Impact of Male Takeovers on Infant Deaths, Births and Conceptions in *Cebus capucinus* at Santa Rosa, Costa Rica

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*Male takeovers are associated with infant wounding and death in 3 of 4 capuchin species. In this paper, I analyze the effects of male takeovers on infant mortality and the subsequent conceptions and interbirth intervals of their mothers over an 18-yr period and test predictions of the sexual selection model of infanticide for white-faced capuchins, (*Cebus capucinus*). Major findings are that infants are significantly more likely to die in the 3- and 12-mo periods following a takeover than in times of peace and that a female whose infant dies experiences a significantly shorter interbirth interval before her next infant is born than she would have had the former infant survived. In the vast majority of cases, the invading males become resident in the group and are present during the subsequent conceptions of the females in the group. However, overall conception rates do not rise significantly in the year after a takeover, there is no relationship between the age of the infant at death and the length of the mother's subsequent interbirth interval, and it is not yet clear if male infants are preferentially targeted by invading males. Most takeovers occur during the 6-mo dry season and most conceptions occur in the wet season, 3–6 mo later. My findings support the major predictions of the sexual selection model of infanticide in primates and demonstrate that male takeovers of social groups have substantial effects on infant survival and maternal parturition patterns in* Cebus capucinus.*

KEY WORDS: takeover; male replacement; capuchins; infanticide; alpha male change.

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INTRODUCTION

In several primate species, males occasionally enter new groups by force, drive out the resident adult males and fatally wound unweaned infants (Paul *et al.*, 2000; Sterck and Korstjens, 2000; van Schaik, 2000a,b). This process whereby immigrant males challenge and replace the alpha male has been called male replacement (Butynski, 1982; Rudran, 1973; Struhsaker, 1977; Sugiyama, 1966; Wheatley, 1982; Wolfe and Fleagle, 1977), but more recently and more commonly is referred to as a male takeover (Clarke *et al.*, 1994; Pope, 2000; Ross, 1993; Steenbeck, 2000; Strier, 2000; Swedell, 2000; van Schaik, 2000b; Zinner and Deschner, 2000).

The concurrence of alpha male changes with the wounding, death and disappearance of infants (as well as females and other males) occurs in *Cebus apella* (Izawa, 1994), *C. olivaceus* (O'Brien, 1991; Valderrama *et al.*, 1990) and *C. capucinus* (Fedigan *et al.*, 1996; Perry, 1998; Rose, 1994; Rose and Fedigan, 1995). In some cases the capuchin male suspected of killing an infant had been previously resident in the group at a subordinate rank before assuming the alpha male role, but in most cases, the suspected infanticidal males are in the process of invading and taking over breeding groups.

At Santa Rosa, we began to note the disappearance of infants in association with male takeovers in 1985, though it was another 6 years before we directly observed a male to fatally wound an infant. At our field site, white-faced capuchins (*Cebus capucinus*) occur in multimale, multifemale groups of *ca.* 16 members (Fedigan and Jack, 2001). Females typically remain in their natal groups, whereas most males disperse several times during their lives (Jack and Fedigan, in press). From long-term life history data, we know that the adult females of a group are often related to each other, but some adult females immigrate into our study groups from non-neighboring groups. In addition, we have seen sibling males disperse and enter new groups together; therefore it is likely that some adult males in a group are also related to one another.

Although all the adult males and subadult males of a group may mate with the adult females with no obvious recrimination from higher ranking males, our preliminary DNA analyses indicate that the alpha males sire a disproportionate number of the infants (Jack and Fedigan, 2003). Males spend little to no time living as solitaries or in all-male groups. Instead, they move quickly out of their former groups and immigrate almost immediately into new ones, either singly or in pairs or triplets. New males may enter groups peacefully and unobtrusively, or they may do so aggressively, attacking the resident males and other members of the group (Jack and Fedigan, in press). Aggressive immigrations—takeovers—almost always result in the wounding and departure of most former resident adult males, and in the wounding

and sometimes death of the infants during and after such events (Fedigan *et al.*, 1996). Peaceful male immigrations are not takeovers because they do not result in eviction of resident males, immediate male rank changes, or wounding and deaths of group members.

