RESEARCH ARTICLE

Social Factors Influencing Natal Dispersal in Male White-Faced Capuchins (*Cebus capucinus*)

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White-faced capuchin males disperse from their natal group at around 4.5 years of age, but there is much variation in dispersal timing: our youngest confirmed disperser was 19 months and the oldest 11 years old. In this study, we investigate possible factors influencing dispersal decisions in this species. Between 1983 and 2010, 64 males were born into three study groups in Santa Rosa National Park, Area de Conservación Guanacaste, and Costa Rica. As of August 2010, 21 died or were presumed dead (< 14 months), 13 remained natal residents, and 30 were presumed dispersers. We used backward logistic regression to identify proximate factors that predict the occurrence of male natal dispersal. The occurrence of a takeover (significant positive association) and group size (nonsignificant negative association) were included in the model. Male age, number of maternal brothers, and number of adult males were not significant predictors of natal dispersal. The resultant model correctly classified 97% of dispersed and 89% of resident natal males, for an overall success rate of 95%. The occurrence of a group takeover was the strongest predictor of male dispersal, with natal males being 18.7 times more likely to disperse in the context of a group takeover than during peaceful times. A linear regression model showed that the tenure length of a male's probable father influences the age of natal dispersal, explaining 15% of the observed variation in age. However, when our oldest disperser was removed (an outlier) this effect disappeared. Collectively, these results indicate that group instability, as evidenced by the occurrence of a takeover, shorter tenure length of a natal male's father, and smaller group size, triggers natal dispersal in this species while the converse leads to a delay. These data add to our growing evidence of the enormous impact that takeovers have on the behavioral ecology of this species. Am. J. Primatol. 73:1–7, 2011.   © 2011 Wiley-Liss, Inc.

Key words: emigration; group stability; male tenure; takeovers

INTRODUCTION

For some mammalian species, male dispersal from the natal group or range may be triggered by changing levels of sex hormones associated with the onset of sexual maturity [Bronson, 1989; Holekamp & Smale, 1998; Smale et al., 1997] while for others the exact timing of dispersal appears to be plastic and often condition-dependent [Ims & Hjermann, 2001]. In species that display little variation in the age at natal dispersal [e.g. Verreauxi's sifaka, *Propithecus verreauxi*: 3–6 years, Richard et al., 1993; blue monkeys, *Cercopithecus mitis*: 6–8 years, Ekernas & Cords, 2007; patas monkeys, *Erythrocebus patas*: 2–3.5 years, Rogers & Chism, 2009], it is likely that changing hormone levels serve as the proximate trigger for emigration. By contrast, when the timing of natal emigration shows greater intraspecific variability [e.g. baboons, *Papio* spp.: 4–9 years, Packer 1979; 6.8–13.4 years, Alberts & Altmann 1995; vervets, *Chlorocebus aethiops*: 2.5–7 years, Cheney, 1983; Milne Edwards' sifakas, *Propithecus edwardsi*: 4.5–9 years, Morelli et al., 2009] it is

unlikely that dispersal is simply a function of achieving sexual maturity but rather that a combination of variables, both physiological and social, are at work.

Many social factors may influence the timing of dispersal from the natal group. For example, in both rhesus (*Macaca mulatta*) and Japanese macaques (*Macaca fuscata*), maternal rank influences male age at natal dispersal, with sons of higher ranking females consistently emigrating at a later age [Colvin, 1983; Koford, 1963]. The death of a natal male's mother influences the timing of dispersal in

both vervets and savannah baboons (*Papio cynocephalus*), with orphaned males generally dispersing at younger ages than those whose mothers remained in the group throughout the juvenile stage [Alberts & Altmann, 1995; Cheney et al., 1981]. Natal dispersal may also be delayed until males achieve adult body size [Belding's ground squirrels, *Spermophilus beldingi*: Holekamp, 1986; Nunes et al. 1998; Smale et al., 1997]. This delay may make dispersing males more competitive in aggressive contests and ultimately affect their ability to achieve higher dominance status in a new group [e.g. *Macaca fascicularis*: van Noordwijk and van Schaik, 2001] or may aid them in surviving the perils associated with dispersing [Alberts & Altmann, 1995]. Similarly, in species where parallel dispersal is common (i.e. where males disperse in cohorts with peers or siblings), males may delay dispersal to await the maturation of dispersal partners [e.g. vervets: Cheney & Seyfarth, 1983; Japanese macaques; Enomoto, 1974; Kawanaka, 1973; baboons: Cheney & Seyfarth 1977; but see Alberts & Altmann, 1995; lions, *Panthera leo*: Bygott et al., 1979].

