dispersers through multiple emigrations (but see van Noordwijk & van Schaik 1985; Sussman 1992; Alberts & Altmann 1995).

This is the second paper in our investigation of the dispersal patterns of male white-faced capuchins in Santa Rosa National Park, Costa Rica. The first of these papers (Jack & Fedigan 2004) focused on the emigration of natal males and the proximate factors influencing their dispersal. In this paper, we document the patterns of secondary dispersal according to male age class and we test several hypotheses for why males engage in secondary dispersal.

Patterns of Age-related Dispersal

Capuchins are characterized by male dispersal and female philopatry, and long-term monitoring of white-faced capuchin groups has demonstrated that male tenure is short and males may change groups repeatedly throughout their lives (Fedigan et al. 1996). Long-term studies of this species at two Costa Rican field sites report that complete change-overs in group males occur approximately every 4 years (Rose & Fedigan 1995; Perry 1998). Although dispersal in many mammalian species is often limited to a specific life history stage (Smale et al. 1997), this pattern of multiple transfers by males has been observed among several primate species and lions, where male dispersal patterns are also reported to be age related (e.g. primates: Sugiyama 1976; Cheney & Seyfarth 1983; Sprague 1992; Strier 2000; reviewed in Jack 2003b; lions: Packer & Pusey 1982; Bertram 1983). For example, in most primates, natal emigration occurs prior to sexual and/or physical maturity (Itani 1972; reviewed in Melnick & Pearl 1987). Dispersing natal males are usually unable to attain a high rank within new groups, because they have not yet achieved the physical strength necessary to defeat the dominant adult males (Cheney & Seyfarth 1983; van Noordwijk & van Schaik 1985; Sprague et al. 1998). Secondary dispersal, on the other hand, typically occurs once a male has attained physical maturity, by which time he is able to compete with resident males and enter a group at a higher rank (van Noordwijk & van Schaik 1985; Strier 2000). Interestingly, in long-lived and slowly developing species like primates (e.g. life expectancy of captive male white-faced capuchins is about 55 years: Hakeem et al. 1996), males appear to reside in several groups before they reach full adult size and begin reproducing (Suzuki et al. 1998; van Noordwijk & van Schaik 2001; reviewed in Jack 2003b).

Regardless of age, entering a new group is a stressful activity (Alberts et al. 1992; Alberts & Altmann 1995) and males can attempt entry in several ways. In species characterized by a single breeding male, new males must successfully defeat the resident male to join the group, usually through aggressive interactions (Hrdy 1977; reviewed in Pusey & Packer 1987a). In multimale species,

several options exist for entering new groups. Males can enter by force, fighting for dominant positions within the group, a pattern observed among baboons (Packer 1979), longtailed macaques (van Noordwijk & van Schaik 1985), and in multimale groups of Hanuman langurs, *Semnopithecus entellus* (Borries 2000). In these cases, resident males often remain in their group at lowered dominance positions after new males have entered their group by force. In white-faced capuchins, coalitions of two to four males have been observed to aggressively take over groups and evict resident males (Fedigan 1993; Rose 1998; S. E. Perry, personal communication). In this species, these aggressive take-overs have been observed to result in the deaths or disappearances of both resident males and females (Fedigan 1993), and infanticides are also common in the year following a group take-over (Fedigan 2003). Male cooperation is not only essential in gaining entrance into a group, but is also the key in retaining membership within it. It is when alpha males lose the support of their co-resident males, usually through their emigration, that they are unable to defend the group from attacks by male coalitions (Rose & Fedigan 1995). Details of these take-overs in white-faced capuchins are very similar to those reported for lions (Packer 1983; Pusey & Packer 1987b) and red howler monkeys, *Alouatta seniculus* (Pope 1990; Crocket & Pope 1993), but this pattern does not appear to be common in other multimale primate species. In many of the multimale primate species, it is more common for males to enter groups peacefully (i.e. quietly and without fighting) and to initially assume lower status in the existing dominance hierarchy (e.g. Japanese macaques: Sugiyama & Ohsawa 1975; Sprague 1992; Sprague et al. 1998; vervets: Henzi & Lucas 1980; longtailed macaques: van Noordwijk & van Schaik 1985). Some species show both aggressive and peaceful patterns of male immigration (longtailed macaques: van Noordwijk & van Schaik 1985; white-faced capuchins: Fedigan 1993; Perry 1996), although there is still little known about the factors influencing the way in which males enter into groups and whether or not these vary according to age.

Explanations for Secondary Dispersal

Dispersal is presumed to reflect a male's attempt to increase his reproductive success (e.g. Greenwood 1980; Moore & Ali 1984; Clutton-Brock 1989; Alberts & Altmann 1995) and may result from intrasexual competition for mates (e.g. Dobson 1982; Moore & Ali 1984; Waser 1985; Pusey 1987; Shields 1987). For example, Sussman (1992) found that adult male ringtailed lemurs preferentially transferred into groups with more favourable sex ratios, and studies of several species of Old World monkeys have demonstrated that males often disperse in an attempt to increase their rank (Altmann & Altmann 1970; Henzi & Lucas 1980; Cheney & Seyfarth 1983). In most species, male dominance hierarchies are the result of intrasexual competition within groups (Walters & Seyfarth 1987) and the majority of wild primate species for which paternity data are available show a significant positive correlation between male dominance rank and reproductive success (reviewed in Jack 2003b). These findings

