

THE DEMOGRAPHIC AND REPRODUCTIVE CONTEXT OF MALE REPLACEMENTS IN CEBUS CAPUCINUS

by

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Summary

Male primates may immigrate into groups by peacefully joining the residents and taking up low-ranking positions in the hierarchy, or they may enter by force, challenging the resident males and attempting to drive them from high rank or from the group. Here we address the questions of how, when, and why immigrating male white-faced capuchins (*C. capucinus*) at Santa Rosa replace the former resident males of our groups, rather than simply joining them. We present data on 15 male replacements in 6 study groups tracked from 1984 through March 2004. During 11 aggressive takeovers, resident males were nearly always outnumbered by coalitions of invading males; lone resident males were particularly vulnerable. Both residents and invaders were wounded and infants often perished during or soon after takeovers. Male replacements also occur when resident males abandon their groups and males from neighboring groups 'waltz in' to become resident. Three such 'waltz in' replacements occurred during the study period. If we combine takeovers with 'waltz in' cases, replacements occur about every 4 years in our study groups, almost invariably during the dry season months of January

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to April, about 3-6 months before the annual peak in conceptions. In the years that groups are subject to takeovers, group composition includes significantly lower proportions of adult males than in no-takeover years. We conclude that: (1) the mechanism of male replacement is usually aggressive takeover, but sometimes abandonment of the group by prior resident males occurs; and (2) aggressive takeovers are more likely to happen when the group is vulnerable because it has a lower proportion of adult males, particularly when all co-resident males have emigrated, leaving only the alpha male in residence. Our long-term study shows that adult males need coalition partners not only to gain entry to a group but also to maintain their membership within it.

Introduction

The dispersal of one or both sexes from the natal group is a universal mammalian phenomenon and a pattern that is strongly male-biased in social mammals (Greenwood, 1980; Waser & Jones, 1983; Waser, 1985). In some species, male emigration does not end with natal dispersal and males may reside in several successive breeding groups during their lifetime (primates: see Jack, 2003b for review; non-primate mammals: see Smale *et al.*, 1997, for review; wild dogs: Creel & Creel, 2002; lions: Pusey & Packer, 1987). Patterns of dispersal have been widely investigated in nonhuman primates, although most studies concentrate on proximate and ultimate explanations for male natal emigration, while less attention has been paid to secondary or breeding dispersal (Clobert *et al.*, 2001; see Jack, 2003b for review on primates). In particular, the process of male immigration into established groups following secondary emigration in multimale species and decisions affecting the selection of target groups remain poorly understood (but see Packer, 1978; Alberts *et al.*, 1992; van Noordwijk & van Schaik, 2001). These data are necessary to gain a more complete understanding of male life-history patterns and life-time reproductive success in male dispersed species.

How males enter established groups appears to be largely influenced by their age-class. For example, van Noordwijk and van Schaik (2001) reported that in long-tailed macaques (*Macaca fascicularis*), and cercopithecines in general, subadult males enter groups peacefully because they have not yet attained full body size and are unable to physically compete with resident adult males. However, when adult male primates immigrate into groups, they may also do so by peacefully joining the residents and taking up low ranking positions in the male hierarchy (for review see van Noordwijk & van Schaik, 2001) or they may enter by force, challenging the resident males

and attempting to drive them from dominant positions or from the group entirely. We have observed somewhat similar patterns of male immigration into our long-term study groups of white-faced capuchins (*Cebus capucinus*) in Santa Rosa, Costa Rica. However, fully adult males appear to be limited in that, when they join a group containing resident males, they always do so aggressively (Jack & Fedigan, 2004b).

