Female dispersal in a female-philopatric species, *Cebus capucinus*

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Summary

White-faced capuchins (*Cebus capucinus*) reside in multimale–multifemale groups characterized by female philopatry and frequent male dispersal. However, over the years we have observed five females immigrate into our study groups and 23 disappear/emigrate. We examined long-term demographic and behavioural data on three groups of *C. capucinus* residing in Santa Rosa, Costa Rica, between 1986 and 2007. During this time, 56 females resided in our study groups and as of June 2007, 23 were still present, ten were confirmed/presumed dead and 23 were missing. Here we review the circumstances surrounding the five immigrations and 23 missing females and evaluate three main hypotheses to explain female dispersal in a female philopatric species: inbreeding avoidance, reduction of intragroup feeding competition and infanticide avoidance. The two main predictions of the inbreeding avoidance hypothesis were not supported by our study; male tenure did not exceed female age at first birth and the majority of dispersers were parous females. The reduction in intragroup feeding competition hypothesis received moderate support; dispersing/disappearing females tend to leave during the dry season and they have fewer matrilineal kin than females remaining in their natal group. Our data were most consistent with the infanticide avoidance hypothesis in that females are more likely to disperse/disappear during years with male replacements, a time when infant deaths are also more common. These data provide further evidence of the large impact that the movement and actions of adult male white-faced capuchins have on the lives of females in this species.

Keywords: female dispersal, parallel dispersal, takeovers, replacements, infanticide.

Introduction

Data on female dispersal in species characterized by female philopatry are by definition anomalous. Given the difficulty of determining the fates of missing group members, the limited data that exist on this phenomenon generally consist of accounts of single individuals observed to transfer into study groups (Manson et al., 1999; Robinson et al., 2000; Sterck & Korstjens, 2000; Payne et al., 2003). In most species characterized by sex-biased dispersal, immigration by the philopatric sex is forcibly resisted (Armitage & Johns, 1982; Hammond et al., 2006) and in several species such immigration attempts can result in the death of the immigrant (e.g., Garret & Franklin, 1988; Miller, 1998; Payne et al., 2003). These observations indicate that dispersal by the philopatric sex is costly, particularly when attempted alone. Dispersal costs are variable (Isbell & van Vuren, 1996), but for the philopatric sex the greatest costs are likely social in nature in that dispersing individuals can lose allies important for winning within-group foraging competition (Sterck et al., 1997), which may also render them targets of intense conspecific aggression (reviewed in Isbell & van Vuren, 1996). These social costs may be offset if individuals engage in parallel dispersal, whereby they disperse together or join groups containing familiar individuals (van Hooff, 2000). Given the high cost of dispersal, the benefits must be large in species where female dispersal is not the norm but nonetheless occasionally occurs.

In this paper we examine female dispersal in white-faced capuchins (*Cebus capucinus*), a primate species in which females are philopatric, natal males disperse (Jack & Fedigan, 2004a) and, approximately every four years, groups experience complete changeovers in adult male membership, usually by way of aggressive coalitionary takeovers (Fedigan & Jack, 2004). Despite this pattern of female philopatry and male dispersal, we have, over the years, observed some females to join our study groups and many of our study females to disappear (suspected dispersal events). Although the genus *Cebus* is unusual among the platyrrhines in being characterized by female philopatry, this pattern appears more flexible than that observed across the cercopithecines, to which *Cebus* are generally compared. Indeed, female dispersal has been reported to occur with some frequency in *C. olivaceus* (Robinson et al., 2000) and *C. apella* (Izar, 2004). In these species, parallel dispersal appears to be common, with entire matrilines joining an existing group in at least one case for *C. olivaceus* (Robinson et al., 2000). While solitary dispersal has been observed in both species, female transfer between groups as

pairs of matrilineal kin has only been reported for *C. olivaceus* (Robinson et al., 2000). Female dispersal in *C. capucinus* has also been reported to occur (Manson et al., 1999), although no estimates of the frequency of dispersal have yet been provided.

A number of hypothesized explanations for female dispersal have been proposed, all of which can be adapted to explain the occasional dispersal of females in female philopatric species: inbreeding avoidance, reduction of predation risk, reduction of intragroup foraging competition, and infanticide avoidance (see Sterck et al., 1997 for review; Table 1).

Hypotheses and predictions for female dispersal (Table 1)

Inbreeding avoidance is the most cited evolutionary explanation for natal dispersal in mammals (Greenwood, 1980; Pusey & Packer, 1987). In species characterized by male dispersal and female philopatry, natal nulliparous females may emigrate when male tenure is extended and exceeds female age at reproductive maturity (Clutton-Brock, 1989; Moore, 1993). According to Sterck & Korstjens (2000), inbreeding avoidance cannot explain the dispersal of parous females, particularly in species characterized by male dispersal. Therefore, we predict that nulliparous female capuchins are more likely to disperse.

One of the ultimate benefits of group living is thought to be reduced susceptibility to predation (e.g., Alexander, 1974; Bertram, 1978; Wilson, 1980; Janson, 1998) and female dispersal may be a means to reduce predation risk (Rasmussen, 1981). Group size is thought to be negatively correlated with predation risk, and if female dispersal functions to reduce predation risk, then females should disperse from smaller to larger groups (Hamilton, 1971; van Schaik, 1983). Unfortunately we do not have comparative data on transfer group sizes, which renders us unable to test this hypothesis.