indicate that dispersal may be a male reproductive strategy in that it functions to increase male dominance rank, which, in turn, confers the potential for increased reproductive success. Male eviction from a group (i.e. forced dispersal) is also a manifestation of intrasexual competition that may lead to secondary emigration (for a review on primates see Pusey & Packer 1987a; lions: Pusey & Packer 1987b; white-faced capuchins: Fedigan 1993). Long-term studies of lions indicate that avoidance of maturing daughters may also be an important factor influencing male secondary dispersal (Pusey & Packer 1987b) and this finding might help to explain short male tenure in several species of polygynous primates. For example, male Japanese macaques have a mean tenure of between 2 and 4 years (Huffman 1991; Sprague et al. 1998) and female Japanese macaques attain sexual maturity at 3.5 years (Melnick & Pearl 1987), with age at first reproduction occurring at 5 years of age (Ross 1992). The voluntary emigration of resident male Japanese macaques may be in response to their maturing offspring, although frequent dispersal has also been attributed to an overall decline in mating success after a male has spent a few years in a group (Furuichi 1985; Huffman 1992; Perloe 1992).

In this paper, we examine the patterns of male secondary dispersal derived from 16 years (1985–2000) of behavioural and demographic data collected on multiple groups of white-faced capuchins in Santa Rosa National Park, Costa Rica. We begin by addressing the effect of male age on patterns of secondary dispersal. For example, does the way a male enters a group change with age? Are males of particular age classes more likely to use cooperative aggression, forcing their way into groups and evicting resident males, or do they enter peacefully and join the resident males already present in the group? Does male tenure within groups vary according to age class, and does the frequency of parallel dispersal decrease with male age, as has been reported for other male-dispersed primate species?

We then examine the two main ultimate hypotheses suggested to explain male secondary dispersal by adult and subadult males: inbreeding avoidance and mating competition.

Inbreeding avoidance

If males engage in secondary dispersal to avoid mating with maturing daughters, we predicted that male dispersal would be voluntary and male tenure within groups would be shorter than female age at first birth (i.e. gestation length plus female age at reproductive maturity). Note that female white-faced capuchins very rarely transfer between groups (they are philopatric), and we have never observed a male re-enter his natal group. For these reasons, it is very unlikely that any immigrant male would be residing in a group with female kin other than maturing daughters.

Intrasexual mating competition

We examined this hypothesis according to whether mating competition occurs (1) between groups (extragroup mating competition) or (2) within groups (intragroup mating competition).

Extragroup mating competition. If male secondary dispersal is related to extragroup competition for mates, we predicted that secondary dispersal due to eviction by extragroup males (i.e. dispersal resulting from aggressive group take-overs) would be high and voluntary dispersal would be low.

Intragroup mating competition. If males emigrate as a result of mating competition occurring within their group, males should disperse in an attempt to increase their dominance rank, which may lead to increased reproductive opportunities. If male reproductive success is correlated with male dominance rank, we predicted that subordinate males should display shorter tenure within groups than alpha males; that subordinate males should disperse voluntarily, whereas alphas should disperse following group take-overs (eviction); and that males should attain higher ranks following group transfer (note that all of these predictions need not be met to accept the hypothesis). We also predicted that males would transfer into groups with more favourable sex ratios.

METHODS

Study Site

Data were collected in the Santa Rosa Sector of the Area de Conservacion Guanacaste, in northwestern Costa Rica. Protection of this sector, formerly known as Santa Rosa National Park (SRNP), the original boundaries of which encompass approximately 108 km² of tropical dry forest in various stages of regeneration, began in 1971. SRNP ranges from 300 m in altitude to sea level, where the park is bordered by the Pacific Ocean. The Guanacaste Province experiences a distinct dry season during December–May, and a rainy season during June–November, during which an average of 1472 mm of rain falls (D. H. Janzen & W. Hallwachs, unpublished data). For a detailed description of the site, see Fedigan et al. (1996) and Fedigan & Jack (2001).

Species

White-faced capuchins reside in groups comprised of multiple immigrant males, related females and their juvenile offspring. Group sizes average approximately 17 individuals (range 7–36) comprised of 4–5 adult males, 5–6 adult females and 7–8 immatures (Fedigan & Jack 2001). Due to the philopatric nature of females and the formation of long-term affiliative relationships observed among them, the species is described as female bonded (Fragaszy et al. 2004). However, the maintenance of long-term affiliative bonds between males has also been described for this species (Perry 1998; Jack 2003a). Adult male white-faced capuchins are 25–35% larger than adult females and, with the exception of the alpha female, are usually dominant over females (Fedigan 1993). White-faced capuchins frequently engage in nonconceptive mating, show no external signs of oestrus (Manson et al. 1997), and although they are not strict seasonal breeders,

they do display a birth peak between January and April (Fedigan et al. 1996). Preliminary DNA analysis has demonstrated that dominant males sire the majority of offspring in this species (Jack & Fedigan 2003).

Study Groups

Behavioural observations of our first two study groups, Sendero (SE) and Cerco de Piedra (CP), began in 1984, with discrimination of all individuals, including juveniles, being achieved in 1985. We added a third group, Los Valles (LV), in 1990 when members of our study groups emigrated into this neighbouring group, a fourth and fifth group, Bosque Humedo (BH) and Cuajiniquil (CU), in 1997, and a sixth group, Cafetal (CA), in 1999, all because we were tracking our study males into new groups. Group SE was observed until 1993 when it dissolved, and groups BH, CU and CA have only been observed intermittently since 2000, when they entered a stage of continuous, rapidly changing membership.