Given that one of the main costs of group living is competition over limited resources, increasing group size may also serve as a proximate trigger for dispersal [Dobson, 1982]. However, foraging competition appears to play a greater role (or has been investigated more thoroughly) in species displaying female natal dispersal [e.g. Sterck, 1997; Teichroeb et al., 2009; VanderWaal et al., 2009]. Indeed some researchers argue that aggressive competition within groups, be it over mates or food resources, does not appear to act as a trigger for male dispersal in most mammalian species [Smale et al., 1997]. However, increased intragroup aggression preceding male natal dispersal occurs in several primate species. For example, some (but not all) cases of male natal dispersal in both patas [Rogers & Chism, 2009] and blue monkeys [Ekernas & Cords, 2007] were directly attributed to the escalation of intragroup aggression, namely from adult males who may treat maturing males as potential competitors for mates. In these and other species, male natal dispersal often occurs in direct response to takeovers or changes in the adult male membership within their groups [*Semnopithecus entellus*: Rajpurohit & Sommer, 1993; *Cercopithecus mitus*; Ekernas & Cords, 2007; *Propithecus edwardsi*; Morelli et al., 2009; *Erythrocebus patas*: Rogers & Chism, 2009]. Under these circumstances, young males may be forcibly evicted from their natal groups, or they may voluntarily disperse perhaps because they are attracted to extra-group males or to dispersing group-mates. In our own research on white-faced capuchins (*Cebus capucinus*) in Santa Rosa National Park, Costa Rica, we found that male natal dispersal is largely voluntary and results from an attraction to other dispersing males in their group [Jack & Fedigan, 2004a], although the trigger

for this *en masse* male movement has not yet been documented.

White-faced capuchins live in groups comprising multiple immigrant adult males, multiple-related adult females, and their offspring. In the Santa Rosa study population, groups average ~15 individuals with approximately equal ratios of adult males to females [Fedigan & Jack, 2011a]. Although females in several *Cebus* species may disperse under specific circumstances [*Cebus apella*: Izar, 2004; Janson et al., 2011; *C. capucinus*: Jack & Fedigan, 2009 and Manson et al. 1999; *C. olivaceus*: Robinson et al., 2000], members of this genus follow the general mammalian pattern of male-biased dispersal from the natal group/range [Dobson, 1982; Greenwood, 1980; see also Handley & Perrin, 2007]. In the Santa Rosa study groups, all natal males *eventually* disperse, and they continue to move between groups at approximately 4-year intervals throughout their lives [Fedigan & Jack, 2004; Jack & Fedigan, 2004b]. Although young males are able to transfer relatively peacefully into a new group, once they reach full body size (~10 years of age) males must either fight their way into a new group, usually through cooperative takeovers accompanied by the eviction of resident males, or they must find a group that has no males [waltz-in; Fedigan & Jack, 2004]. Both forms of male secondary dispersal almost always involve the complete replacement of adult males residing in a group.

Although our previous research indicated that males disperse from the natal group at around 4.5 years of age [Jack & Fedigan, 2004a], we have observed considerable variation in the timing of natal dispersal. In addition, the mean age at natal dispersal at our Santa Rosa study site is much younger than that reported for the nearby site of Lomas Barbudal, where natal males disperse at a mean age of 7.6 years [Perry et al., 2011]. In this study, we provide updated information on male age at natal dispersal in the Santa Rosa population of *Cebus capucinus* and investigate possible social factors influencing dispersal decisions in three of our long-term study groups. We address the following two research questions:

(1) What proximate factors influence *the occurrence of male natal emigration*?
(2) What proximate factors influence *male age at natal emigration*?