Increased within-group feeding competition may also lead to female dispersal if groups become too large (van Schaik, 1983). In such cases, female dispersal is more likely to occur during times of food shortage and females should move from larger to smaller groups (Sterck, 1997). In addition, females with lower foraging success due to decreased competitive abilities are predicted to disperse, either voluntarily or via eviction (Dobson, 1982). The ability to compete for access to resources is often determined by dominance rank (e.g., Janson, 1985; Saito, 1996; Koenig, 2000; Vogel, 2005), which,

Table 1. Hypotheses and associated predictions relevant to explaining occasional female dispersal in *Cebus capucinus*.

Hypothesis	Associated predictions	Supported in this study?	Overall support
Inbreeding avoidance	a. Dispersing females are nulliparous b. Male philopatry or male tenure exceeds female age at menarche	a. No b. Rare	No
Reduction of predation risk	a. Disperse from smaller to larger groups	a. Unable to fully test; however, the mean size of groups joined by immigrants is slightly smaller than those departed by dispersers	Unable to fully test
Reduction of intragroup feeding competition	a. Disperse from larger to smaller groups b. Dispersal occurs during times of food shortage c. Dispersers are low ranking d. Dispersers have fewer matrilineal kin e. Group females aggressively resist the immigration attempts of other females	a. Unable to fully test; however, the mean size of groups left by disperses is only slightly higher than those joined by immigrants b. Marginal support (65% occur in dry season) c. No d. Yes, but connection of kin to dominance rank and food acquisition is questionable in this species e. No — only mild resistance to immigrations	Moderate

in turn, may be determined by the number of close matrilineal kin available for agonistic support in female philopatric species (e.g., Gouzoules & Gouzoules, 1987). Sterck et al. (1997) suggest that in female philopatric, resident-nepotistic species (such as *Cebus*), the main costs to dispersing females are social; they lose access to allies (namely kin), which are important in gaining access to resources. Therefore, we predict that emigration should be more common for low ranking females and females with fewer kin in the social group. If feeding competition is linked to group size, as it is in most primate species (e.g., van Schaik, 1983, 1989; Janson 1988; Sterck et

Table 1. (Continued.)

Hypothesis	Associated predictions	Supported in this study?	Overall support
Reduction of infanticide risk (sub-hypotheses):			
1. Stay with the father	1a. Females with dependent infants (and pregnant) disperse with ousted male 1b. Dispersal coincides with male replacements	1a. Marginal evidence 1b. Yes	Yes
2. Choosing the best male	2a. Females do not disperse with dependent offspring 2b. Females disperse after infanticide during intergroup encounters 2c. Dispersal is voluntary	2a. Yes (only 3 of 19 females left with dependent offspring) 2b. No — infants have disappeared after intergroup encounters but we have not had females disappear after these encounters 2c. Yes	Moderate
3. Reducing the risk of male-takeovers	3a. Risk of infanticide/group takeovers increases with an increasing number of breeding females 3b. Group females aggressively resist the immigration attempts of other females 3c. Eviction of maturing, nulliparous females	3a. No 3b. No — only mild resistance to immigrations 3c. No — Dispersal appears to be voluntary and dispersers are parous	No

al., 1997; Knopff & Pavelka, 2006), resident females are predicted to aggressively resist immigration attempts by outsider females (Dobson, 1982; Sterck & Korstjens, 2000).

Female dispersal may also function as a means of avoiding infanticide and infanticide has been documented in the three well-studied capuchin species (*C. olivaceus*: Valderrama et al., 1990; *C. apella nigritus*: Ramirez-Llorens et al., 2008; *C. capucinus*: Fedigan, 2003). Three main sub-hypotheses have been proposed for infanticide avoidance (see Sterck & Korstjens, 2000 for review). (1) 'Remaining with the father': dispersing females can increase survival chances of dependent infants if they disperse (voluntarily) with the

father who has just been ousted from the breeding group by a new male (Rudran, 1973; Hrdy, 1977). (2) 'Choosing the best male': females disperse (voluntarily) in order to seek another group with a male who may be better able to protect their future offspring from infanticide (e.g., *Gorilla gorilla beringei*: Harcourt et al., 1976; Watts, 1989; and *Procolobus rufomitratus*: Marsh, 1979). In both gorillas and colobus monkeys, female dispersal has been observed following infant deaths during intergroup aggression. Females dispersing to seek better protector males should not disperse with dependent offspring as these would be susceptible to infanticide within the new group (Sterck & Korstjens, 2000). (3) Reducing the chance of male takeovers: in some species aggressive group takeovers and subsequent infanticides have been linked to larger female group size (e.g., *Theropithecus gelada*: Dunbar, 1984; *Alouatta seniculus*: Crockett & Janson, 2000; *Presbytis thomasi*: Steenbeek & van Schaik, 2001). If female dispersal functions to reduce risk of male takeovers and, consequently, infanticide, then females should act to keep the number of breeding females to an optimal level. To do this, they are predicted to aggressively resist immigration attempts and evictions should be directed against maturing, nulliparous females (Sterck & Korstjens, 2000).