Study groups were monitored for membership at least twice per month, and were usually the focus of intensive behavioural observations collected on a daily basis (with the exception of 21 months spread over five rainy seasons: a 6-month hiatus in 1991, 3 months in 1995, 4 months in 1996, 5 months in 1997 and 3 months in 1999). Data presented here incorporate 8 years of observations collected on the SE group (1985–1993), 14 years on the CP group (1985–2000), 10 years on the LV group (March 1990–May 2000), 3 years on groups CU and BH (1997–2000), and 2 months on the CA group (1999). The age breakdown for male white-faced capuchins used here was: infant: ≤ 1 year; juvenile: 1–7 years; subadult: 7–10 years; adult: ≥ 10 years (Fedigan et al. 1996). Male white-faced capuchins are not estimated to attain sexual maturity until approximately 8 years of age (Freese & Oppenheimer 1981) and within our study groups, we have only once observed a juvenile male (an immigrant male aged 6–7 years) engage in sexual activities with group females (see Jack & Fedigan 2004). Life expectancy of captive male white-faced capuchins is 55 years (Hakeem et al. 1996), and although the exact life expectancy of wild male capuchins is unknown, the oldest known male in our study groups was estimated to be 20 years. He appeared in our study groups as an adult (≥ 10 years) in 1993 and was still present as of January 2003. However, in general, it is very difficult to estimate the exact age of adult male white-faced capuchins with any accuracy.

Definitions

Where appropriate, we distinguish between a 'confirmed emigration', defined as the departure of a male from a group and his confirmed immigration into a different group, and a 'disappearance', defined as all departures where the survival and/or subsequent immigration of a male could not be established. Confirmed emigrations plus disappearances are collectively referred to as 'dispersals'. Following Fedigan (2003), we define a 'take-over' as the aggressive challenge and replacement of group males

by extragroup males. We distinguish between emigration events according to whether males dispersed from the group voluntarily or whether they were evicted. A dispersal event was labelled as 'voluntary' if it did not occur in the context of, or within 3 months following, a group take-over. The term 'eviction' is used to describe those dispersal events that occurred within 3 months of a group take-over (i.e. resident males were attacked, wounded and repeatedly driven out of the group's range by newcomer males). Likewise, we categorize immigration types as being either 'peaceful' (involving no aggression between incoming and resident males) or 'aggressive' (occurring in the context of a take-over). A group was considered 'abandoned' when there were no adult or subadult males present.

Data Analysis

SPSS SURVIVAL analysis was used to determine the length of male tenure in the study groups. This analysis allows for the use of both completed/uncensored intervals (i.e. known male tenure within groups), and incomplete/censored intervals (i.e. males who were present in groups when the study began, or males that remained in the groups in May 2000). This method is preferred because analyses based solely on completed intervals create a bias towards shorter intervals. SPSS SURVIVAL analysis generates the median survivorship for each group and performs a Wilcoxon (Gehan) test for comparing survival distributions between groups. We used Wilcoxon matched-pairs signed-ranks tests to compare the sex ratios of the groups between which males transferred, and the rank of these males before and after their transfer between known groups. We used Spearman's rho to test for correlation between the mating peak and the timing of male secondary emigration. We also used a chi-square analysis, with Yates correction for small sample size, to test for differences between subordinate and dominant males in the frequency of voluntary dispersal and forced dispersal (eviction). Significance was set at $P \leq 0.05$ (two-tailed probabilities) for all statistical analyses.

RESULTS

Patterns of Age-related Dispersal

How male white-faced capuchins enter groups

Table 1 summarizes the types of immigrations of the 34 males (19 adults, 4 subadults and 11 juveniles) who entered our three main study groups (SE, CP, LV) during the specified periods. One juvenile male was excluded from the analysis because he entered one of our study groups during a period of researcher absence. The sample of juvenile males that moved into the study groups includes several males that were known to be arriving directly from their natal groups, and it is likely that many of these juvenile males were transferring for the first time. We included these males here to allow for a comparison of immigration styles among the three age classes. In contrast, all subadult and adult males that entered study groups were considered secondary immigrants, because

Table 1. Type of immigration according to male age class

Type of immigration	Adult	Subadult	Juvenile	Total
Aggressive take-over	13	0	0	13
Peaceful	6	4	10	20
Unknown	0	0	1	1*
Total	19	4	11	34

*Excluded from analysis due to researcher absence.

we have never observed a male to remain in his natal group beyond 8 years of age (average age of natal dispersal is ~4.5 years; Jack & Fedigan 2004).

Thirteen of the 33 males, or 39% of the immigrant sample, entered into the groups aggressively and in all but one case ousted the resident male(s) (Table 2). All of the males involved in group take-overs were adults and they represent 68% of the immigrant adult males in our sample. However, researchers in SRNP have also observed or inferred take-overs in nonstudy groups in which subadult and even juvenile males were involved, although the participation of these young males was minor (e.g. facial threats). The 13 adult males involved in aggressive group take-overs represent only seven actual take-over events that occurred within our three long-term study groups during the specified periods. Of these seven take-overs, three were brought about by single males, while the remainder involved the cooperation of two or more males. Of the three take-overs by solitary adult males, two occurred in groups containing only a single resident male (one of these attempts was unsuccessful), and the third solitary male take-over was directed at a group with one adult and one subadult male. The latter take-over was the only case in which invaders were outnumbered by resident males and one of two cases (see also LV 2000) where a resident male remained in the group following a take-over. In all other cases, resident males were either outnumbered by invaders ($N = 3$), or their numbers were equally matched ($N = 3$), and all resident males were aggressively evicted from the group.