Sexual selection models of infanticide in primates predict that infants that are still regularly suckling their mother's milk and thereby suppressing her reproductive cycles (Recabarren *et al.*, 2001) will be killed by invading males during or soon after takeovers (Hausfater and Hrdy, 1984; Hrdy, 1977, 1979). Therefore mortality rates of infants should be higher during and after takeover events than at other times. Furthermore, lactating mothers that lose an infant by natural death/infanticide are predicted to resume cycling and mating sooner than they would have had the infant survived, as has been documented for baboons (Altmann *et al.*, 1978). Thus, mothers of infants that die should experience shorter interbirth intervals (IBIs) than mothers with infants that survive. And because all of the group's adult females are hypothesized to mate with newly-resident invader males as a counterstrategy to infanticide (Hrdy, 1979; van Schaik, 2000b), conception rates are predicted to be higher after takeover events.

It has also been argued that younger infants should be targeted by invading males because the younger the infant is when it dies or is killed, the higher impact it has via nursing on her reproductive cycles and the more efficient this male strategy is in shortening the mother's subsequent IBI (Crockett and Sekulic, 1984; Hrdy, 1979; Sommer, 1994; van Schaik, 2000a). We also predict the positive correlation between the age of the infant at death and the length of the mother's subsequent interbirth interval.

In addition, in some species (Hanuman langurs: Sommer, 1994; mantled howlers: Clarke, 1983 and chimpanzees: Hiraiwa-Hasegawa and Hasegawa, 1994) male infants are differentially targeted, leading to the prediction that more male than female infants die in association with takeovers. Sommer (1994) argued that invaders may target male infants for a couple of adaptive reasons: to eliminate future potential competitors of their sons and to spare female infants that might grow up to be future mates. Finally, the sexual selection hypothesis for infanticide predicts that the perpetrating males are not the fathers of their victims, but will become or remain members of the mother's group, gain mating access to her, and be present at the time of her next conception (Borries *et al.*, 1999; Sommer, 1994).

As Janson (2000) noted, the old debate about whether infanticide by male primates is adaptive has shifted to a consideration of the consequences of such behavior for female fitness and female counterstrategies. The objective of this first of two papers analyzing the effects and context of male takeovers is to test the above predictions by examining the impact of such takeovers on infant mortality and on the subsequent conceptions and

interbirth intervals of their mothers, i.e., the consequences of aggressive male behaviors for infant survival and female reproductive success in the Santa Rosa population of *Cebus capucinus*.

METHODS

Study Site

Santa Rosa National Park (SRNP) was established in 1971 to protect 108 km^2 of tropical dry forest in northwest Costa Rica, near the Nicaraguan border. SRNP consists of a series of stepped plateaus that range from 300 m in altitude to sea level (where the park is bordered by the Pacific Ocean) and encompasses a mosaic of forest types in various stages of regeneration from a differential history of human disturbance. In the late 1980s, a project was undertaken to purchase ranchlands surrounding the original park and Santa Rosa became a sector of the larger Area de Conservación Guanacaste (ACG). Allen (2001) provided details of the site and the history of the park and conservation area. There are three monkey species in ACG: white-faced capuchins (*Cebus capucinus*), mantled howlers (*Alouatta palliata*), and black-handed spider monkeys (*Ateles geoffroyi*). Many aspects of their demography, behavioral ecology and social systems are known (capuchins: Chapman and Fedigan, 1990; Fedigan, 1993; Hall and Fedigan, 1997; howlers: Bergeson, 1996; Gebo, 1992; Larose, 1996; spider monkeys: Chapman, 1989; Chapman and Chapman, 1991; Chapman *et al.*, 1989; Fedigan *et al.*, 1988).

The area experiences two distinct seasons: a dry season from December through May, and a rainy season from June through November. From mid-December to mid-May, virtually no rain falls and most of the trees lose their leaves. Annual rainfall in the park averages 1472 mm and mean high temperatures range from 21.6°C in the rainy season, e.g., September, to 34.4°C in the dry season, e.g., April, (Janzen and Hallwachs, unpubl. data).