Based on long-term behavioural and demographic data collected on three social groups of *C. capucinus*, we describe the circumstances surrounding immigrations into our study groups and the disappearances/emigrations of females from our groups. We also evaluate the inbreeding avoidance, reduction of intragroup resource competition, and infanticide avoidance hypotheses for their utility in explaining the motivation behind occasional female dispersal in this species.

Methods

This 21.5 year study was conducted between January 1986 and June 2007 in the Santa Rosa sector of the Area de Conservacíon Guanacaste located in northwestern Costa Rica. Formerly known as Santa Rosa National Park and herein referred to as Santa Rosa, the study site is comprised of approximately 108 km^2 of tropical dry forest that experiences a dry season from mid-December to mid-May, during which rainfall is absent or minimal. For additional details on the study site, see Fedigan and Jack (2001, 2004).

This study focuses on the immigrations, dispersals, and disappearances of female white-faced capuchins. Based on our park-wide censuses, average group size ($N = 31$) in the Santa Rosa population is 17.2 individuals with an adult sex ratio approaching $1 : 1$ (Fedigan & Jack, 2001). Both sexes form discernable dominance hierarchies, and adult males are 25–35% larger than adult females and generally dominant over them (Ford & Davis, 1992; Fedigan, 1993). While white-faced capuchins are not strict seasonal breeders (copulations and births occur throughout the year), our Santa Rosa population experiences a dry season birth peak, from February through mid-May (Fedigan, 2003; Carnegie et al., 2005). Paternity analyses of two of our long-term study groups indicate that resident alpha males sire the majority of the infants (Jack & Fedigan, 2006).

In this species, all natal males disperse (Jack & Fedigan, 2004a) and groups experience complete changeovers in adult male membership approximately every four years (Fedigan & Jack, 2004). These changeovers in male group membership, referred to herein as male replacements, almost always involve coalitions of multiple males joining groups together. Male replacements are associated with infant deaths, wounding of other group members, and usually the eviction of resident males (Fedigan & Jack, 2004). Male replacements usually occur during the dry season birth peak (Fedigan, 2003). During our study we also documented two cases of male successions. These successions involved the abandonment of the group by the alpha male enabling a lower ranking male from within the group to assume the alpha position. In both cases, the result of the succession was the same as we have observed during male replacements: infants died when new males assumed dominant positions.

Our study commenced in 1983, although reliable biweekly observations during which both behavioural and life history data were collected did not commence until January 1986, which we use as the starting point for this study. For details of long-term data collection methods, see Fedigan et al., 2008. Here we use 48 group-years of data collected on our three most intensively studied groups over the following time periods: CP group, 1986 through June 2007 (22 years); SE group, 1986 until 1993 when it became extinct (8 years), and; LV group, 1990 through June 2007 (18 years). With the exception of seven gaps of 2–7 months each, study groups have been continuously monitored since group observations began. These gaps combine for a total of 29 months during which groups were not observed. For those

females that disappeared from study groups during one of these data gaps
($N = 3$) we estimate their date of disappearance as the mid-point between
the date last observed and first missing. The exact dates for the appearance
of immigrant females are known in all cases.

Analyses were conducted using SPSS 15 for Windows. In most cases
non-parametric two-tailed tests were employed and significance was set at
$p < 0.05$. Number of close matrilineal kin refers to an r-value of 0.25 to 0.50
and includes mother, grandmother, siblings, offspring and grandchildren.

Results

During this study, 56 females resided in the three study groups; 17 (30%)
were present in the groups when observations began and their origins are
unknown (includes 16 adult females and a 1.5 year old female), 34 (61%)
were born into our study groups, and five (9%) immigrated into our groups
as adults (Table 2). As of June 2007, 23 females were still residing in our
study groups, an additional ten were confirmed or presumed dead, and 23
were missing. In contrast, all but one of the natal males dispersed from our
study groups prior to reaching adult body size (10 years) and the mean age
of natal dispersal is 4.5 years (Jack & Fedigan, 2004a). The average tenure
for adult male immigrants is 40 months in length (Jack & Fedigan, 2004b).

Immigrant females

Five of the 56 females (9%), or five of 36 adult females (14%), that resided in
our study groups were confirmed immigrants. Four of these five immigrant
females were judged to be parous due to their age or reproductive status when
they entered the study groups (two were pregnant), while the fifth immigrant
was recorded as a young adult (estimated at seven years) whose parity could

Table 2. Number of females (adults) that have resided in the study groups.

Group	Total females	In group when obs. began	Natal	Immi-grants	Alive 2007	Confirmed dead	Missing
SE (1986–1993)	4 (4)	4 (4)	0	0	0	1 (1)	3 (3)
CP (1986–2007)	28 (19)	7 (7)	19 (10)	2	14 (6)	2 (2)	12 (11)
LV (1990–2007)	24 (13)	6 (5)	15 (5)	3	9 (5)	7 (0)	8 (8)
Total	56 (36)	17 (16)	34 (15)	5	23 (11)	10 (3)	23 (22)

not be directly established although her youthful appearance led us to infer that she was nulliparous (Table 3). Of these same five immigrant females, three were parallel dispersers, in that they immigrated into our study groups in the company of others; one immigrated in with two juveniles, while the other two transferred together and in the company of two weaned juveniles and their ousted alpha male. These latter two females were known members of a neighboring group and were visibly pregnant when they joined our study group. Their dispersal coincided with an aggressive takeover of their group, during which the alpha was ousted.