Aggressive group entries by newcomer males have been described for many Old World monkey species (e.g. *Cercopithecus mitis*: Butynski, 1982; Henzi & Lawes, 1987; *Colobus vellerosus*: Sicotte & MacIntosh, in press); *Erythrocebus patas*: Ohsawa, 2003; *Macaca fascicularis*: van Noordwijk & van Schaik, 2001; *Macaca fuscata*: Sprague *et al.*, 1996; *Papio hamadryas*: Swedell, 2000; Zinner & Deschner, 2000; *Presbytis entellus*: Reena & Ram, 1992; Agoramoorthy, 1994; *Presbytis thomasi*: Steenbeck *et al.*, 2000; *Theropithecus gelada*: Mori & Dunbar, 1985). They have also been described for a few neotropical species (*Alouatta caraya*: Zunino *et al.*, 1986; *Alouatta palliata*: Clarke *et al.*, 1994; *Alouatta seniculus*: Crockett & Janson, 2000; *Cebus capucinus*: Fedigan *et al.*, 1996, Perry, 2003; *Cebus apella*: Izawa, 1994; *Cebus olivaceus*: Valderrama *et al.*, 1990; *Saimiri boliviensis*, *S. sciureus*, *S. oerstedii*: Boinski, pers. comm.). The aggressive entry of a new male into a unimale social system almost always results in the eviction of the former resident male (e.g. *Presbytis entellus*: Reena & Ram, 1992; Agoramoorthy, 1994; Rajpurohit *et al.*, 2003; *Presbytis thomasi*: Steenbeck *et al.*, 2000; *Erythrocebus patas*: Enstram *et al.*, 2002). However, in most multimale species, newly arrived males will tolerate the continued presence of prior resident males as subordinates or *vice versa* (e.g. *Alouatta palliata*: Glander, pers. comm.; *Macaca fascicularis*: van Noordwijk & van Schaik, 2001; *Chlorocebus aethiops*: Henzi & Lucas, 1980; *Macaca fuscata yakui*: Sprague, 1992; *Papio cynocephalus*: Alberts & Altmann, 1995; *Papio anubis*: Sapolsky, 1996).

Although several of these species show frequent changeovers in male membership over the course of several years, the complete and simultaneous replacement of resident males in multimale primate species has only been reported to occur commonly in *Alouatta seniculus* (Crockett & Pope, 1993; Pope, 2000) and *Cebus capucinus* (Fedigan *et al.*, 1996; Perry, 2003) (see Pusey & Packer, 1987, for similar reports of male replacements among lions; see Creel & Creel, 2002, for African wild dogs). We have shown previously that male white-faced capuchins moving between groups experience

an increase in reproductive opportunities and that the dispersal of adult males appears to be the result of covert intragroup mating competition, rather than intergroup mating competition or inbreeding avoidance (Jack & Fedigan, 2004b). Here we examine the proximate causes of resident male replacements. In particular, this paper addresses three key issues about the process, context and causes of male replacements in *Cebus capucinus*: (1) How do resident male replacements occur? We describe the process of male replacements, the characteristics and numbers of invading vs. resident males, and the consequences of male replacements to other group members (*e.g.* wounding, deaths and disappearances). (2) When do male replacements occur? In terms of timing, how often do male replacements occur and do they occur at a certain time of the year? (3) Why do male replacements occur? Following and building upon Crockett and Janson's (2000) findings on the relationship between howler male invasions and group demography, we examine the predictions that the risk/occurrence of male replacement increases with the proportion of females in the group and decreases with increasing group size and proportion of males in the group. We also address the question of why incoming males replace resident males rather than tolerating them as low ranking members, as has been observed in most other multimale primate species.

Methods and materials

Species

White-faced capuchins are characterized by year-round associations of multiple immigrant males, multiple related females and their immature offspring. Group sizes in our study population range from seven to 36 individuals (mean = 17.2; Fedigan & Jack, 2001). Males are transient, dispersing from the natal group at approximately 4.5 years of age (Jack & Fedigan, 2004a) and continuing to disperse approximately every four years throughout their lives (Jack & Fedigan, 2004b). Some males form long-term coalitions with siblings, cousins, or unrelated males and these are maintained through parallel dispersal (Jack, 2003a; Jack & Fedigan, 2004b). All-male bands are rare and temporary, as males usually move directly out of one group into another. Females form the core of the group and establish close affiliative and cooperative bonds with other females. These relationships, which are based along kinship lines, are stable over many years (Perry, 1995; Fragaszy, Visalberghi & Fedigan, 2004).

The Santa Rosa study population experiences a distinct birth peak between January and April; however they are not strict seasonal breeders (Fedigan *et al.*, 1996). Instead, white-faced capuchins engage in copulations throughout the year, many of which are nonconceptive (Manson *et al.*, 1997), and females do not show any visible signs of ovulation. Female white-faced capuchins can be considered reproductively mature at age 5 when they begin to cycle

for the first time. But, in our study groups, females do not usually give birth to their first infant until they are nearly 7 years of age (Fedigan, unpubl. data). Little to no overt mating competition occurs among group males (Jack & Fedigan, 2004b); although preliminary DNA evidence indicates that dominant males are siring the majority of the offspring born into our study groups (Jack & Fedigan, 2003).

Study site

Data for this study were collected between 1984 and March 2004 on several groups of white-faced capuchins (*Cebus capucinus*) resident in the Santa Rosa sector of Area de Conservación Guanacaste (ACG). ACG is home to three monkey species: white-faced capuchins (*C. capucinus*), mantled howlers (*Alouatta palliata*) and black-handed spider monkeys (*Ateles geoffroyi*). The basic demographic, ecological and behavioral patterns of these species in ACG have been described (see references in Fedigan, 2003). Detailed descriptions and history of the site can be found in Allen (2001) and Evans (1999).