Study Groups

I describe takeovers and births in 7 focal groups that have been followed for variable lengths of time (Table I). We began to follow SE in 1984, until it was rendered extinct by multiple deaths that occurred during a male takeover in 1993. We began to observe CP in 1985 because they were interacting frequently with SE, and continue to follow them to the present day. We started to collect data on LV in 1990, when they moved south into our study

Table I. Summary of groups and years studied, takeovers and associated infant deaths, and subsequent interbirth intervals

Groups	Years studied	Date of takeover	# Infants dead	Sex of dead infants	Age of infants at death (mos)	Time between takeover & death (mos)	Degree of infanticide certainty	Mom's subsequent IBI (mos)
SE	1984–1993	Mar–Apr 1985	?	—	—	—	—	—
		Apr 1989	1	M	5	2	3rd	10.97
		Apr 1991	1	M	12	1	3rd	22.40
		Feb–Mar 1993	1	?	2	Same month	3rd	No further infs
CP	1985–present	Mar–Apr 1989	1	M	10	Same month	2nd	12.17
		Aug 1990	2	?	1	Same month	2nd	21.27
				?	2 days	8 months	1st	No further infs
		Jan–Feb 1993	3	M	9	Same month	3rd	No further infs
				M	7	Same month	3rd	15.67
				M	3	Same month	3rd	13.17
LV	1990–present	Feb 1993	1	M	1	3	1st	12.37
		Apr 1997	1	M	1 day	12	1st	20.17
		Apr 2000	2	M	5	Same month	2nd	16.23
				M	4	Same month	2nd	12.20
BH	1997–2000	Jan 1997	?	—	—	—	—	—
CU	1997–2000	Jan–Mar 1997	?	—	—	—	—	—
		Feb 1999	?	—	—	—	—	—
CA	1997–2000	Jan–Mar 1999	?	—	—	—	—	—
NA	1995–1997	Feb 1997	1	?	3	Same month	3rd	Unknown

area and gradually displaced SE from their former range, and continue to follow it until the present. They are the three main study groups that provide the bulk of the data that I analyzed for this paper. We tracked 3 groups immediately to the north of our core study groups (BH, CU and CA) between 1997 and 2000 when our habituated males emigrated into them (Jack, 2001 and Fedigan, unpubl. data). The seventh group (NA) was tracked between 1995 and 1997 as part of a doctoral student project (Rose, 1998).

Data Collection, Classification of Infants, and Data Analysis

During 18 years of research, 7 graduate students participated in the project and each was trained by me and the preceding graduate student to collect data on births, deaths, dispersal and social behavior. Between 1985 and 1995, a Costa Rican field biologist worked almost continuously as a field assistant and helped to collect data on the groups. Between 1998 and 2002, two other trained field assistants collected life history data during rainy season months when no researcher could be present. Interobserver reliability was practiced as part of the training process for each new researcher. During most of the 18 years the groups were under near-daily observation between January and the end of August. Between September and November (the height of the rainy season), the groups were monitored at least twice a month and usually more often than that. Nonetheless, 6 gaps (totaling to 24 mo) occur in the data set: a 6-mo hiatus in 1991, 2 mo in 1995, 4 mo in 1996, 5 mo in 1997, 3 mo in 1999, and 4 mo in 2000. Although it is certainly possible that takeover attempts occurred during our absences, we believe that successful takeovers did not happen during the data gaps because we never returned to the field to find a new alpha or beta male in place.

I report on takeovers and infant births that occurred in the SRNP study groups between 1985 and 2002. In the early years of the project, we kept good track of the takeovers and births but not of the deaths and infant sex ratios. Furthermore, we do not have such close observation of infant deaths in the 4 short-term study groups as in our 3 main groups. Thus, I used different tallies of years, groups and infants when analyzing takeovers (1985–2002, all groups), births/conceptions (1986–2002, all groups), sex ratios (1987–2002, all groups), total infant deaths (1989–2002, 3 main groups) and mortality rates in given years (1989–2001, 3 main groups).

Operationally infants are 0–12 mo of age. Weaning age is variable, but most infants travel independently and suckle infrequently by one year of age.

Because it is very difficult and rare to observe directly an adult male fatally wound an infant, instead I analyzed and discuss infants that

die/disappear during and soon after takeovers. I contrast them with two other categories of infants: ones that survive beyond 12 mo and ones that die/disappear when there is no sign of emigrating males, rank change, male aggression, or a takeover. It can be argued, however, that in our observations of infant deaths, there are 3 degrees of certainty regarding infanticide: first degree: infants directly seen to be fatally wounded by a male; second degree: infants found wounded during times of takeover that were dead or later died; and, third degree: infants that disappear during or soon after a takeover. I also classified infants as dying of causes other than takeovers and infanticide, i.e., we observed them to be weak or ill before they died/disappeared and there was no evidence of wounding, male rank change, or non-resident male invasion.