We cannot be certain that we did not miss other unsuccessful take-over attempts. Members of the SRNP research team have frequently observed single males or small groups of males ‘checking out’ the study groups, possibly with the intent of taking over (or of joining peacefully). However, these males were always chased away by the resident males before any overt take-over attempts began. Rose (1998) detailed an unsuccessful take-over attempt of the LV group by a single male.

A higher percentage of males, 61% ($N = 20$; six adults, four subadults, 10 juveniles), entered the study groups in a peaceful fashion (Table 1). Ten of these 20 males did so on their own, whereas the remaining 10 males entered in the company of other males. All of the adult males who peacefully entered groups joined groups that were temporarily without resident males, and these adult immigrants were able to nonaggressively assume dominant positions within the group. We have never observed an adult male entering a group peacefully and joining the resident males as a low-ranking group member.

Why males leave groups: voluntary or forced dispersal?

A total of 56 secondary dispersal events occurred during the specified periods for the five study groups (36 adults, 10 subadults and 10 juveniles). Twenty-six of these were confirmed emigrations (i.e. the males were later observed residing in other groups), whereas the remaining 30 were disappearances. Three of the 30 disappearances were not included in this analysis because one juvenile male disappeared during a period of researcher absence and we are fairly certain that two adult males died rather than dispersed. We examined the circumstances surrounding the remaining 53 dispersal events to determine whether they were the direct result of eviction following a group take-over by extragroup males, or whether they were voluntary in nature. These data are summarized in Table 3. Forty-six of the 53 dispersals met our criteria for ‘voluntary’ (i.e. they were not preceded by increased male–male aggression and did not occur within 3 months of a take-over). However, seven of the dispersals were observed to result from eviction following group

Table 2. Summary of immigration through aggressive take-over in the three main study groups (SE, CP, LV)

Invading males (group invaded)	Target group			Notes
	Size before invasion	Male:female sex ratio before invasion	Male:female sex ratio after invasion	
1 One male (SE 1991)	9	1:3	1:3	
2 One male (CP 1990)	14	2*:5	3:4	The former alpha was tolerated as a group member after several months.
3 One male (LV 1997)	14	1:4	1:4	Take-over was unsuccessful; the same male joined LV several months later during take-over 5.
4 Two males (SE 1993)	6	1:2	2:2	Group dissolved 3 months later.
5 Four males (CP 1993)	16	2:4	4:4	One of the four males disappeared after 2 months.
6 Two males (LV 1997)	14	1:4	2:5	An adult female joined the group with an immigrant male.
7 Two males (LV 2000)	14	2:4	3:4	The group’s former beta male remained.

All invading males were adults. The ratio of males to females in each target group includes adult females and males, except where noted.
*Includes one subadult male.

Table 3. Stimulus for male dispersal (confirmed emigrations)

	Adult	Subadult	Juvenile	Total
Eviction	6 (2)	0	1	7 (2)
Voluntary	28 (13)	10 (6)	8 (5)	46 (24)
Total	34 (15)	10 (6)	9 (5)	53 (26)

take-overs (i.e. resident males were attacked, wounded and repeatedly driven out of the group's range by newcomer males; one alpha male that tried to return was fatally wounded by new resident males). With the exception of one juvenile male who disappeared with his group's alpha male following a take-over, all of the remaining evictions involved adult males ($N = 6$). All of the subadult males ($N = 10$), the remaining juvenile males ($N = 8$) and 82% of the adult males ($N = 28$) dispersed from their groups under what appeared to be voluntary circumstances.

How males leave groups: frequency of parallel dispersal according to male age class

Dispersal events were further examined to determine whether the frequency of parallel dispersal, that is dispersal with co-resident males or into groups containing familiar males (van Hooff 2000), was age related. Overall, the frequency of parallel dispersal was very high in our sample and the results for each age class are summarized in Table 4. Of the 53 dispersal events (34 adult males, 10 subadults, nine juveniles), 36 (68%) were parallel (20 confirmed emigrations) and four additional males (three adults and one juvenile) dispersed in the company of female co-residents (two confirmed emigrations). Excluding these latter emigrants, the rates of parallel dispersal according to male age class were: 74% (23/31) for adult males, 80% (8/10) for subadult males and 63% (5/8) for juveniles.

Male age class and tenure length

Since our study began, a total of 61 immigrant males (32 adults, 10 subadults and 19 juveniles; age classes were assigned to males according to their estimated age at group entry) have resided in the five study groups (SE, CP, LV, BH, CU). Of these 61 males, we were unable to calculate the exact length of tenure for 24, because they either were present in the groups when observations began, or were still residing in the groups as of May 2000. In these cases, we assigned a censored (incomplete) interval to each male's tenure length. SURVIVAL analysis

Table 4. Frequency of parallel dispersal according to male age class (confirmed emigrants)

	Adult	Subadult	Juvenile	Total
Disperse with female co-residents	3 (2)	0	1	4 (2)
Parallel*	23 (10)	8 (5)	5 (5)	36 (20)
Disperse alone	8 (3)	2 (1)	3	13 (4)
Total	34 (15)	10 (6)	9 (5)	53 (26)

*Includes dispersal with co-resident males or joining familiar males in the new group.

showed that median tenure for all of the 61 males was 41 months (range 4–67 months). We then compared the data for differences between the three age classes of immigrant males (adult, subadult, juvenile) within our study groups. According to SURVIVAL analysis, the median tenure was 48.9 months ($N = 32$; range 9–53 months) for adult males, 27.7 months ($N = 10$; range 19–36 months) for subadults and 42.7 months ($N = 19$; range 4–67 months) for juveniles. Adult males had significantly longer tenure within groups than subadult males (Wilcoxon Gehan test: $Z = 6.186$, $N = 42$, $P = 0.01$), whereas the other age class comparisons did not yield significant differences.