Study groups

This paper describes male replacements in six study groups that were followed for variable lengths of time between January 1984 and March 2004. The Sendero group (SE) was observed for a total of nine years, beginning in 1984 and ending in 1993 when the group was rendered extinct by multiple deaths and disappearances that occurred during a male takeover. Observations of our second study group, Cerco de Piedra (CP), began in 1985 and continue through the present, while our third main study group, Los Valles (LV), has been observed since 1990 and continues to be under intensive observation. Three additional groups have been studied intermittently throughout the last decade. Two of these groups (BH and CU) were tracked between 1997 and 2000 when our habituated males immigrated into them (Jack, 2001 & Fedigan, 2003), while the third group (NA) was tracked between 1995 and 1997 as part of a doctoral student project (Rose, 1998).

Data collection and analyses

Between 1984 and 2004 the study groups were tracked nearly continuously by a number of graduate students and research assistants that we trained in the field to collect data on births, deaths, dispersal and social behavior. Interobserver reliability was practiced as part of the training process for each new researcher. Although study groups are monitored on a near daily basis between January and August and at least twice a month between September and November, there are six gaps (totaling to 24 months) that occur in the data: a six month hiatus in 1991, two months in 1995, four months in 1996, five months in 1997, three months in 1999, and four months in 2000. It is possible that during these periods, takeover attempts were launched; however, we know that no successful replacements occurred during our absence as we never returned to the field to find new adult males in our study groups.

Whenever researchers became aware of the possibility that a male replacement might occur (*e.g.* nonresident males observed in the vicinity of our study groups), extra time and care was devoted to tracking and noting the details of daily interactions between the newly-arrived males and the study group. Extensive ad libitum notes from several researchers, in addition to the regular data collection sheets, were used to extract the patterns reported here.

The age categories of invading males were estimated based on features we have observed in males of known ages that we tracked over nearly two decades in our study groups. We categorize males as subadult from 7-10 years of age, young adult from 10.1 to 15 years, middle-aged from 15.1 to 20 years, and old from 20.1 to 25 years. We have seen, although on only one occasion, a large juvenile male (aged ~7 years) mount to ejaculation. However, males do not reach full adult body size until 10 years of age, nor do they attain high ranks within groups until that time (see Jack & Fedigan, 2004b). There may well be an error factor in our classification of middle-aged males, but it is easy to distinguish young adult males from old adult males. Young adult males typically have few scars and are robust with shiny fur and athletic locomotor patterns. Old adult males typically have multiple scars, dark pock marks on their faces and heads, and are often missing digits. They are also typically thin with scraggly fur and move more stiffly and cautiously than younger males.

We use non-parametric tests (*e.g.* Wilcoxon signed ranks tests) for analyses of replacement patterns. For the analysis of demographic data, we used logistic regression. We used SURVIVAL analysis to compare alpha male tenure in takeover and waltz-in replacements, and a Wilcoxon Gehan (generated by SURVIVAL analysis) to statistically compare these two types of male replacement.

Results

We present data on 15 male replacements in six study groups tracked from 1984 through March 2004 (Table 1). Eleven of these events occurred in our three continuously studied groups (SE, LV, and CP). Our more complete descriptions and data sets come from these eleven occurrences, as well as a twelfth replacement that was recorded in great detail by Rose for group NA (1998). However, even for the remaining three cases (BH97, CU97, CU99), we have some information on the number and origin of resident and invading males and their estimated ages.

How do replacements occur?

Replacements usually occur when outsider males aggressively enter our study groups and fight with resident males for group membership. Aggressive takeovers often result in severe wounding and the eventual eviction of resident males and they almost invariably coincide with the deaths and disappearances of infants, and the injury or death of other group members (Fedigan, 2003). However, the resident adult males of our study groups occasionally disperse without apparent provocation, and leave the group without adult males, at which time another male, or coalition of males, will immigrate into the group (see Pusey & Packer, 1987 for similar behavior among

male lions). In one sense, newly-arrived adult males are 'taking over' the position(s) of the resident male(s) whenever there is a turnover in male membership of a group, such that prior males disperse and new males establish residence in the group, whether by force or abdication. But here we distinguish between these two types of resident male replacements: takeovers are defined as aggressive invasions involving fights between residents and invaders, while those cases where an adult male(s) joins a group that is without resident males are termed 'waltz-ins'. We use the term 'replacement' to refer to the larger category of all cases involving a turnover of adult males. Both types of male replacement are distinct from peaceful male immigration, where a male joins an on-going group as a subordinate male and no resident males leave — thus far, we have only seen large juvenile and subadult males immigrate peacefully into on-going, stable groups of Santa Rosa capuchins (Jack & Fedigan, 2004b).

