

Predictors of Reproductive Success in Female White-Faced Capuchins (*Cebus capucinus*)

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ABSTRACT Early investigations into variable reproductive success in nonhuman primates tended to focus on the benefits conferred by high dominance rank. However, the effect of high rank on individual reproductive success has been found to vary both intra- and interspecifically, requiring researchers to expand their investigations to include additional factors. Here we examine the age and rank of the mother, sex of the infant, group size, number of close kin, replacement of group males, and resource availability as possible predictors of female reproductive success in white-faced capuchins (*Cebus capucinus*) in the Santa Rosa sector of the Area de Conservación Guanacaste, Costa Rica. We examine the length of interbirth intervals (IBI) and infant survivor-

ship as measures of individual reproductive success for the 31 adult females that resided in our three study groups between 1986 and 2007. The greatest predictor of IBI length was whether or not the first infant in the interval survived (number of matrilineal kin and resource availability were also significant predictors); while infant survivorship was most significantly predicted by the occurrence of a turnover in group males in the year following the birth of an infant (infant sex was also a significant factor). Based on these findings, we conclude that male and female reproductive strategies are at odds in this species, with male strategies strongly influencing female reproductive success. *Am J Phys Anthropol* 137:82–90, 2008. © 2008 Wiley-Liss, Inc.

Many factors may affect the pace of a female monkey's production of infants and the survival of those offspring. In primatology, the dominance rank of the mother has been most often investigated in studies of reproductive success (e.g., Ellis, 1995; Pusey et al., 1997), although results have been equivocal. In some studies (e.g., *Macaca fascicularis*: van Noordwijk and van Schaik, 1999; *Papio hamadryas cynocephalus*: Altmann and Alberts, 2003; *Gorilla beringei beringei*: Robbins et al., 2007) female dominance rank and reproductive success are significantly correlated, with high ranking females displaying shorter interbirth intervals (IBI) and/or experiencing higher infant survivorship. In other studies, however, such relationships are not found (e.g., *Chlorocebus aethiops*: Cheney et al., 1988; *Macaca fuscata*: Koyama et al., 1992; *Papio hamadryas ursinus*: Cheney et al., 2004; *Macaca sylvanus*: Kümmerli and Martin, 2005).

The inconclusive and contradictory results surrounding investigations of female dominance rank and reproductive success indicate that a female's reproductive schedule and infant survival rates may be influenced by several factors in addition to, or other than, maternal rank. For example, maternal age may be important to fecundity and infant survival patterns, although the relationship between these factors is also inconsistent. While most primate species experience some decline in reproductive output with increasing maternal age, a decline that is largely attributable to decreased fertility and increased IBI (e.g. *Gorilla beringei beringei*: Robbins et al., 2006; see review by Fedigan and Pavelka, 2007), in at least some species greater rearing success by older females offsets the higher fecundity of younger females (e.g., *Presbytis entellus*: Borries et al., 1991; *Chlorocebus aethiops*: Fairbanks and McGuire, 1995).

The sex of the infant produced may also affect female reproductive success in that the length of IBI may be longer and infant survivorship will increase if a mother preferentially invests in one sex over the other. For example, a mother may wean one sex earlier than another thereby shortening the interbirth interval; however, no consistent pattern of a preferred sex has emerged from the primate data (see reviews by Brown, 2001 and Silk and Brown, 2004). It is clear, however, that in many mammalian species male infants generally experience higher mortality than females (Kraemer, 2000; see review by Setchell and Lee, 2004), which given the long periods of gestation and lactation, will have a strong impact on the lifetime reproductive success of a female primate.