Causes of Secondary Dispersal

Rank differences in why males leave groups: voluntary or forced dispersal?

We examined the proximate reasons for male secondary dispersal according to male rank to determine whether alpha and subordinate males differed in why they left their groups; that is, forced or voluntary dispersal. We removed females from the hierarchies and calculated male ranks. Subadults were excluded from this analysis because they all dispersed under what appeared to be voluntary conditions (see Table 3), they differed significantly from adult males in their tenure within groups (see above), and they always ranked below adult males. We also excluded juveniles from the analysis because of this latter reasoning and because their ranks were not always recorded or obvious. A total of 32 adult males resided in our study groups during the specified periods. Of these males, 13 were alphas and 19 were subordinates. Of the 13 alpha males in our sample, two were still residing in the study groups as of May 2000, and one left the group during a period of researcher absence and so we cannot be sure of the direct cause of his emigration (he was later observed as a member of a neighbouring group). Only seven males in our sample dispersed due to eviction from the group (Table 3) and six of these cases involved adult males (the seventh case involved a juvenile male). Of these six males, five were alphas and only one was a subordinate. This means that 50% of the alpha males (i.e. five of the 10 alpha males for which we had data) were forced from their groups and the other 50% dispersed voluntarily (Fig. 1). The rate of forced dispersal for adult subordinate males was much lower, with only one of the 19 (5.3%) being evicted from his group (Fig. 1). In the latter instance, the subordinate male was evicted following a take-over of his group by four adult males, during which the resident alpha male died from the wounds he received. After these events, the subordinate male disappeared from the group's range. These data clearly show that subordinate males were more likely to disperse voluntarily than were alpha males and this difference was significant (chi-square with Yates correction: $\chi_1^2 = 5.497$, $P = 0.019$).

Male rank and tenure length

We further examined adult male tenure according to male rank to determine whether alpha and subordinate males

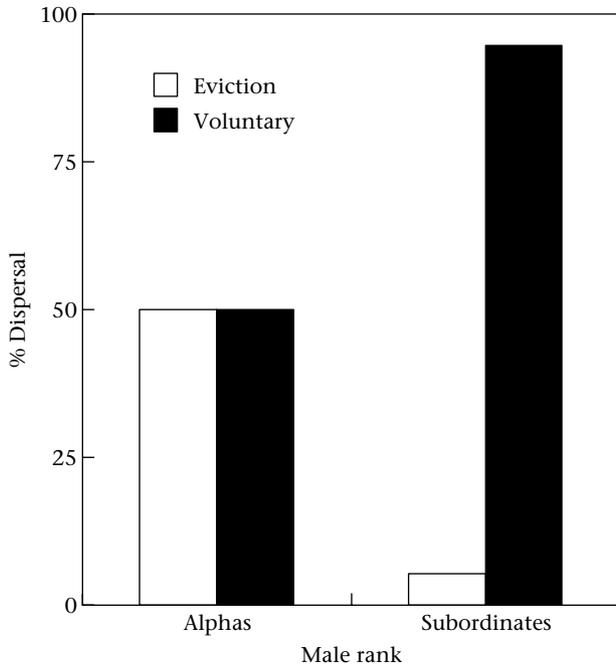


Figure 1. Rank differences in males that left groups voluntarily or due to eviction.

differed in the length of time they spent in groups. Only those males who entered our study groups as fully adult individuals, or were adult when observations began, were included in this analysis, again due to the influence of age class on male tenure within groups and the fact that all subadults and juveniles rank below alpha males. We also excluded one adult alpha male (from the total of 13) because

he remained temporarily in the study group as a subordinate after the take-over of his group. SURVIVAL analysis indicated that subordinate males ($N = 19$) had a slightly higher median tenure in groups (51.4 months; range 9–51 months) than alpha males ($N = 12$; 47.92 months; range 23–54 months), but this difference was not significant (Wilcoxon Gehan test: $Z = 0.028$, $N = 31$, $P = 0.87$).

We also examined the tenure length of alpha males to determine whether there were any differences according to whether they dispersed voluntarily or were evicted from the group. SURVIVAL analysis showed that the median tenure length for alpha males voluntarily leaving their group was 54 months ($N = 5$; range 24–51 months), whereas those dispersing due to eviction had a shorter tenure length of 33 months ($N = 5$; range 23–53 months). These differences were not significant (Wilcoxon Gehan test: $Z = 1.601$, $N = 10$, $P = 0.2$). Note that in all five cases where an alpha male voluntarily emigrated from his group, he was actually abandoning the group because all co-resident males had previously dispersed.