When an infant capuchin <12 mo of age disappears, it can be assumed to have died because capuchins <24 mo old have never been seen to disperse, and have never been relocated in other groups after vanishing from their natal group. Older individuals that disappear from their groups are frequently located in neighboring groups. For the analyses in this paper, I combined infants that disappeared with those whose bodies we found.

Additionally, it is difficult for even experienced observers to sex very young white-faced capuchins, especially when they cling to their mother's bodies, which is why a sizable proportion of infants go unsexed if they die early. Given that we have identified 57% of our new infants as males, only 25% as females and 18% of unknown sex, it is likely that we are underestimating female births. It is harder to conclusively sex a female infant, and all of the unsexed infants may well be females. However, a male-biased sex ratio also occurs in the juveniles of our groups, in which we are certain of the sex of all individuals in them - 66% of 70 well known juveniles are males.

Even with 18 years of data, sample sizes remain small and I employ nonparametric tests: chi-square, binomials. For some of the directional predictions, e.g., more male than female infants will be targeted, more conceptions will occur in wet than dry seasons, I present one-tailed tests. All other tests are two-tailed.

RESULTS

Summary of Takeovers and Infant Births and Deaths

We observed 15 takeovers in 7 study groups between 1985 and 2002 (Table I). During the years that births were reliably recorded (1986–2002), 97 infants were born into them. During the period that sex ratios were reliably recorded (1987–2002), 91 infants were born and sexed. Deaths were reliably

Fig. 1. One-day old victim of infanticide (observed by K. MacKinnon,1998), showing extensive wounds to right side of chest and lower back (possibly where the adult male's two canines made deep puncture wounds; arrows). Photo by K. Jack.

recorded from 1989–2002, during which time 87 infants were born and 23 died/disappeared. Birth dates are known for 84 infants to within a 10-day period, and we used the birth dates to infer conception dates by counting back 164 days (5.4 months) from the birth dates (Fedigan and Rose, 1995; Robinson and Janson, 1987).

Between 1989 and 2002, 14 infants died/disappeared after 9 separate takeovers in 4 different groups. For the additional 5 takeovers, we do not have sufficiently precise data to analyze the occurrence and pattern of infant deaths. Of the 14 infants, 3 were fatally wounded by an adult male (first degree certainty; Fig 1), 4 were found severely wounded during or after a takeover and later died of their wounds (second degree), and 7 disappeared during or soon after a takeover (Table I). Nine infants died of apparently natural causes, i.e., no recent takeover and no sign of male aggression directed at the infant. Of the 87 infants born in this period, 64 survived longer than 12 mo., which indicates an infant mortality rate of 26.4% for all the study groups over a 14-year period.

Infant Mortality Rates in the Years Subsequent to Takeovers

For this analysis, I took data from only the 3 best known groups, in which all deaths were carefully recorded over 5 years (SE: 1989–1993), 13 years

(CP: 1989–2001) and 12 years (LV: 1990–2001). In the sample there are 9 takeover events and 30 study years, in which groups were followed for one year after a point in time when takeovers occurred or did not occur. Because most takeovers occur in January–April, I calculated years as beginning April 1 and continuing through to March 31.

Infants died (of any cause) in all 9 of the years after takeovers, but only in 4 of the 21 years following a period of peace with no takeover, a difference that is significant ($\chi^2 = 16.81$, df $= 1$, $p = 0.000$). In the years after a takeover, 82.4% of the infants under one year of age perished. In the years following a peaceful period (no takeover) only 11.9% of the infants under one year of age died (Fig. 2). This difference in mortality rate is significant ($\chi^2 = 27.51$, df $= 1$, $p = 0.000$). Note also that only 17.6% of infants, i.e., potential victims of invaders, survived for one year after takeovers in the 3 groups.