METHODS

Study Site and Subjects

Our study population inhabits Santa Rosa National Park/Santa Rosa Sector, Area Conservación Guanacaste, Costa Rica and our observations have been ongoing since 1983 [see Fedigan & Jack, 2001, 2011b for additional details of this long-term study].

In this study, we use data collected from three contiguous social groups tracked for various periods between 1983 and 2010. For Cerco de Piedra group (CP), we use 24 years of data, beginning in 1986 (when we first began to collect reliable dominance and reproductive data) through May 2010. Data from Sendero group (SE) spanned the 9-year period from 1983 to 1993 when this group became extinct. Data from the Los Valles group (LV) came from a 20-year period, 1990 through May 2010. We monitored groups continuously during these periods except for six gaps of 2–6 months each. The birth dates of infants born during the ''data gaps'' were estimated based on their size when we first encountered them and our experience with infants of known age. We estimated disappearance dates for males that left study groups during ''data gaps'' as the mid-point of the period.

In May of each year, we construct group dominance hierarchies for all adult group members using behavioral data collected during the prior 5 months. For group females, we construct interaction matrices using the I&SI method [De Vries, 1998] to determine a linear rank order matrix based on all approach–retreat interactions (i.e. supplants) and the direction of submissive signals (i.e. cower, bared teeth display) in dyadic interactions. Individual females are arranged in the order that produces the fewest reversals and by focusing on dyadic interactions we are able to construct hierarchies for all group females. Alpha males are easily identifiable using both physical and behavioral cues. However, linear ranking of subordinate males is less straightforward due to the infrequency of agonistic interactions. Therefore, for this study we distinguish only between alpha and subordinate males.

Data Analysis

Using SPSS 16.0, we used linear and logistic regressions to analyze male dispersal patterns. The dependent variable for regression 1 was dispersal status (dispersed/natal), whereas the dependent variable for regression 2 was male age in months at the time of dispersal. Each regression uses a different combination of the following predictor variables: (1) male age, (2) group size, (3) number of adult males in group, (4) number of maternal brothers in group, (5) maternal rank (coded as either ''1'' if the mother ranked among the bottom 50% of group females and ''2'' if she ranked among the top 50% of group females at the time of the male's birth), (6) time spent residing in the natal group with the probable father (coded as tenure length of the male's probable father), and (7) the occurrence of a takeover at or in the 3 months preceding dispersal or during the life of a resident natal male (i.e. if the natal male remained in his group following a takeover). All variables were calculated at the time of dispersal or

at the end of the study period (May 11, 2010) for those males still in their natal groups.

The identity of all mothers were known and fathers were either identified through genetic analyses ($N = 11$) or assumed to be the group's alpha male at the time of conception [based on a gestation period of 158 days; Carnegie et al., 2011]. Paternity studies at both Santa Rosa and Lomas Barbudal have shown that alpha males sire the majority of group offspring (70–100%) [Jack & Fedigan, 2006; Muniz et al., 2010]. In the sole instance where the group's alpha male was the father of a natal male's mother, paternity analysis confirmed that the infant was sired by the group's sole subordinate adult male. Although there is some variation in expected gestation length, there were no cases in our samples where a changeover in group alpha male occurred within $+/-$ one month of the estimated conception.

The research reported here complied with the protocols approved by the Institutional Animal Care and Use Committee at both Tulane University and the University of Calgary and adhered to all the legal requirements of the Costa Rican government and the Principles for the Ethical Treatment of Non Human Primates as outlined by the American Society of Primatologists.