Group transfers: changes in rank and sex ratio

Nine males (seven adults and two subadults) moved between our three long-term study groups and seven males (four adults and three subadults) moved into nonstudy groups on which observations began after their transfers ($N = 16$; see Table 5). One juvenile individual also moved between groups, but was not included in this analysis because his rank was unknown. The circumstances surrounding the transfer of two males in our sample (males 1 and 2 in Table 5) were unknown because these males moved into the LV group where studies did not begin until almost a year later. Four of the 16 males

Table 5. Male rank and sex ratios within groups before and after group transfer

Males	Target group (status)*	Rank		Sex ratio†		
		Prior group	New group	Prior group (M:F)	New group (M:F)	
1	CP adult male	LV (unknown)	5	3	6:6	5:4
2	CP subadult	LV (unknown)	6	5		
3	CP adult male	SE (abandoned)	2	1	6:6	1:3
4	SE adult male	CP (abandoned)	3	1	4:3	2:5
5	SE subadult	CP (abandoned)	4	2		
6	LV subadult	CP (peaceful)	5	2	4:5	2:3
7	LV adult male	SE (take-over)	2	1	4:4	1:3
8	CP adult male‡	LV (peaceful/take-over)	1	1	3:2	5:5
9	LV adult male‡	CP (abandoned)	4	1	5:5	1:3
10	CP adult male	LV (take-over)	2	1	3:2	4:5
11	CP adult male	LV (take-over)	3	3		
12	LV adult male	BH (take-over)	2	1	7:4	4:4
13	LV adult male	CU (take-over)	3	1	7:4	2:2
14	LV subadult	CU (take-over)	5	2		
15	CU adult male	CA (take-over)	1	1	2:2	5:6
16	CU subadult	CA (take-over)	2	2		
Wilcoxon matched-pairs signed-ranks test			$Z = -3.109$, $P < 0.01$		$Z = -3.057$, $P < 0.01$	

*Abandoned: the transferring male(s) entered a group that did not have resident males; take-over: the male(s) evicted the resident males present in the group; peaceful: the male(s) joined resident males within the group; unknown: the circumstances surrounding the group entry were unknown.

†Sex ratio includes subadult males.

‡This is the same male. He entered the LV group peacefully after his two CP co-resident males had aggressively defeated LV's sole resident male. He assumed the alpha male role without opposition from his former subordinate males.

joined a group that had been abandoned by its resident males, one of whom (male 8/male 9 in Table 5) returned to the group that he had abandoned 9 months earlier. Nine males in our sample transferred into groups with resident males, and these groups were either joined peacefully, if the transferring male was a subadult ($N = 1$), or the resident males were aggressively evicted by the invading males ($N = 8$). The remaining male that transferred between study groups, CP male 8, took over as the alpha male of the neighbouring LV group after his two former co-resident males in the CP group (males 10 and 11 in Table 5) aggressively invaded and took over LV. CP male 8 appeared to assume the alpha male rank without any resistance from his two former subordinate males and the dominance hierarchy for these three males within LV was identical to what it had been in CP.

We compared the ranks of males in their groups before and after their transfer (Table 5). None of the 16 males in our sample experienced a decrease in their rank; four retained the same rank and 12 increased their rank by at least one position. The increase in male rank after transfer was significant (Wilcoxon matched-pairs signed-ranks test: $Z = -3.109$, $N = 16$, $P = 0.002$). We also compared sex ratios (males to adult females, including subadult males but excluding juveniles) between the groups from which males emigrated and to which they transferred (calculated after the transferring males had immigrated). Two of the 16 males (males 1 and 2 in Table 5) were observed 11 months after their disappearance as residents of the LV group, which at that time had a higher ratio of males to females than in their previous group (CP). The remaining 14 males in our sample transferred into groups with a lower ratio of males to females and, overall, the sex ratio decreased significantly ($Z = -3.057$, $N = 16$, $P = 0.002$) as a result of group transfer.

DISCUSSION

Patterns of Secondary Dispersal

Previous accounts of immigration in white-faced capuchins indicated that males enter groups in one of two ways: they either immigrate alone, joining resident males (Perry 1996), or cooperatively and aggressively enter a group and evict resident males (Fedigan 1993). In our study population, the way males enter social groups varied according to age class. Unless they were in the company of supportive adult males, physically immature males (subadults and juveniles) were restricted to entering groups in a peaceful fashion. We never observed an adult male peacefully enter a group at a low rank and join the adult males already present. If there were resident males in a group, immigrating adult males entered aggressively, most often evicting resident males, and always assumed the top dominance positions within the groups. It appears that the only way that an adult male can enter a group in a nonaggressive manner is by joining a group that is temporarily without resident males (an abandoned group). A total of 32% of our adult male sample entered groups in this manner. These immigrating adult males did not display wounds following their entry and they

appeared to enter the new groups opportunistically when resident males either were away from the group or had previously dispersed. We often observed males to be missing from our study groups for days at a time, and we also observed neighbouring males close to our study groups. At these times, males may be assessing their opportunities within new groups before their departure from their former groups (see Smale et al. 1997 for similar findings in other mammals).

The majority of the adult males in our sample (68%) entered new groups aggressively and in all but one of the seven take-overs in our sample evicted the resident males present in the group. Four of these seven take-overs involved multimale cooperative invasions of the type that has been previously reported for this species (Fedigan 1993). However, three of the take-overs involved a single adult male aggressively entering a social group and taking over as the group's dominant male. In these cases, the target group contained only one resident adult male and one of these take-over attempts was unsuccessful.