The size of groups joined by immigrants ranged from 13 to 21 (mean = 16.6), with the number of adult males ranging from 1 to 4 (mean = 2.4) and all target groups contained four adult females. The four parous immigrants moved into our study groups in the context of male replacements while the nulliparous female entered one of our study groups during a time of relative stability, although there was some movement of subadult males between groups at the time. Four of the five immigrations occurred in the dry season.

Three of the five females (two parous, one non-parous) were the recipients of some aggression from resident females upon entering the new groups, although only the non-parous female received minor wounds during the first week of residency. The entry of the other two immigrants occurred at an early stage of our study during a period where only demographic data were being collected; we do not, therefore, have details surrounding their immigration and integration into the groups. In our many years of studying the Santa Rosa capuchins, we have never observed an unsuccessful immigration attempt by an extra-group female.

Qualities of immigrants vs. natal females

Tenure: We compared the tenure of natal females through their death or disappearance from the study group (or as ongoing if they were still resident in June 2007), with those of immigrant females. We used 6.5 years as the starting point of residency for natal females as this is the average age at first birth in our study group (i.e., adulthood) and enables us to equalize the starting points for natal vs. immigrant females, as all immigrants were estimated to ⩾7 years. Females who were group residents when our study began were not included in this analysis, as their immigration status was unknown. Tenure for immigrant females was calculated from the date of their immigration into the study group through their subsequent disappearance (note: all immigrant

Table 3. Details on female immigrations into the study groups.

Immigrant	Parity	Size of group joined (No. AD♂, AD♀)*	Tenure (months)	Total offspring (rate of offspring production)	Male replacement	Notes
CP-IMM1	Parous	21 (4,4)	33	2 (0.73)	Yes	Immigrated alone
CP-IMM2	Parous	13 (1,4)	14	0	Yes	Immigrated with two juveniles
LV-IMM1	Nonparous (suspected)	15 (1,4)	37	1 (0.32)	No	Immigrated alone; minor wounds noted during first week
LV-IMM2	Parous	17 (3,4)	80	3 (0.15)	Yes	Immigrated with ousted former alpha, LV-IMM3 and two juvenile males; visibly pregnant; minor aggression received
LV-IMM3	Parous	17 (3,4)	14	0	Yes	Immigrated with ousted former alpha, LV-IMM2 and two juvenile males; visibly pregnant; minor aggression received

* AD = adult (>10 yrs): these figures do not include the immigrants themselves or those individuals that immigrated with them.

females eventually disappeared from our study groups and none of the females currently residing in our study groups are immigrants). Using SPSS SURVIVAL analysis, the median tenure of natal females was 216 months ($N = 15$, range $= 18$–216 months), while the median tenure for immigrant females was significantly lower at 30 months ($N = 5$, range $= 14$–80 months) (Wilcoxon Gehan test: $Z = 7.903$, df $= 1$, $p = 0.005$).

Number of offspring: Two of five immigrant females (40%) did not produce offspring in their new groups, while only one of 15 natal females (6%) that reached adulthood in our sample did not reproduce, and this female disappeared at eight years of age following a male takeover of her group. Excluding those females that did not reproduce ($N = 3$) the rate of offspring production (# of offspring produced per year) was slightly higher for immigrant (mean $= 0.50$, $N = 3$) versus natal females (mean $= 0.34$, $N = 14$), but the differences were non-significant (Mann–Whitney U: $Z = -1.260$, $p = 0.244$) and are likely a reflection of sample size rather than any qualitative differences in reproductive rate.

Rank: All of the females that joined our study groups did so at the bottom of the hierarchy and remained at low ranks (bottom 50%) throughout their tenure in the group.

Deceased, missing and dispersed females

Deceased females

Ten of the 56 females that resided in our three study groups died or were presumed dead during our study period. Four of these were under 1 year of age, three of which disappeared within one month of a male replacement and the fourth disappeared following an intergroup encounter. There have been additional infants born into our study groups that died or disappeared before we were able to definitively sex them ($N = 14$), and it is quite likely that a portion of these infants were female, but they are not included here. Three additional immature females are presumed dead due to the circumstances surrounding their disappearance or their young age; one four-year-old female disappeared after a predatory attack by a puma (*Puma concolor*), while the other two females were under 2.5 years of age when they disappeared during two of the periods of researcher absence from the field site. These females are presumed dead due to their young age and the fact that no other group residents went missing during this period.

The remaining three females classified as deceased were adult females; one was >23 years of age and is presumed to have died of old age and the other two females were found dead following male takeovers of their groups (one from SE and one from CP). We were unable to determine if the deaths of these last two females were the result of trauma received during the takeover (no wounds were visible on the bodies found) or due to an illness that seemed to spread through the group (several infants also perished at this time). Members of our research team noted both females as lethargic prior to their deaths or disappearance.