Since all but one of the takeovers occurred between January and April, I designated April–June as the critical phase for possible negative effects of invading males on infant survival. We then took a more focused look at infant deaths in these 3-mo periods following a takeover versus a comparable no-takeover period (April – June of years with no takeovers). This method
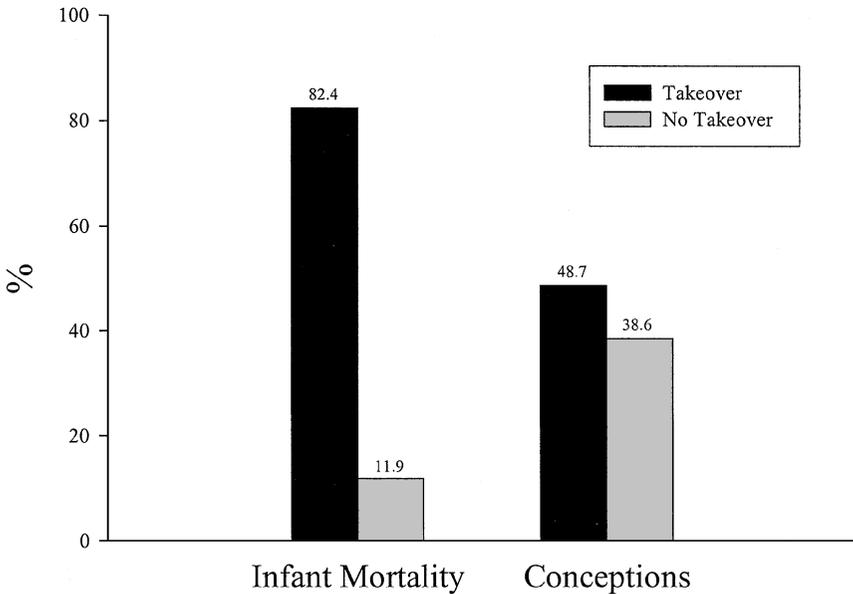

Fig. 2. Infant mortality and conception rates in the 12 mo following a takeover versus an equivalent period with no takeover.

controls for other sources of mortality that might be related to seasonal effects. Infants died in 7 of the 9 3-mo periods after a takeover, but only in 4 of the 21 comparable 3-mo periods, a significant difference ($\chi^2 = 9.36$, df $= 1$, $p = 0.004$). The infant mortality rate in the 3-mo period following a takeover is 70.6%, whereas it is 11.9% in the comparable no-takeover 3-mo periods ($\chi^2 = 20.32$, df $= 1$, $p = 0.000$).

Mean Age at Death in Infants

The mean age at death for infants that die in the context of male takeovers is 133.43 days, or 4.4 mo. Mean age at death for infants that die naturally, i.e., when there is no male takeover, is 110 days or 3.7 mo. Clearly the two values are not significantly different. However, the 3 infants that we saw killed by males, rather than being inferred to be killed, were 1-day, 2-days, and 1-mo old at the time of death, far younger than the average. Infants died in the context of takeovers up to the age of 12 mo, which is the definitional end of infancy. Wounding and death of small juveniles (n $= 2$) was only observed during one takeover out of 15. After 12 mo of age, infants suckle infrequently and their deaths should not shorten a mother's subsequent IBI.

Interbirth Intervals

If the prior infant survives, then study group females experience a mean interbirth interval (IBI) of 27.54 mo (n $= 33$). If the prior infant dies and there is no evidence for a male takeover, the subsequent IBI for the mother averages 12.35 mo (n $= 9$). If the prior infant dies in the context of a male takeover, the subsequent IBI for the mother averages 15.67 mo (n $= 10$). A one-way ANOVA comparing the 3 types of IBI results in a significant difference ($F = 47.011$, df $= 46$, $p = 0.000$). Planned comparisons show that there is no difference in IBIs by type of infant death (during takeover vs. other causes) ($t = 1.3$, df $= 46$, $p = 0.200$). However, there is a significant difference in IBIs experienced by females whose prior infant survives versus those whose prior infant dies during a male takeover ($t = 7.02$, df $= 46$, $p = 0.000$).

Because there was no difference in subsequent IBI by type of infant death, and because of small sample sizes, I combined all infant deaths to look for a relationship between infant age at death and the length of the mother's subsequent IBI. There is no correlation between the age of the infant when it died and how long it took the mother to produce her next infant (n $= 17$, $r = 0.160$, $p = 0.541$).