Immigrant male tenure within groups of white-faced capuchins was relatively short, averaging just less than 3.5 years when we considered males of all ages together. Of the three age classes, adult males had the longest tenure within groups and this probably reflects the higher risks adult males face during dispersal. The results of our study show that natal males (Jack & Fedigan 2004), as well as immigrant juvenile and subadult males, enter groups peacefully, unless they are in the company of more aggressive, physically mature males. Adult males, on the other hand, are much more likely to be the directors and recipients of conspecific aggression. Given that this aggression can be lethal, adult males benefit the most from longer tenure within groups.

It is curious that male dispersal, which is inevitably rife with increased risk of predation, aggression from conspecifics, or even starvation once males leave familiar areas in search of a new social group (e.g. Dittus 1977; van Schaik 1983; Johnson & Gaines 1990; Isbell et al. 1993; Alberts & Altmann 1995), is occurring at all life stages in white-faced capuchins. This anomaly is intensified when we take into account the fact that the majority of secondary dispersals are voluntary (88% in our study sample). As with natal dispersal, eviction as a proximate cause of secondary dispersal was infrequent for adult males (only 18% of our sample) and almost nonexistent for subadults and juveniles (only one juvenile male emigrated directly following a group take-over). Male white-faced capuchins may be offsetting the risks of dispersal by maintaining a high frequency of parallel dispersal at all life stages (i.e. juvenile, subadult and adult). In other primate species where males disperse in the company of groupmates, this phenomenon is much more commonly observed among young males than among adults (reviewed in Pusey & Packer 1987a) and Cheney (1983) proposed that parallel dispersal diminishes with male age because the risks of attack by conspecifics in the new group decrease with age. As males mature, they are better able to defend themselves and, therefore, there is a decreased need for male allies. However, in our study population, parallel dispersal remained high for all age

classes: 71% of natal males (see Jack & Fedigan 2004); 63% of juveniles; 80% of subadults; and 74% of adults. Given our finding that adult male white-faced capuchins are more at risk of conspecific aggression than are juvenile and subadult males (i.e. only adult males enter groups aggressively and have been known to die from wounds received), and previous reports that male coalitions are more successful at entering and maintaining membership within social groups (Fedigan 1993), parallel dispersal remains beneficial even into adulthood. Long-term data from Santa Rosa have clearly shown that males rely on allies throughout their lives; they need allies to get into groups and to retain membership within them (L. Fedigan, unpublished data). Although we do not have abundant data on how long males maintain coalitions with specific partners, we have observed several pairs of males through multiple emigrations and we have also seen many cases where males join familiar males who had dispersed as many as 5 years earlier (Jack 2001, 2003a). This indicates that males maintain their alliances over multiple emigrations. Such long-term alliances may serve to maintain male kinship within groups and we await further genetic analyses to test this possibility.

Causes of Secondary Dispersal

Within our study groups, a complete change-over in group males occurs approximately every 4 years (Fedigan 2003). Given the many risks associated with dispersal, particularly for adult male white-faced capuchins, the question of why these males disperse continually throughout their lives also arises. In reviewing the limited literature available, we identified two main ultimate explanations for secondary dispersal: (1) inbreeding avoidance, whereby males are dispersing to avoid mating with maturing daughters, and (2) intrasexual mating competition, whereby males are dispersing as a result of either (a) extragroup mating competition (i.e. they are evicted from the group by invading males) or (b) intragroup mating competition and males are changing groups to increase reproductive opportunities. We consider each of these explanations for secondary dispersal in adult and subadult male white-faced capuchins. We excluded juveniles from these analyses because they could not be reliably assigned a dominance rank within our study groups and because we have never observed a male under the age of 7 years to engage in copulations with females in our study groups.

Inbreeding avoidance

If male white-faced capuchins disperse in an attempt to avoid mating with maturing daughters within the group, we predicted that dispersal would be voluntary, and that male tenure within groups would be shorter than female age at first reproduction (this represents the time necessary for a group female to give birth and for that infant to reach sexual maturity). Within our study groups, male secondary dispersal was largely voluntary, with 82% of adult males and 100% of subadult males meeting our criteria for voluntary dispersal. The median tenure length

for adult males was 49 months (range 9–53 months), whereas that of subadults was 27.7 months (range 19–36). In the Santa Rosa study groups, we observed six females from birth through to the birth of their first infant (L. Fedigan, unpublished data), and their median age at first birth was 7 years (range 6–8 years) or 84 months, which is surprisingly advanced. The tenure length of both adult male and subadult males within our study groups was, therefore, much shorter than female age at reproductive maturity.

Given our previous finding that alpha males sire the majority of the offspring that are born into our study groups (see Jack & Fedigan 2003), we also examined tenure length of alpha males alone. For all 10 alphas, the median tenure length was 48 months. However, when we limited our examination only to those males that emigrated voluntarily ($N=5$), as would be predicted by the inbreeding hypothesis, the median tenure length was 54 months. In all five of the cases where alpha males voluntarily dispersed, the males actually abandoned their groups, leaving mates and offspring vulnerable to male invasions (see Fedigan 2003). Therefore, even when we restricted our analysis to alpha males that voluntarily dispersed from their groups, their tenure length was much shorter than female age at sexual maturity (i.e. 4.5 years versus 6–8 years).