Takeovers: aggressive replacements of resident males

Of the 14 male replacements for which we have sufficient data to determine the proximate cause (*i.e.* takeover or waltz-in; excluding CU97), eleven (79%) were the result of aggressive group takeovers. These takeovers almost always involve coalitions of two or more males (10 of 11 cases, Table 1). Five of the eleven groups that were aggressively taken over had only one resident male (the alpha male) at the time of the invasion, and, in general, invading males outnumber the residents. We have two exceptions in our sample of group takeovers. The first (SE85) involved a case where invaders and resident males were matched in number but not in strength (*i.e.* resident males were either too young or too old to win the battle), and the other exception (CP90) was the only takeover where resident males actually outnumbered invader males. However, in this case the lone invading male was of prime age (mid-aged adult) while the alpha male was a small, young adult male and his coresident was subadult.

There were 37 invading males involved in the eleven takeovers that occurred within our study groups. Fifteen of these males were mid-aged adults, twelve were young adults, and ten were subadults. Although subadult males are often coalitionary partners to young and mid-aged adult males during group takeovers (subadults were involved in five of the eleven takeovers), we have never observed a takeover solely involving subadult males, probably because they are not physically strong enough to win fights against adult

TABLE 1. *Characteristics of male replacements*

	# σ^{σ} invaders: resident	Transition Length (mos.)	Origin Invading Related?	Who is wounded? (Deaths also noted)	Age of Invading σ^{σ} ,***	Tenure & age of resi- dent α σ^{σ} and coresi- dent σ^{σ} ***
SE 85	2 : 2	2	Unknown/Unknown	1 invader and α & $\beta\sigma^{\sigma}$	2 young σ^{σ}	Unknown; old α and 1 young coresident
SE 89*	1 : 0	1	Neighbor grp/1 invad- ing σ^{σ}	No wounds noted; 1 inf dies	1 mid-aged	48 mos; mid-aged α
SE 91*	1 : 0	1	Neighbor grp/1 invad- ing σ^{σ}	$\alpha\sigma^{\sigma}$ is wounded 1 mo. earlier by in- vader during intergroup; 1 inf dies	1 mid-aged	23 mos; old α
SE 93	2 : 1	1	Unknown/Unknown	1 invader wounded; $\alpha\sigma^{\sigma}$ leaves, 2 σ^{σ} & 1 inf die; grp rendered extinct	2 mid-aged	22 mos; old α
CP 89*	2 : 0	2	Neighbor grp/Sibs or cousins	12 residents leave the home range; 1 inf dies	1 young & 1 subadults	>39 mos; young α
CP 90	1 : 2	1	Unknown/1 invading σ^{σ}	Invader and $\alpha\sigma^{\sigma}$ wounded; 2 infs die	1 mid-aged	17 mos; young α and 1 sub. Coresident
CP 93	4 : 2	2	Unknown/Unknown	2 invaders; resident deaths: $\alpha\sigma^{\sigma}$; 2 σ^{σ} ; 2 juvs; 3 infs	3 young & 1 subadults	29 mos; mid-aged α and 1 small mid-aged coresident
LV 93	2 : 1	2	Unknown/Unknown	1 invader, all coresident σ^{σ} disappear; 1 inf dies	2 mid-aged	>35 mos/mid-age α
LV 97	2 : 1	3	Neighbor grp/Unknown	Invaders, $\alpha\sigma^{\sigma}$ & $\alpha\sigma^{\sigma}$ wounded; 1 inf dies	2 mid-aged	50 mos; mid-aged α

TABLE 1. (*Continued*)