Missing/dispersed females:

Which females disperse/disappear? Twenty-three females (22 adults and 1 juvenile) went missing from our study groups during the study period. The sole juvenile female disappeared when she was three to four years old during a period of researcher absence. Although it is possible that she dispersed, it is more likely that she died and we do not consider this young female for any of the analyses that follow. One of the 22 missing adult females is also strongly suspected to have died as she disappeared suddenly, leaving behind an unweaned infant. The only time we have observed a female to desert a dependent offspring was due to her own death. This female is not considered in further analyses.

Only one of the 21 females that went missing from our study groups was nulliparous, and she disappeared at 8 years of age following an aggressive takeover of her group. Of the 21 females in our missing sample, we were only able to definitively confirm one group transfer. In this case, the dispersing adult female and the alpha male who was ousted from the LV study group were observed shortly after their disappearance as members of an unhabituated neighboring group. One additional adult female was provisionally observed as a member of another group shortly after the dissolution of our SE study group following an extended period of male instability. It is possible that some of the other missing females in our sample died rather than dispersed, and some of these departures may represent group fissions rather than isolated dispersal events (Robinson, 1988). Because we were unable to confirm the fates of the majority of the missing females in our sample, and we have never observed our missing group members to form a new group, we include all 21 together and refer to them as dispersals/disappearances.

Using a Fisher's Exact Test, we analyzed the residency status (in group, natal, immigrant) of the adult females that remained in our study groups ($N = 15$) versus those that dispersed/disappeared ($N = 20$). For these analyses we have included those adult females known or suspected to have died ($N = 4$) as non-dispersers because they remained in the group until their death. All four of these females were residents within the groups when our study began. We have excluded one natal female who reached adult status only a few months prior to the end of our study, as she would not have had sufficient time to allow dispersal. Overall there was a significant effect of residency status on female dispersal from our study groups (Fisher's Exact = 6.295, df = 2, $p = 0.042$). Breaking the analyses into two independent tests showed that immigrants were significantly more likely to disperse than natal females (Fisher's Exact = 8.03, df = 1, $p = 0.022$), while there was no difference between natal and in-group females (Fisher's Exact = 2.17, df = 1, $p = 0.136$).

We tested the effect of female rank at the time of dispersal/disappearance from the group. For this analysis each female in our missing sample was scored in one of three rank categories according to the percentage of group females that she outranked: 0–30, 30–70 and 70–100. We have excluded one SE female from this analysis as she was the sole remaining female in the group when the group dissolved in 1993. The observed frequencies of females in each rank category that emigrated were 7 in the 0–30 range, 8 in the 30–70 range and 5 in the 70–100 range, and these did not differ significantly from the predicted proportions (Chi-square Exact Test: $\chi^2 = 0.876$, df = 2, $p = 0.669$).

We also examined the effect of the number of close matrilineal kin present in the group on female dispersal. We classified each adult female group member present at the time of each dispersal/disappearance event into one of three categories: those having 0–1 close kin members in the group, those with 2–3, and those with 4–6 (6 was the maximum number of known close kin for any one female in our sample). We have again excluded the one SE female from this analysis in addition to those females for whom we did not know the number of close matrilineal kin (i.e., those resident in the group when observations began). Overall, the number of close matrilineal kin that a female had in the group had a significant effect on whether or not a female dispersed/disappeared (Fisher's Exact = 5.994, df = 2, $p = 0.046$). Females with zero to one close kin in the group left twice as often

Table 4. Chi-square goodness of fit test for the effect of the number of close matrilineal kin residing in the group on female dispersals/disappearances.

No. of close matrilineal kin	Dispersed/disappeared		Stayed in group	
	Expected	Observed	Expected	Observed
0–1	4.3	8	11.7	8
2–3	7.1	6	18.9	20
4–6	4.6	2	12.4	15

The number of close matrilineal kin refers to an r-value of 0.25 to 0.50 and includes mother, grandmother, siblings, offspring and grandchildren.

as expected, females with two or three close kin left slightly less often than expected, and females with four to six close kin members in the group left much less often than expected (Table 4). These results indicate that females with more close kin were less likely to disperse/disappear than those with few kin in the group.

With whom do females disperse/disappear? Five of the 21 females were solitary disappearances/dispersers, while the remaining 16 (76%) females disappeared with one to 16 other members of their social group (Table 5). In the case where 17 group members disappeared, with two adult females among them, we suspect that a group fission occurred. However, we never observed a splinter group in the areas adjacent to our study groups as would be expected in a group fission (Robinson, 1988) and, with the exception of two males (one adult and one subadult) who joined a neighboring study group, none of the group members were observed again. Given that we were unable to discern the circumstances surrounding the disappearance of these two females, they are not treated differently from the other 'missing' females in our sample.

None of the 21 females left dependent infants behind and at least eight of the missing females (38%) in our sample disappeared with known kin; either dependent infants or older offspring. Two of the three females who disappeared with dependent young were the only group members missing at that time (i.e., they were not dispersing with a potential father of their offspring), while the disappearance of the third female and her 11-day-old infant, coincided with that of one subadult and three adult males. These males had been part of a seven-male coalition that aggressively entered the study group 5 months earlier and had been moving in and out of the social group since

their arrival. Given that gestation length in white-faced capuchins is estimated at 5.5 months (Nagle & Denari, 1982), it is possible that the father of the missing infant was among them.