RESULTS

A total of 64 males were born into the three study groups during the specified study periods. As of May 2010, 21 were known or presumed dead (disappeared from the natal group at <14 months of age), 13 remained as natal residents (aged 12–112 months), and 30 were presumed dispersers (i.e. they were old enough to disperse or they were confirmed dispersers in that they were later observed as members of other social groups). Dispersing males ranged in age from 19 months (our youngest confirmed disperser) to 134 months (11 years; our oldest disperser and also a confirmed disperser; Fig. 1). As shown in Figure 1, the majority of natal males in our study groups (77%) dispersed between the ages of 2 and 6 years . The mean age at natal dispersal for all presumed dispersers was
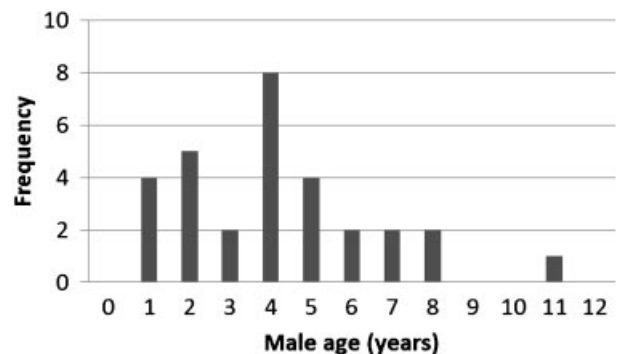

Fig. 1. Distribution of ages for male natal dispersal or disappearance from three study groups 1983–2010 ($N = 30$).

TABLE I. Logistic Regression Predicting the Occurrence of Male Natal Dispersal

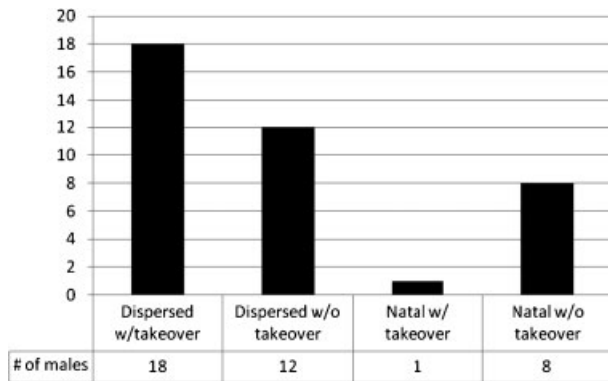| Predictor	B	Wald χ^2	P	e^{β} (odds ratio)
Group size	−0.937	2.911	0.088	0.392
Takeover	2.931	4.430	0.035	18.747

Fig. 2. The distribution of dispersal events that co-occur with group takeovers.

54.5±SD 28.4 months (4.5 years; $N = 30$). If we limit this analysis to confirmed dispersers, the mean age at dispersal is one year later at 65.7±27.4 months (5.5 years; $N = 14$).

Proximate Factors That Influence the Occurrence of Male Natal Emigration

We examined possible proximate stimuli that might act to trigger male natal dispersal. The data set included the 30 dispersed males (all ≥19 months) and nine males still residing in their natal groups, who ranged in age from 20 to 112 months, and were thus older than our youngest confirmed disperser. We used a backward conditional logistic regression to predict the probability of dispersal based on five predictor variables: male age, number of maternal brothers in the group, group size, number of adult males in the group, and the occurrence of a takeover. The final model ($\chi^2(2,\ N = 39) = 26.160,\ P < .001$) included group size and the occurrence of a takeover (Table I).

The model correctly predicted the dispersal status of 88.9% of natal males and 96.7% of dispersed males, for an overall success rate of 94.9%. The occurrence of a takeover was the only significant variable included in the model (Table I). The odds ratio for takeovers indicates that when holding all other variables constant, dispersal is 18.7 times more likely to occur following a takeover than during peaceful times (Table I and Fig. 2). Although it was a nonsignificant predictor in the model, the effect of group size was negative, with males more likely to disperse from smaller than from larger groups. When group size was excluded (i.e. only takeovers were included), the model was unable to correctly predict
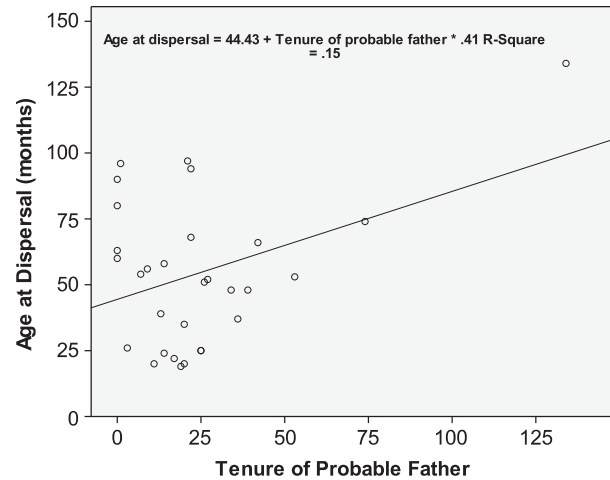