	# $\sigma\sigma$ invaders: resident	Transition Length (mos.)	Origin Invading $\sigma\sigma$ / Related?	Who is wounded? (Deaths also noted)	Age of Invading $\sigma\sigma^{***}$	Tenure & age of resi- dent α σ and coresi- dent $\sigma\sigma^{***}$
LV 00	4 : 2	3	Unknown/Unknown	3 invaders, α and $\beta\sigma$ and 4 ad f's wounded; 2 inf's die	2 young & 2 mid- aged	37 mos; mid-aged α
LV 04	5 : 3	2	Unknown/Unknown	2 invaders and 2 juvs wounded; all resident $\sigma\sigma$ & 1 juv disappear; 1 inf wounded but recovers, second inf dies	2 mid-aged, 2 young, 1 subad	45 mos, mid-aged α ; and mid-aged coresi- dent
NA 97	7 : 3	0.5	Unknown/Unknown	4 invaders wounded, $\beta\sigma$ killed; 1 inf dies	4 mid-aged, 1 young and 2 subadults	Unknown/mid-aged α , 1 old and 1 subadult coresident
BH 97	5 : 1	Unknown	Neighbor grp/Adult $\sigma\sigma$ unrelated, sub- adults sibs & cousins	$\alpha\sigma$ and 1 invading σ wounded; Un- known for other group members	1 young & 4 subadults	Unknown/Mid-aged adult
CU 97**	2 : ?	Unknown	Neighbor grp/Sibs	Unknown; no wounds noted on new males	1 young & 1 subadults	Unknown
CU 99	3 : 1	2	Unknown/Unknown	$\alpha\sigma$ wounded; 1 formerly pregnant female observed with no infant after takeover	1 young & 2 subadults	24 mos; young adult α

* Indicates waltz-in rather than takeover.

** This study group was not observed prior to these males moving in, so we are unsure of the number of males prior to replacement and whether this was a waltz-in or a takeover.

*** Ages are estimates and all males are adults unless otherwise indicated (sub = subadult male).

males. We have not yet seen an old male act as an invader. Alpha males of groups that experience a takeover are typically middle-aged ($N = 7$), while two alpha males were old and two were young adults (Table 1). In ten of the eleven takeovers, resident males were permanently evicted from the group by the invading males, and in the one case where an alpha male was only temporarily evicted (CP90), he returned to hold a very peripheral position in the group.

In nine of the eleven takeovers both invader and resident males were wounded. In two cases (CP93, NA97) adult resident males were confirmed to have died as a result of their wounds. Infants were wounded and died during or soon after takeovers in all eight of the takeovers for which we have sufficiently detailed records (SE93, CP90 through NA97 in Table 1). In all takeovers for which we have sufficient data (excludes CU97), at least one resident group member was injured. Two of the eleven takeovers were launched by invaders from neighboring groups; while the invaders in the nine remaining cases were unknown to us (*i.e.* they did not emigrate from neighboring groups).

Failed takeovers

During the study period, we also documented two takeover attempts that failed and it is possible that additional takeover attempts were launched during times of researcher absence. The first failed takeover that we documented involved a single young adult invader who had just been ousted as alpha male by a coalition of males and he in turn attempted to aggressively invade a neighboring group containing a single mid-aged adult male. However, with the cooperation of group females, the lone resident male was able to hold on to his position in the group, although only for a short time before a coalition of males successfully evicted him three months later (LV97). The second failed takeover was extremely complicated and actually involved the subordinate coalition partner changing allegiance following a takeover and usurping alpha male status for himself. This is a special case in many respects – first, the resident male was known to the two invaders, as all three had lived together in a different group several years earlier; and second, the invading males were thought to be maternal siblings. In addition, the male who changed allegiances following the takeover managed to rise to the position of alpha male, while the former resident male dropped to beta male, and the second coalition partner was evicted from the group.

Waltz-ins: replacements occurring during periods of resident male absence

We have occasionally observed adult males to enter groups with no resistance by taking advantage of the absence of adult males in the group and simply 'waltzing-in'. Of the fourteen male replacements for which we have sufficient data to determine the proximate cause of the replacement, three are best categorized as waltz-ins (CP89, SE89 & SE91).

Groups without resident males may be the result of a fission, which we have observed on one occasion (CP89), or they may be groups that have been completely abandoned by all resident males after an intergroup encounter (SE91). The SE91 case is rather telling in that the immigrating male, who was a member of our LV study group, and one of his coresident LV males, had mildly wounded the SE alpha male during an intergroup encounter one month prior to the replacement. After this interaction the SE alpha was not seen again, leaving the group without any resident males, and the immigrating LV male was then able to enter with no further aggression.

It is possible that similar pre-replacement interactions between resident males and replacement males took place in the other case that we have labeled as a 'waltz-in' (SE89). We do know that in the SE89 replacement the four resident males (three adults and one subadult) all disappeared from the group several weeks before the replacement male moved in. The replacement male was noted as being on the periphery of the SE group one month prior to 'waltzing' in, but it is unlikely that this single male could have aggressively ousted four resident males.

When do replacements occur?