Subsequent Mating Access to Mothers

Of the 14 cases in which infants died during a male takeover, the invading males (n = 21) remained in the group 76% of the time and also stayed in the group long enough to be present at the mother's subsequent conception. Two males were not able to remain in the group because the takeover brought about the group's extinction, and 3 males were not sufficiently tracked. Preliminary DNA analyses indicate that alpha males sire 63–84% of the infants in their groups (Jack and Fedigan, 2003). Because 2–3 males sometimes form coalitions to invade groups but only the alpha male may benefit from subsequent mating access to females, we also calculated the percentage of time that invading males who took up the position of alpha males remained in the group long enough to be present at the subsequent conception of the deceased infant's mother. Of former invaders that became alpha males, 100% were present in the group at the time of the mother's subsequent conception.

Sexes of Infants Lost During Male Takeovers

Between 1987 and 2002, 91 infants were born into the study groups: 57% males, 25% females and 18% of unknown sex. Of the 14 infants lost after male takeovers, 71% were males, 0% were females and 29% were of unidentified sex. Although, *prima facie*, the infants lost after male takeovers seem quite biased toward males, in fact, our study population has an infant birth ratio that is biased toward males, and has remained so over the many years of study (Fedigan and Jack, 2001).

There is no significant difference between the sex ratio at birth and the sex ratio of infants that died/disappeared in the context of male takeovers. This is the case when we classify all the unidentified infants as females ($\chi^2 = 0.240$, df $= 1$, $p = 0.379$), and even when we carry out this as a one-tailed test ($p = 0.190$), because of the directional prediction that more males than females will be killed. However, if 3 sex classes are compared (males, females and unknowns), then there is a significant difference ($\chi^2 = 5.9$, df $= 2$, $p = 0.05$).

Timing of Infant Death Subsequent to Takeovers

In 9 of 14 cases, the infant died in the same month as the sudden presence of newly invading males. In three cases, the infants died 1–3 mo after the takeover. In the final two cases, we saw the infants killed by the alpha

males of their groups 8 and 12 mo after they had invaded and taken over. In both cases, there is reason to believe that a male other than the alpha male fathered the infant. For example, in 1998 when the alpha male killed a newborn infant in LV, researchers were able to obtain tissue samples of the infant and hair samples from all adult males and females of the study groups (MacKinnon, 2002). Molecular DNA analysis showed that the infant had been fathered by the top-ranking male of neighboring CP (Jack and Fedigan, 2003). He had been temporarily resident in LV 6 mo before the infant's birth (apparently taking advantage of the other male's takeover). In the 1991 example, the alpha killed an infant that we strongly suspect had been fathered by the popular beta male (Rose, 1994). He had been deposed from the alpha position and evicted from the group by the invading male 8 mo earlier, but after 2 mo returned to hang around the group in a subordinate, peripheral position, in which he continued to receive frequent grooming and sexual solicitation from the females.

Conceptions

I used data from the 3 best-known groups (SE: 1985–1993; CP: 1986–2001; LV: 1990–2001), which comprises 9 takeovers and 38 study years during which groups were followed for one year after the point in time when takeovers occurred or did not occur.

Conceptions rates rose slightly but not significantly in the 6 mo after a takeover versus a comparable 6-mo period after no takeover (25% vs. 18%, Fisher's Exact Test, $p = 0.212$, one-tailed). Conception rates also rose somewhat but not significantly in the year after a takeover versus no takeover (Fig. 2; 48.7% vs. 38.6%, $p = 0.179$, one-tailed).

Therefore, although the specific females that lost infants during and soon after takeovers conceived their next infant sooner than they would had the infants survived, i.e., shorter IBIs, the overall conception rate of females in the group is not significantly increased after takeovers.