Fig. 3. Regression of male age (months) at natal dispersal and the tenure length of his probable father (months).

which males remained in the natal group indicating that group size is an important variable to consider in predicting male natal dispersal.

Proximate Factors That Influence Male Age at Natal Emigration

We conducted a stepwise multiple linear regression with male age (months) at dispersal as the dependent variable and the following five predictor variables: maternal rank at male's birth, number of male siblings present in the group, group size, number of adult males present in the group, and the tenure length of probable father (i.e. the length of time the natal male resided in the group with his probable father). The tenure of the male's probable father was the only factor included in the final model ($F(1,\ 30) = 4.998,\ P = .034$; Fig. 3) although it accounted for only 15% of the variance in male age at dispersal. However, when we remove our oldest disperser, who is an obvious outlier in the data set (see Fig. 1 and Fig. 3), this relationship disappeared and none of the variables investigated were significant predictors of male age at natal dispersal.

DISCUSSION

Although all members of the genus *Cebus* follow the pattern of male-biased dispersal and female philopatry [Fragaszy et al., 2004], long-term data on dispersal patterns are only available for two species; *Cebus capucinus* and *Cebus apella* [now referred to as *Sapajus*, see Lynch Alfaro et al., 2011]. These two species are similar in that the age of natal dispersal is highly variable, although it most often occurs well before males attain full body size between 9 and 10 years of age [*Sapajus*: Janson et al., 2011]. Based on their long-term studies of *Sapajus* in Iguazú National Park, Argentina, Janson et al. [2011] report that most males disperse between 5 and 7 years of age (70%), with a mean of 5.7–6.5

years (the latter mean excludes infants that disappeared with their mothers and dispersals that coincided with group fissions). This is younger than the mean of 7.5 years reported by Perry et al. [2011] for their Lomas Barbudal population of *C. capucinus*, but older than the 4.5 year mean we observe in our Santa Rosa study groups. Given these findings and the huge range of ages within which male natal dispersal occurs (our youngest confirmed disperser was only 19 months and the oldest was 11 years), it is clear that the age of natal dispersal is a highly plastic trait for at least two of the species included in this genus.

Indeed our analysis of the proximate triggers for male dispersal from the natal group did not find that age played a significant role in predicting when males would leave their birth groups. Of the five variables investigated (male age, number of maternal brothers in group, group size, number of adult males in group, and the occurrence of a takeover) only the occurrence of a takeover was significant in predicting the timing of dispersal. In our study groups, 60% (18/30) of the natal males have dispersed in the context of a group takeover. Takeovers occur approximately every 4 years [Fedigan & Jack, 2004], which corresponds well with our mean age at natal dispersal (4.5 years). A takeover can occur at any point in a natal male's life (i.e. they occur independent of male age); if it occurs when a male is old enough to disperse, then he will disperse [see Ekernas & Cords, 2007 for similar findings in blue monkeys]. If he is too young (<1 year) he will likely die in the course of the takeover [Fedigan, 2003; see Janson et al., 2011 for similar findings for *C. apella*] or if he is >1 year but not old enough to disperse, he may remain in the natal group. In our sample of natal males, only one male (aged 9.3 years at the end of this study period) had experienced a takeover during his lifetime and remained in his natal group. This LV male, a son of the group's alpha female, was just over 2 years of age when the takeover occurred and the group has remained relatively stable since that time (i.e. some adult males have emigrated but no new males have joined the group).