Our three main study groups have been tracked for 9 years (SE), 15 years (LV) and 19 years (CP). During the periods that they have been studied, SE experienced four replacements for an average rate of one every 2.3 years, LV experienced four replacements for an average rate of one every 3.8 years and CP experienced three replacements for an average rate of one every 6.3 years. However, CP in recent years appears an anomaly in that the current alpha male has been in place for 11 years. He deserted his group for nine months in 1997 after a tenure of 51 months, but no males attempted to invade his group while he was away and he subsequently returned for another term as alpha male in CP. If we consider this alpha male's desertion of CP in 1997 to have been the 'normal' time for a male replacement to have occurred, then

CP's average would be 4.8 years between turnovers. Using the adjusted rate for CP, male replacements occur on average every 3.6 years in our long-term study groups.

We also examined the tenure length of alpha males ($N = 11$; SE89 through LV04 and CU99 in Table 1) according to the type of replacement that occurred within the study groups. Using SURVIVAL analysis, which enables us to take into account incomplete tenure lengths (*i.e.* those males who were group residents when our observations began), the median tenure length for alpha males whose group was the target of an aggressive takeover ($N = 8$) was 35 months. In the 'waltz-in' cases where the prior alpha male deserted his group ($N = 3$ cases), the median tenure length was 45 months. This difference is not significant (Wilcoxon Gehan = 0.567, $df = 1$, $p = 0.4514$).

Fourteen of the 15 male replacements occurred in the dry season months of January to April. In fact, all forms of male secondary dispersal in our study animals (peaceful entries, takeovers, waltz-in) are significantly more likely to occur in the dry season (binomial test, observed proportion = 76%, $p < 0.001$, $N = 67$; Jack, 2001).

Why do male replacements occur?

When we compare our three best known study groups for the years in which they experienced takeovers versus the years they did not, we find some demographic patterns typical of groups that experience takeovers (Table 2). These analyses include only those replacements that were classified as takeovers because the 'waltz-in' replacements, by definition, would occur when the groups have lower numbers and proportions of males, altered sex ratios, and possibly smaller overall group sizes.

The demographic trends show that groups subjected to takeovers had lower numbers and proportions of adult males, and of subadult/adult males combined. They also had slightly lower proportions (but not numbers) of adult females and juveniles and greater numbers and proportions of infants. Group size is also somewhat lower in takeover years, whereas the ratio of females to males is higher (2.7 in takeover years and 1.7 in non-takeover years). We used logistic regression to predict the likelihood of a takeover occurring within our three long-term study groups as a function of group size and of the proportion of adult males, adult and subadult males combined, and adult females within groups. While all four of these variables had a negative effect,

TABLE 2. Comparison of group composition in takeover versus no takeover years for 3 study groups (CP, SE & LV)*

	Mean #/proportion Adult Males	Mean #/proportion Sub & Ad M's	Mean #/proportion Adult Female	Mean #/proportion Juveniles	Mean #/proportion Infants	Mean Group Size	Mean Adult Sex Ratio (F:M)
CP Takeover Years (N = 2)	1.5/0.1	3.5/0.23	5/0.33	4.5/0.30	2/0.13	15	3.75
CP No Takeover Years (N = 16)	3.4/0.23	4.3/0.29	4.4/0.30	4.7/0.32	1.3/0.09	14.7	1.6
SE Takeover Years (N = 2)	1.5/0.18	3.5/0.35	2/0.24	3/0.35	0.5/0.06	8.5	1.5
SE No Takeover Years (N = 5)	2.6/0.25	3.8/0.36	3.2/0.30	2.6/0.25	1.0/0.09	10.6	1.8
LV Takeover Years (N = 4)	2.3/0.14	3.8/0.23	5.0/0.30	6.0/0.36	2.0/0.12	16.7	2.8
LV No Takeover Years (N = 11)	3.3/0.17	5.4/0.29	4.9/0.26	7.3/0.39	1.2/0.06	18.7	1.7
All Takeover Years (N = 8)	1.8/0.14	3.4/0.27	4.0/0.29	4.5/0.34	1.5/0.10	13.4	2.7
All No Takeover (N = 32)	3.1/0.22	4.5/0.30	4.2/0.29	4.9/0.31	1.1/0.08	14.7	1.7

* Group composition in No Takeover years was always calculated from January census data, whereas for Takeover Years, group composition was determined at one month prior to the time of male invasion (usually January, February or March).

only the proportion of adult males within our study groups had a significant effect on the likelihood of a takeover (regression coefficient = -18.550 , Wald = 4.516 ; $df = 1$; $p = 0.034$). The lower the proportions of adult males in the group, the greater the likelihood of a takeover.

Discussion

How do male replacements occur?