Although our findings do not refute the inbreeding avoidance hypothesis, they do not provide overwhelming support for it. If males disperse as a means of avoiding mating with maturing daughters, these emigration events should occur at or near female age at reproductive maturity, rather than years before, as was the case in our study groups. In addition, there are many examples in the primate literature of males experiencing longer-than-average tenures within groups and it has been suggested that there are mechanisms other than dispersal that function to deter inbreeding avoidance (reviewed in Jack 2003b). For example, recent paternity studies have shown that alpha male tufted capuchins, *Cebus apella* (Escobar-Parámo 1999) and longtailed macaques (De Ruiter et al. 1992) sire the majority of offspring in their groups, and when males experience long breeding tenures, beta males sire the offspring of the alphas' daughters. Additionally, in female-dispersed primate species, secondary dispersal by adult females is rare, indicating that other mechanisms (e.g. kin recognition) must be at play (reviewed in Jack 2003b).

Intrasexual mating competition

Extragroup mating competition. If males engage in frequent secondary dispersal as a result of extragroup mating competition, we predicted that secondary dispersal would be the direct result of eviction, rather than voluntary emigration. Although previous reports (Fedigan 1993; Fedigan et al. 1996) indicated that eviction was a major factor influencing the lives and behaviour of adult male white-faced capuchins, it was not the primary factor influencing male dispersal patterns in the study groups. Given our finding that none of the dispersals by subadult males and only 18% of all dispersals by adult males were

the direct result of eviction from their groups, it does not appear that extragroup intrasexual competition for mates is a primary factor influencing secondary dispersal in male white-faced capuchins.

Intragroup mating competition. If males engage in frequent dispersal as a result of mating competition within their groups, secondary dispersal should result in increased reproductive opportunities. Overt or direct mating competition among males living within groups of white-faced capuchins is almost nonexistent. These monkeys are nonseasonal breeders, females do not show any external cues to ovulation, and nonconceptive copulations are common (Manson et al. 1997). In terms of male mating behaviour, co-resident male white-faced capuchins are extremely egalitarian. Males appear to make no effort to hide their mating activities, regardless of their rank. It has been suggested that, in these types of mating systems, the alpha tolerates the mating activities of his subordinates as a sort of 'staying incentive' so that they will remain in the group and assist him in defending it (i.e. maintaining residency in the group by cooperatively resisting male take-over attempts; Vehrencamp 1983; van Hooff 2000).

However, if all males in our study groups experienced mating success, why were the rates of voluntary dispersal so high? When we examined the data more closely to determine whether males left voluntarily or due to eviction, we discovered that subordinate males were more apt to disperse voluntarily than were alpha males. The frequency of voluntary dispersal by alpha males was 50%, much higher than initially expected, but the rate for subordinate males was staggering, at 95%. As mentioned, adult male dispersal is an extremely risky undertaking; unless males can find an abandoned group, they must fight their way into groups containing resident males. If co-resident males receive their so-called 'staying incentives' in terms of mating opportunities, then why do they leave voluntarily? One answer is suggested by DNA paternity analyses on our study groups, which indicated that, although all co-resident males experience mating success, reproductive success is largely restricted to alpha males (Jack & Fedigan 2003). These data show that some form of male mating competition is occurring within groups, be it through sperm competition or female choice or some other type of nonovert competition.

Having established that intragroup mating competition in white-faced capuchins does occur and that an individual male's reproductive success is closely tied to his dominance rank, we now examine the hypothesis that males engage in secondary dispersal as a means of increasing reproductive opportunities. To increase their access to reproductive opportunities, we predicted that subordinate males would display shorter tenure within groups, that males would transfer into groups with more favourable sex ratios and that dispersing males would attain higher ranks following group transfer. We did not find differences in the mean tenure length of subordinate and alpha males. We suspect that this might be because alpha male tenure length was reduced by evictions following aggressive group take-overs and that forced dispersal may have counterbalanced any proclivity that

alpha males might have shown to remain longer in groups than subordinate males. Indeed, alpha males that dispersed voluntarily displayed a median tenure length (54 months) that was slightly longer than that of subordinate males (51 months), whereas evicted alpha males experienced much shorter tenure lengths (33 months). We did find that males in our sample transferred into groups with significantly lower ratios of males to females and that transferring males experienced a significant increase in their rank following transfer.

Our findings that alpha males sire the majority of offspring, that subordinate males are more likely than alphas to disperse from groups voluntarily, that males experience a significant increase in their rank within new groups, and that males disperse into groups with more favourable sex ratios all support the hypothesis that secondary dispersal in male white-faced capuchins is driven by intragroup mate competition and results in an increase in reproductive opportunities.

Acknowledgments

We are grateful to the National Park Service of Costa Rica for allowing us to work in SRNP from 1983 to 1988 and to the administrators of the Area de Conservacion Guanacaste (especially Roger Blanco Segura, the Research Director) for permission to continue research in the park to the present day. Many people contributed to the male life history and dispersal database, and we thank them all, especially Rodrigo Morera Avila, Lisa Rose, Katherine MacKinnon, Craig Lamarsh, Dale Morris and Sasha Gilmore. Katharine Jack gratefully acknowledges financial support from the Natural Sciences and Engineering Research Council of Canada (NSERCC), the Royal Anthropological Institute, Sigma-Xi, the Faculty of Graduate Studies and Research/Department of Anthropology at the University of Alberta, the Alberta Heritage Scholarship Fund, the Killam Foundation, and the National Geographic Society. Linda Fedigan's research is funded by an ongoing operating grant from NSERCC (No. A7723). This manuscript was improved with the comments and suggestions made by Dr Jim Moore and an anonymous referee. This research was approved by the Biosciences Animal Policy and Welfare Committee of the University of Alberta (Proposal No. 319104).

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