When do females disappear from groups? Excluding the sole remaining female in the dissolving SE group, the size of groups prior to the dispersal/disappearances of females ranged from 7 to 22 (mean = 17.6, $N = 20$), with one to six adult males (mean = 3.45, $N = 20$) and 3–7 adult females (mean = 5.25, $N = 20$). We examined our data set to determine if there are certain circumstances under which females disappear, including times of food shortage (i.e., dry season) and during times of group instability, namely when male replacements occur. We also examined our data set to see if there are certain demographic traits associated with the occurrence of male replacements.

We found a tendency for female dispersal/disappearance to occur in the dry season ($N = 13$) versus the wet season ($N = 8$). The seasonal effect on female dispersal/disappearance is more pronounced when we consider that four of the five immigrations also occurred during the dry season. Collectively, 65% of dispersals (disappearances/dispersals plus immigrations) occurred during the dry season months (Dec–May).

We examined our data set to determine if female dispersal/disappearance was associated with a changeover in the group's alpha male. There were 12 group-years during which our groups experienced a changeover in alpha male (through a succession or male replacement event) and 36 years during which no change occurred. Eleven of the 21 females (52%) disappeared from our study groups within one year of a changeover of the group's alpha male. Using a Mann–Whitney U-test, we found that a significantly higher proportion of group females dispersed/disappeared during years with changeovers in the group's alpha male than during years of alpha male stability ($Z = -2.807$, $p = 0.005$).

Three additional females disappeared from our study groups during times of male instability within the group. These disappearances did not involve a replacement of the group's alpha male, but they coincided with the dispersal/disappearance of subordinate adult males from the group, which left the alpha male as the sole resident male remaining with the group. When we consider these females together with the 11 that disappeared in the context of alpha male replacements, 67% of our sample of missing females dispersed/disappeared during times of group instability.

Table 5. Details regarding female disappearances from the study groups.

Group-female	Immi-gration status	Group size at time of departure (No. AD♂, AD♀)*	Month missing	Disappears with?					Total missing (including ♀)	No. of kin
				AD♀	AD♂	SAD♂	Inf	Juv		
CP[1]-DIS1	In group	25 (6, 6)	April	1	5	1	1	8	17	min. 1
CP[1]-DIS2	In group	25 (6, 6)	April	1	5	1	1	8	17	min. 1
CP[2]-DIS3	In group	13 (4, 4)	January	1		1		1	4	min. 2
CP[2]-DIS4	Natal	13 (4, 4)	January	1		1		1	4	0
CP[3]-DIS5	In group	18 (6, 7)	September	1	1				3	0
CP[3]-DIS6	In group	18 (6, 7)	September	1	1				3	0
CP[4]-DIS7	Natal	19 (4, 5)	February		1				2	0
CP-DIS8	Natal	17 (2, 5)	February				1+		2	1+
CP-DIS9	Immigrant	15 (2, 6)	October					2	3	0
CP-DIS10	Immigrant	14 (1, 5)	August						1	0
CP-DIS11	Natal	19 (2, 5)	May				1+		2	1+

Table 5. (Continued.)

Group-female	Immigration status	Group size at time of departure (No. AD♂, AD♀)*	Month missing	Disappears with?					Total missing (including ♀)	No. of kin
				AD♀	AD♂	SAD♂	Inf	Juv		
LV-DIS1	Natal	18 (3, 5)	July		5		1[+]		7	1[+]
LV-DIS2	In group	22 (3, 6)	July		1				2	0
LV-DIS3	In group	20 (2, 5)	October			1			4	1
LV-DIS4	In group	20 (4, 6)	October		1			2	2	0
LV-DIS5	Immigrant	23 (2, 5)	May						1	0
LV-DIS6	Immigrant	16 (3, 5)	May						1	0
LV-DIS7	Immigrant	17 (3, 6)	February						1	0
SE-DIS1	In group	7 (1, 3)	March						1	0
SE-DIS2	In group	13 (5, 4)	February		2				3	0
SE[5]-DIS3	In group	4 (2, 1)	February		2			1	5	1

* Group composition includes the dispersing/disappearing female and other group members.

[1,2,3] Single dispersal events in which more than one adult female dispersed at the same time.

[4] This is the sole nulliparous female in our sample; she went missing during an aggressive group takeover where it was suspected. That the alpha male was fatally wounded; we found bodies of an adult female and her nine-month old infant, and two additional infants went missing at this time and were presumed dead. Only the alpha male is included here as a disappearance.

[5] This was the last time the SE group was observed; it dissolved after a long period of instability.

[+] A dependent infant to the missing females.

Using a multiple stepwise (backward elimination) logistic regression we examined the number of adult females, number of adult males, and a modified sex ratio that calculated the proportion of group adults that were male (AdultPropMale = ADM/ADM + ADF) for years during which a male replacement occurred ($N = 10$) with that of non-replacement group-years ($N = 38$). Because we are looking for demographic trends that might attract extra-group males to a group (e.g., a large number of adult females) and thereby increase the likelihood of a male replacement, we have excluded the two cases of successions from these analyses as they do not involve new males moving into our groups. Only the proportion of adults that were male was included in the resultant model (the probability of a replacement = $1/(1 + \exp(-3.54 - 16.433 * \text{AdultPropMale}))$, Wald $\chi^2 = 7.532$, df = 1, $p = 0.006$). This model demonstrates that the probability of a replacement increased when the proportion of adult males in a group was low relative to the proportion of adult females.