Although there is variation in the 14 male replacement episodes for which we were able to document the proximate cause of the replacement (takeover vs waltz-in), distinctive patterns emerge. The process by which in-coming males replace residents most often (79% of our sample) involves repeated aggressive encounters and often severe wounding of both resident and newly-arrived males (Fedigan, 2003). During aggressive takeovers and the months following them, females and juveniles may also be wounded, but usually superficially, whereas unweaned infants commonly perish during and after takeovers (Fedigan, 2003). The period of transition and fighting lasts from two weeks to three months (Table 1) and invaders typically arrive in coalitions that outnumber the resident males (see Gros-Louis *et al.*, 2003 for similar findings in the Lomas Barbudal *Cebus capucinus* population). In most cases these invaders are not known to us, and given that we can recognize most males in groups surrounding our study groups, we suspect that these males come from farther away.

Takeovers occur when certain features in the invaders and residents coincide. Potential invaders typically have a partner or multiple partners and must be of the right age. Invading male coalitions usually consisted of a mix of young and middle aged adult males, often accompanied by subadults, but we have yet to see an old male take part in an aggressive group takeover. Subadult males are less likely to participate in contact aggression with adult males during takeovers, but we found that they were just as likely to be members of aggressive coalitions as either mid or young aged adult males. This suggests that subadults are important, albeit slightly less compatible, coalition partners. There is a slight shift in ages of protagonists and recipients such that young and middle-aged adult males are more likely to invade whereas middle aged males are more likely to be evicted. A similar age effect, where young ('prime-aged') males are the most likely to aggressively

takeover groups, has been reported for long-tailed macaques (van Noordwijk & van Schaik, 2001) and lions (Pusey & Packer, 1987).

Resident male replacements that occur as a result of new males moving into groups when former resident males are no longer present (waltz-ins) occur much less frequently in our study groups (21% of male replacements). Interestingly, all three of the waltz-in type of male replacements involved males transferring in from neighboring groups. This may indicate that males from neighboring groups are able to take advantage of frequent intergroup interactions, which are even more common during the dry season when most dispersal events take place, to assess their competitors in neighboring groups (see Smale *et al.*, 1997 for similar findings in other mammals). We often see extragroup males around the periphery of our study groups who appear to be 'checking out' the group and indeed we also have group males who will disappear for days at a time and when followed, also appear to be assessing opportunities in other groups. This 'visiting' behavior is more frequent during the dry season.

When do male replacements occur?

Male replacements occur about every 2-6 years in our study groups and we have attempted to identify the proximate variables that co-occur with these periodic social upheavals.

On average, we see a complete replacement of resident males approximately every four years. However, the timing of these replacements in terms of the tenure of the former alpha male is highly variable, ranging from 17 to 50 months for takeover episodes and 23 to 48 months for waltz-in cases. Our finding that alpha males who are replaced as a result of a takeover do not have much shorter tenure lengths than males who desert their groups is in contrast to what has been reported for male lions, where males are evicted much sooner than they would voluntarily leave their groups (Pusey & Packer, 1987). In further contrast, Pope (pers. comm.) reports that although subordinate male red howler monkeys (*Alouatta seniculus*) will often emigrate voluntarily because they are seeking breeding positions within other groups, breeding males never desert their group. With a mean tenure length of 35 months before eviction and 45 months before deserting their groups voluntarily, alpha males in our study are replaced long before their daughters become sexually mature at approximately 60 to 72 months of age.

Although not the focus of this paper, we briefly address here the issue of why resident males would ever abandon their groups. We have previously shown that in our study population of white-faced capuchins, male transfers between groups result in increased mating opportunities for subordinate males and that dispersing alpha males are also moving towards groups with an increased number of potential mates and more preferable sex ratios while maintaining their high rank (Jack & Fedigan, 2004b). Pusey & Packer (1987) also report that male lions desert groups in search of better mating opportunities. In addition, our cases of 'waltz-in' replacements following abandonment of the group by former resident males, show that alpha males may 'waltz-out' because their group fissions and they can only reside in one of the two resulting groups (CP89), or due to the mere threat of an invasion (SE91) or because their co-resident males have already emigrated and they are trying to take advantage of a takeover in a neighboring group (the alpha male of CP in 1997).