Of course the occurrence of a group takeover is intimately linked to the tenure of the adult males in a group (and a natal male's potential father); when takeovers occur, we almost always see complete replacements of group males [see Janson et al., 2011 for similar findings in *Sapajus*]. Although our attempt to identify factors to explain the observed variation in male age at dispersal was inconclusive, there is a trend toward males delaying dispersal if their father is still present in the group. Interestingly, Perry et al. [2011] report a much later mean age of natal dispersal, 7.6 years, for their study groups of *C. capucinus* at the nearby site of Lomas Barbudal, although there is some overlap in the ranges of dispersal ages between the two sites (SR range = 19 months –11 years; Lomas range = 4–11

years). This later age at natal dispersal may be, in large part, explained by the increased group stability and extraordinarily long alpha male tenures reported for the Lomas Barbudal study population [8, 15, and 18 years for three respective groups; Perry & Manson, 2008]. Although the mean tenure length for alpha males in our study groups is 4 years [Jack & Fedigan, 2004b], we recently had a case of an alpha male with an extremely long tenure (14 years) in our CP group. When this alpha male finally did disperse, three of his sons (aged 11, 6 and 4 years) went missing at the same time. Given the prominent pattern of parallel dispersal reported for this species [Jack & Fedigan, 2004a,b; Perry et al., 2011], it is likely that this was a dispersal event rather than coincidental deaths of four related males. It does seem that the tenure of alpha males, who are responsible for siring the majority of group infants in all Cebus species for which paternity data exist [*Sapajus*: Escobar-Paramo, 2000; *C. capucinus*: Jack & Fedigan, 2006; Muniz et al., 2010; *C. olivaceus*: Valderrama et al., 2000], is intimately linked with male age at natal dispersal. Janson et al. [2011] report mean alpha male tenures of 5.3 years, a number that corresponds well to the mean age at natal dispersal (5.7 years) that they report for their study population of *Sapajus*.

In further support to our finding of the impact of takeovers on male dispersal patterns, the three youngest dispersing natal males (four years of age) in the Lomas study population occurred in the context of an aggressive group takeover [Perry et al., 2011]. We are not yet sure why alpha male tenures are shorter and takeovers occur more frequently in our Santa Rosa study population, but plans to compare the ecology and demography of the two populations are underway and may help us understand what has led to such differing dispersal patterns. We do know that the Lomas study groups tend to be larger than ours [Perry et al., 2011] and the results presented here show that natal males residing in larger groups are less likely to disperse than those in smaller groups. Although group size does not predict the occurrence of a takeover [the odds of a takeover increase with a decreasing proportion of resident males in the group; Fedigan & Jack, 2004], large group size does reflect group stability in our study population; the longer the alpha male tenure, the more infants that are born and survive, and the larger the group becomes [see Fedigan et al., 2008; Fedigan & Jack, 2011a]. Younger males residing in larger groups may, in essence, be reaping the benefits of this stability.

In summary, for natal male white-faced capuchins, age alone (and implicitly, sexual maturity) is not enough to predict dispersal events. Data presented here accompanied by those coming out of the nearby study site of Lomas Barbudal, provide strong evidence that stable adult male tenure may

encourage natal males to prolong their group residency. Although we do not have data on the survivorship of dispersing males in our study population, Janson et al. [2011] estimate that 38% of dispersing male *Sapajus* do not survive. Although *Sapajus* differ from *C. capucinus* in that they disperse alone (rather than into neighboring) and greater distances (rather than into neighboring groups, which is often the case in *C. capucinus*), both of which likely increase dispersal-related mortality, it is possible that delaying dispersal until males are closer to reaching adult body size (and competitive ability) may increase their immigration success as has been shown in other primate species [e.g. long-tailed macaques: van Noordwijk & van Schaik, 2001; baboons: Alberts & Altmann, 1995]. Our long-term analysis of male dispersal indicates that the variation in the age at which young natal males disperse is largely determined by the movement of adult males between groups. Indeed the occurrence of a group takeover was the strongest predictor of male natal dispersal, adding to growing evidence of the profound effect that takeovers exert on the lives of white-faced capuchins.

ACKNOWLEDGMENTS

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