Discussion

Overview

These long-term data provide a glimpse into the life of an immigrant female white-faced capuchin. Immigrant females were mostly parous (4/5), joined the group at the bottom of the dominance hierarchy, and remained at low ranks throughout their time as residents. Two of the five immigrants never reproduced in their new group, likely as a result of their shortened group tenure. The rate of offspring production for the three immigrants that reproduced in their new group did not differ significantly from that of reproducing natal females. Immigrant females experienced significantly shorter tenure than natal females who reached adult age; immigrants spent a median of 2.4 years in a group whereas natal females who reach adulthood remained in the group for >17 years. Four of the five immigrant females that joined our study groups did so during times of group instability. That is, they joined the group in the midst of a male replacement.

In terms of females that disperse/disappear from our study groups (excluding known deaths), they are parous adults, with few close matrilineal kin residing in the group at the time of their departure, and they are of varying ranks (i.e., low, medium and high ranked females were equally likely to

disperse/disappear). Over half (52%) of the female disappearances from our study groups coincided with a changeover in the group's alpha male (through succession or replacement) and most females went missing at the same time as other group members (76%), many of which are known matrilineal kin (38%). Given that we have not known genetic relatedness among many of these disappearing group members (e.g., among those females who were residents when our study began), it is likely that an even higher percentage of the individuals that disappear at the same time are closely related. Interestingly, 42% of the female disappearances coincided with the disappearance of adult males from their group. Regardless of the relatedness among dispersing individuals, this coordinated dispersal, known as parallel dispersal, can serve to offset the high costs associated with dispersing (see Schoof et al., 2009: this issue) and is a practice common among male white-faced capuchins at all ages (Jack & Fedigan, 2004a,b).

Evaluating the hypotheses for female dispersal in white-faced capuchins (Table 1)

Inbreeding avoidance

The avoidance of mating with close kin is the most commonly cited ultimate explanation for sex-biased dispersal from the natal group (Greenwood, 1980). This hypothesis does not, however, explain the cases of female dispersal that we observed in our study population. Females who disperse as a means of inbreeding avoidance are expected to be nulliparous, whereas four of five immigrants into our study groups and all but one of the 21 missing females were parous. Additional evidence against the inbreeding avoidance hypothesis is the fact that natal males disperse from their groups at approx. 4.5 years of age (Jack & Fedigan, 2004a) and male tenure is short (Jack & Fedigan, 2004b). At approx. 40 months, male tenure within our study groups is much shorter than female age at first birth in our population (80 months or 6.5 years, $N = 11$, range = 6–8 years: Fedigan, unpubl. data). Our preliminary paternity data also indicate that males do not reproduce within their natal group (Jack & Fedigan, 2006; Fedigan, unpubl. data).

We have had, however, one adult male who remained in the same group as alpha for 15 years. During his tenure, three of his daughters began reproducing in the group and his only son also remained in the group through adulthood; the son was 11 years when he finally dispersed with his father in

September 2008. Although inbreeding was possible within this group (particularly given our earlier findings that alpha males sire the majority of group offspring, Jack & Fedigan, 2006), our most recent genetic analyses show that a subordinate immigrant adult male sired the offspring of the alpha's daughters (Fedigan, unpubl. data). Muniz et al. (2006) reported similar findings within their groups of *C. capucinus* in the nearby site of Lomas Barbudal, Costa Rica. These results indicate that there are mechanisms in place other than dispersal, such as kin recognition or mating aversions, that serve to prevent breeding among close kin (e.g., Moore, 1993; Lehmann & Perrin, 2003; Pusey, 2005).

Reduction of intragroup feeding competition

Prior research on *C. capucinus* has shown that intragroup feeding competition does occur (Vogel & Janson, 2007) and this hypothesis was somewhat supported by our data set. While we were unable to directly test the prediction that females move from larger to smaller groups, the data that we have on group sizes joined by immigrants (mean = 16.6, N = 5) versus those left by dispersers (mean = 17.6, N = 20) indicate little difference between the two. Females show a tendency to disappear/disperse during the dry season, which coincides with a time of low resource availability in our population. However, we have previously shown that male replacements are significantly more likely to occur in the dry season (Fedigan & Jack, 2004), making it difficult to separate the influence of food availability from the effects of male-replacements.

In a female philopatric species such as capuchins, dispersing females are predicted to have fewer close kin than those who remain in the group — a prediction that was supported by this study. However, the benefits of cooperative resource defense with kin are usually cited as important for between group competition, rather than within group competition (Wrangham, 1980; Sterck et al., 1997). In white-faced capuchins females play a very small role during intergroup aggression (Rose, 1994; Perry, 1996; Crofoot et al., 2008) whereas males are the main participants and the resources in contention are thought to be mates rather than access to food (Rose & Fedigan, 1995). The extent to which food acquisition rates, or even dominance rank, are influenced by the presence of kin in this species remain unclear (see Manson et al., 1999), however, a link has been found between male and female dominance rank and food acquisition (Vogel & Janson, 2007). If female dispersal

in this species is related to intragroup feeding competition we would expect dispersing females to occupy lower ranks within their groups. This prediction was not supported in this study. In fact, four of the 21 females that dispersed or disappeared from our groups were top ranked females, and one of these was a confirmed transfer.