In terms of seasonal timing, we have puzzled over the finding that these replacements occurred almost entirely during the dry season months of January to April, which is about 3-6 months before the peaks in conceptions (July and Oct). In the seasonally arid forests of Santa Rosa, capuchin groups become 'central place foragers' around water holes during the dry season (Fedigan *et al.*, 1996), and more intergroup encounters occur at this time. Perhaps groups become more visible and locatable targets for invading males during this period when the trees are largely leafless and capuchin home ranges are smaller. It is also possible that males are using intergroup encounters as a way of assessing neighboring groups as possible targets for immigration, which has been reported for samango monkeys and baboons (Packer, 1979; Henzi & Lawes, 1987). This suggestion is supported by our finding that six of the 15 replacements involved males immigrating from neighboring groups. In addition, we have been tracking dispersing males for many years, and our data indicate that most males move into neighboring groups, traveling farther and farther from their natal group with each subsequent emigration (see van Noordwijk & van Schaik, 2001, for similar findings in long-tailed macaques and Cheney & Seyfarth, 1983, for vervets). It may also be the case that male replacements, and dispersal in general, occur more frequently during the dry season because most infants at Santa Rosa are born January-April (Fedigan, 2003), and females at our site sometimes experience a brief (non-fertile) post-partum phase during which they will mate with males. It is

possible that the attractivity/proceptivity signals of post-partum females are conveyed to non-group males as well as residents.

Our previous finding that males who immigrate into groups (either through replacement or simple dispersal) experienced increased mating opportunities (Jack & Fedigan, 2004b) may also shed light on the seasonal bias in male dispersal found in these white-faced capuchins. Fedigan (2003) has shown that infant deaths in replacement years are significantly increased over non-replacement years and here we report that even waltz-ins, where males peacefully enter into groups, are associated with infant deaths. Most infant deaths (Fedigan, 2003) and male replacements (present paper) occur during the six month dry season and although white-faced capuchins are not strict seasonal breeders, they do display a birth peak (Jan-April), which directly corresponds to the dry season. It is possible that males time their entry into new groups so as to ensure that they will be in place during the upcoming conception peak that occurs three to six months later. Recabarren *et al.* (2000) found that captive brown capuchin females, *Cebus apella*, who lost their infants experienced resumption of their menstrual cycles 31 to 150 days after parturition, but such cycle resumption was followed by periods of up to five months of residual infertility (mating but no pregnancy). If residual infertility is also occurring in our white-faced capuchins, this could explain the three to six month time lag between male replacements and the peak in conceptions and why we see more males moving between groups during the dry season (birth season).

Why do male replacements occur?

We predicted that the risk/occurrence of male replacements (specifically takeovers) would increase in years when our study groups have higher proportions of adult females, lower proportions of adult males, lower combined proportions of subadult and adult males, and smaller group size. Of these variables, only the proportion of adult males in our groups had a significant effect on the occurrence of aggressive replacements of resident males, indicating that the odds of a takeover increase with a decreasing proportion of resident adult males.

We have previously noted (see Fedigan, 1993; Rose & Fedigan, 1995; Perry, 1998; Jack, 2003a) that it is when alpha males lose their coalition partners, usually through the emigration of subordinate coresident males,

that their groups become more susceptible to aggressive group takeovers. Indeed in our study groups that were subject to aggressive takeovers, invading males almost always outnumbered resident males, and in nearly 50% of our sample the alpha male was the sole male resident in the target group. This finding underlines the importance of coalition partners for male white-faced capuchins: males not only need allies to gain entry into a group but to retain their membership within it.

The importance of coalition partners in this species may also shed light on the question of why complete replacements of resident males occur in white-faced capuchin groups, rather than the integration of new males into established groups, as is seen in most other multimale primate species. Our long-term analysis of male dispersal patterns has shown that males of all ages form migration alliances that last over multiple emigrations and this dispersal pattern may be one way in which kin relations are maintained among coresident males in some groups (Jack & Fedigan, 2004b). If male kinship within groups is maintained through parallel dispersal, which we strongly suspect, then subordinate males may experience inclusive fitness benefits even though alpha males are siring the majority of infants. Similar findings have been reported for red howler monkeys (*Alouatta seniculus*: Pope, 2000) and lions (Packer *et al.*, 1991) where males are more likely to remain in a group in a non (or low) reproductive capacity only if they are residing with male kin. If similar circumstances exist within coalitions of male white-faced capuchins, then it would not make reproductive sense for a former resident male to remain as a subordinate group member and reside with new and unrelated invader males since his reproductive success would become minimal to nonexistent. In addition, lethal aggression in this species has been well-documented (*e.g.* Fedigan *et al.*, 1996; Rose, 1998; Gros-Louis *et al.*, 2003) and it appears that in most cases former resident males do not have the option of remaining in the group as a subordinate – the risks of being seriously or fatally wounded by the new males are too great. The data we have collected and analyzed on replacement and dispersal patterns indicate that white-faced capuchins pursue reproductive success in the context of an intricate web of adult male relationships maintained through agonistic support for coalition partners and fierce animosity to those outside the coalition.

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