Seasonality of Takeovers and Infant Births/Conceptions

All but one of the 15 takeovers occurred during the months of January–April (dry season, see Fig. 3). In prior papers, we showed that births and male dispersals are more likely to occur in dry season (Fedigan et al., 1996; Jack and Fedigan, in press). From these findings, I predicted that conceptions would be more likely to occur in wet season. I separated immigrations that were carried out aggressively as takeovers from those that occurred peacefully
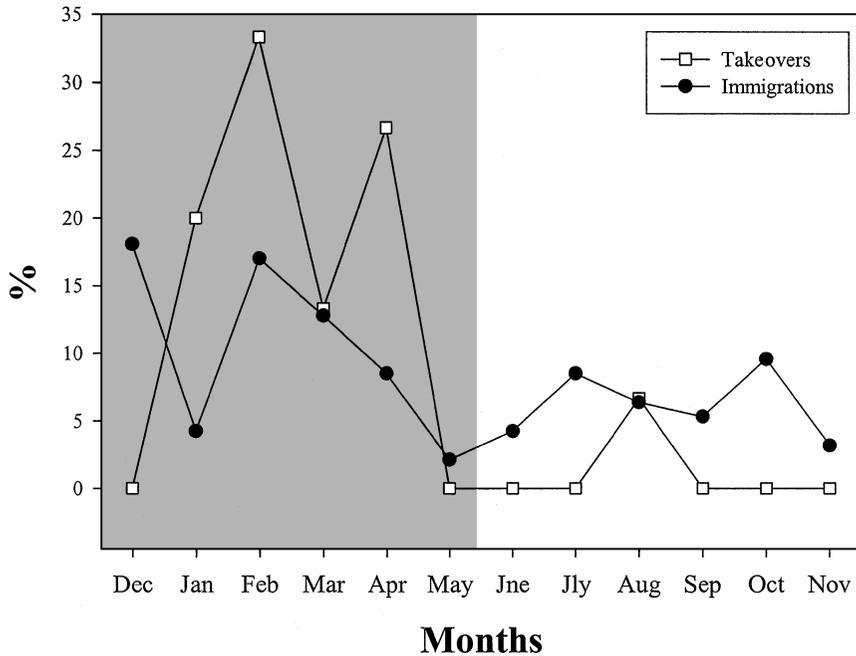
Fig. 3. Monthly and seasonal (dry/wet) distributions of takeovers, and of peaceful male immigrations during which no takeover occurred. Darker background shading from mid-December to mid-May represents the dry season, light background the wet season.

and I predicted that immigrations without takeovers would also be more likely to occur in dry season, a prediction that was substantiated (binomial test, observed proportion = 64%, n = 47, $p = 0.04$, one-tailed).

Conceptions overall are more likely to occur in the wet season (binomial test, observed proportion 60%, n = 84, $p = 0.05$, one-tailed). To determine if takeovers have any effect on seasonality of conceptions, I then divided conceptions into those that occurred in the 12 mo subsequent to a takeover versus those that occurred in the 12 mo subsequent to years with no takeover (Fig. 4). Seventy-one percent of conceptions occurred in wet season after takeovers (a significantly biased pattern, binomial test, n = 24, $p = 0.03$, one-tailed), whereas 55% of conceptions occurred in wet season after years with no takeover (not significantly biased toward wet season, binomial test, n = 60, $p = 0.26$, one-tailed). However, even though the percentage of wet season conceptions rose after takeover years, the bias toward wet season conceptions in takeover years is not significantly higher than in no-takeover years ($\chi^2 = 1.78$, $p = 0.138$, one-sided).
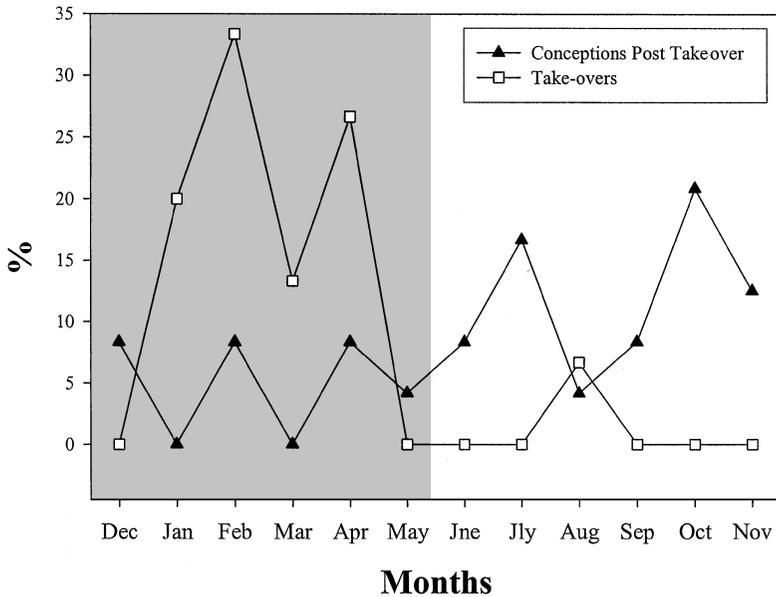
Fig. 4. Monthly and seasonal (dry/wet) distributions of takeovers and of conceptions that occurred in the 12 mo after a takeover. Darker background shading from mid-December to mid-May represents the dry season, light background the wet season.