The feeding competition hypothesis also predicts that the immigration of females should be aggressively resisted by resident females. While we have observed some resistance to female immigration in our study groups, the aggression directed towards immigrants is mild in comparison to that observed in other species or even what we have observed among group females during dominance disputes in our study groups. Indeed we have not observed any lethal or severe wounding of an immigrant or any unsuccessful immigration attempts.

Infanticide avoidance

Over the years we have observed first hand a number of infanticide events and inferred many more, the majority of which occur within the context of changeovers in alpha males (Fedigan, 2003). We have clearly documented that infant deaths are significantly more common during years with male replacements than during times of group stability. Recently, we have shown that male replacements and infanticides have a profound effect on the long-term reproductive success of group females (Fedigan et al., 2008). Fourteen of 21 females (67%) dispersed/disappeared from our study groups during times of group instability, 11 of which occurred in the context of a male replacement event. This finding provides strong evidence that the movement of males between groups, which is intimately tied to infant deaths, is driving female dispersal in this species. These data are further bolstered by the fact that four of five immigrations also occurred during times of group instability (i.e., in the midst of male takeovers), with at least two of these females joining our study group after their own group had been aggressively taken over.

In regards to the three sub-hypotheses, it does not appear that female dispersal in this species serves to reduce the risk of male-takeovers by reducing female group size as has been proposed for red howlers (Crockett & Janson, 2000). The only demographic factor significantly associated with the occurrence of male replacements was the proportion of group adults that were male. These results indicate that it is not the absolute number of females in

a group that attracts extra-group males, but rather a high number of adult females in proportion to the number of adult males (i.e., groups with low proportion of males in comparison to females are targeted). Further evidence against this sub-hypothesis comes from our observations that female immigrations are not aggressively resisted nor are maturing natal females evicted.

Our data do show some support for the 'Remaining with the father' hypothesis. For example, two of the five females who immigrated into our study groups did so with the ousted alpha male of their former group and they were obviously pregnant at the time. In addition, 42% of our missing females disappeared at the same time as adult males in their group. Some of these females may have been pregnant and dispersing with the father, but only one left with a dependent offspring and the possible father in the context of a male replacement (as is predicted by this hypothesis). While these data lend support to the idea that females may disperse in order to remain with the father and avoid infanticide from new males in the group, the fact that some infants are killed by incoming males indicates that other females are not choosing this strategy. Indeed, 'Remaining with the father' is a challenging prospect for a female, given the way that white-faced capuchin males must usually fight their way into groups (Fedigan & Jack, 2004). According to the 'Choosing the best male' hypothesis, females may also disperse in order to find a male better able to protect their future offspring from infanticide attempts. Dispersal in such cases may be prompted by an infanticidal attack during an intergroup encounter. While we have had at least three cases where an infant went missing in the immediate context of an intergroup encounter, we did not witness what happened to the infant during these events and they did not lead to the dispersal of the mother. Vogel and Fuentes-Jiménez (2006) recently reported a case of severe aggressive harassment of a female and her dependent offspring when they were separated from their group during an intergroup encounter. This incident, accompanied by observations that females and infants are the first to flee when intergroup encounters occur, indicates that infants are at real risk during these events.

Conclusions

Cebus capucinus is typically considered a female-philopatric species. This characterization may not be entirely accurate, however. Over a 21.5-year period, we found that at least 14% of the adult females that resided in our

study groups were immigrants. Although, to our knowledge, the rates of female dispersal have not been published for other *Cebus* species, the data we present here add to the growing evidence that the genus displays flexibility in its dispersal pattern. This flexibility has led some researchers to suggest that bisexual dispersal was the ancestral platyrrhine condition (e.g., Strier, 1999). Given that the closet living relative to *Cebus* is *Saimiri*, a genus that displays all three possible patterns of dispersal (female-biased, male-biased and bisexual dispersal) (Boinski et al., 2005; Jack, 2007), and the overall behavioural plasticity that characterizes *Cebus*, our finding of greater flexibility in female residence patterns is, in retrospect, perhaps not so surprising.

The majority of the dispersers in our sample were parous females. This finding, accompanied by the finding that male tenure is much shorter than female age at first birth, provides strong evidence against the inbreeding avoidance hypothesis as an explanation for the occasional female dispersal that we observe in our study groups. While we cannot rule out that female white-faced capuchins may be dispersing due to the increased demands of foraging competition within their groups, the link between the two is weak at best and it is difficult to separate the influence of male movement between groups from seasonal effects on the timing of female dispersal. On the whole, the dispersal and/or disappearance of female white-faced capuchins, seems to be intimately linked with the movement of males in our study population. Although our data set is limited in that we do not know the fates of most missing females in our sample, the end result (be it death or dispersal) is the same; females are disappearing during male replacement events. We have previously shown that these male replacements have an enormous reproductive impact on group females (Fedigan et al., 2008) and the results of this study provide a strong indication that male replacements are the driving force behind female dispersal/disappearances in this species. The data presented here add to our growing evidence of the profound influence that males have on the lives of female white-faced capuchins.

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