DISCUSSION

Analysis of 18 years of data on 3 main and 4 auxiliary groups of white-faced capuchins demonstrates that aggressive male takeovers of social groups have considerable impact on the survival of infants and the parturition patterns of their mothers. In the Santa Rosa groups, infants are significantly more likely to die in the 3- and 12-mo periods after aggressive male takeovers of their groups, and the infant mortality rate rises from the overall average of 24.4% to 82.4% in the years following a takeover. Furthermore, a female whose infant dies during a male takeover, experiences a significantly shorter interbirth interval before her next infant is born. And in 76% of the cases where in an infant dies in the context of a takeover, the invading male gains mating access to the deceased infant's mother and is still present during the subsequent conception by the mother. All invaders that became alpha males of the groups they took over were present in the group at the time of the mother's next conception. These findings indicate that 3 of the critical predictions of the sexual selection model of infanticide—higher infant mortality, shorter interbirth intervals and subsequent mating access to the mother—are operating in *Cebus capucinus*.

However, 3 other predictions are not strongly supported by the data set: those concerning conception rates after takeovers, and age at death and sex of infants targeted. Overall conception rates rose, but not significantly, in the 6-mo and one-yr periods following a takeover. Further, although the mean age at death of infants in the context of takeovers is quite young (4.4 mo), it is little different from the mean age at death for infants that died/disappeared in times of peace (3.7 mo). Moreover, while there is a large range of variation in how old the infants were when they died/disappeared (1 day to 12 mo), there is no correlation between the age of the infant at death and the subsequent interbirth interval of the mother. The issue of whether more male than female infants are targeted is still unresolved because of the high percentage of young infants we are unable to sex. If we classify all unsexed infants as females, the sex ratio at birth and the sex ratio of infants killed in the context of takeovers are not significantly different.

Adding to our understanding of the effects of male takeovers on infant births and deaths is the finding that infants usually (71%) die in the same month as the takeover or 1–3 mo later (14%). However, it appears that if the infant is fathered by a male other than the new alpha male, it may be killed many months after the takeover event. With a sample of only 2 cases of infant killings long after the takeover event, we do not yet conclude that the new alpha male can detect when an infant born into his group 8–12 mo after his takeover is not his own progeny. However, if he can do so, it is likely to be based on his perception of mating history with the mother (van Schaik, 2000a).

Perhaps the most perplexing finding of the study is that takeovers occur overwhelming in the dry season months of January–April, at the same time as a peak in infant births. 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 then. Perhaps groups become more visible and locatable targets for invading males during the dry season. Females at Santa Rosa often experience a brief postpartum estrous period, during which they solicit males for mating, and it is possible that the estrous signals are conveyed to non-group males as well, or the presence of young infants may attract them.

Conceptions overall are significantly more likely to occur in the wet season (June–November), and takeovers shift the bias even more toward wet season conceptions, such that there is a pattern of conception rates rising in the 3–6 mo (July–October) following the January–April takeovers (Fig. 4). Thus, there appears to be a time lag before the mothers that have lost their infants resume cycling and conceive again. Recabarren *et al*. (2001) found that captive brown capuchin females (*Cebus apella*) that lost their infants experienced resumption of their menstrual cycles 31 to 150 days after

parturition, but such cycle resumption was followed by periods of ≤ 5 mo of residual infertility (mating but no pregnancy). If residual infertility is also occurring in Santa Rosa white-faced capuchins, this could explain the 3–6 mo time lag between takeovers and the rise in conceptions, and it might also explain the lack of relationship between the age of the infant at death and the length of the mother's subsequent interbirth interval.

On the whole, the results of this long-term study suggest that *Cebus capucinus* in large part fit the sexual selection model of infanticide. The findings offer support for the hypothesis that male white-faced capuchins will sometimes kill infants sired by former resident males as part of a larger reproductive strategy that involves aggressively invading breeding groups, ousting former males, taking up residence, and then fathering infants with the females of their new groups sooner than they would have done had the prior infants survived. Such a strategy has major consequences for infant survivorship and female reproductive patterns.

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