Broad ecological and demographic variables have also been shown to have a profound effect on individual female reproductive success. Resource availability

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greatly affects female fecundity (e.g., Suzuki et al., 1998; van Noordwijk and van Schaik, 1999) and several studies have shown that group size can also play an important role, although once again the effect is inconsistent across the primates. For example, in wedge-capped capuchins (*Cebus olivaceus*: Robinson, 1988), common marmosets (*Callitrix jacchus*: Koenig, 1995), and Japanese macaques (*Macaca fuscata*: Suzuki et al., 1998), large groups have been shown to experience higher birth rates, which appears to be linked to the greater success of larger groups during intergroup resource competition. However, larger group size does impose foraging costs in that the time and distance traveled must increase to obtain needed resources (Janson and Goldsmith, 1995), factors that can impart higher energetic costs for females and reduce reproductive output (Srivastava and Dunbar, 1996; Hill et al., 2000). Indeed female baboons residing in larger groups, particularly those containing an increased number of same-sex competitors, experience longer IBI and these effects are even more marked for low ranking females (Altmann and Alberts, 2003). In a number of primate species no relationship, either negative or positive, has been found between group size and birth rates (e.g., Hsu et al., 2006; Robbins et al., 2007).

Infant mortality due to predation is predicted to decrease with increasing group size (van Schaik, 1983) and the same pattern may hold in species where infanticide plays a key role in infant mortality (e.g., see review by van Schaik, 2000; Robbins et al., 2007). The composition of a group may also influence female reproductive schedules and infant survivorship. For example, in mountain gorillas (Robbins et al., 2007), infant survivorship is strongly influenced by the number of silverbacks in the group and for some primate species studies have found a link between female reproductive success and number of close kin in residing in the mother's group (e.g., Fairbanks and McGuire, 1986; Pope, 2000).

There is as yet little known about patterns of female reproductive success in the neotropical cebids. Most platyrrhines exhibit female dispersal, a norm to which the male-dispersed capuchins are a striking exception (Strier, 1999). Long-term research on white-faced capuchins, *Cebus capucinus*, has shown that these New World monkeys exhibit female philopatry and form dominance hierarchies based on affiliative support networks (Manson et al., 1999; Fragaszy et al., 2004; Perry et al., 2004). Furthermore, female white-faced capuchins experience differential competitive success such that dominant individuals exhibit higher nutrient/energy intake rates than do subordinates and the former are able to consistently supplant the latter from preferred food trees, limited water holes, and safer sleeping sites (Vogel, 2004). Thus, dominance rank has the potential to affect rates of reproduction and infant survival in this species, via individual variation in nutrient intake and stress levels. However, other important aspects of the behavioral ecology of white-faced capuchins also have the potential to exert a strong influence on the classic measures of female reproductive success—fecundity and infant survival. For example, within our study groups we see a complete replacement of resident males approximately every 4 years (Fedigan and Jack, 2004). Infant deaths are significantly more common following these replacements than they are during stable times (Fedigan, 2003), indicating that these events play a large role in determining female reproductive success.

In this article, we use a multiway, model-building approach to examine seven possible predictors of variable reproductive success and their possible interactions in our study population of *Cebus capucinus* in the Santa Rosa Sector of the Area de Conservación Guanacaste. Our goal in so doing is to examine the individual and possibly combined effects of these variables on female reproductive success in the Santa Rosa white-faced capuchins. Data were collected over a period of 21 years, between 1986 and 2007, on all infants born in our three long-term study groups. For each infant born we examine: 1) the mother's age and 2) rank at the time of an infant's birth, 3) the sex of the infant, 4) the size of the group, 5) the number of close matrilineal kin residing in the mother's group at the time of her infants' births, 6) the occurrence of a male replacement within the group in the 12 months following an infant's birth, and 7) the availability of resources, as reflected by rainfall during the 12 months subsequent to an infant's birth. Each of these variables has been documented as a source of reproductive variance in a number of well-known primate species and our central research question is: how do these seven factors affect female reproductive success in the lesser-known white-faced capuchin?

METHODS

Study site and species

This study took place between 1986 and June 2007 in northwestern Costa Rica in the Santa Rosa sector of the Area de Conservación Guanacaste. The Santa Rosa sector encompasses about 108 km² of tropical dry forest and experiences a dry season from approximately mid-December to mid-May. There are three species of primates in the park (white-faced capuchins: *Cebus capucinus*; mantled howlers: *Alouatta palliata*; black-handed spider monkeys: *Ateles geoffroyi*). The site has been described in detail elsewhere (e.g., Fedigan et al., 1996; Allen, 2001; Fedigan and Jack, 2001).

White-faced capuchins live in multimale, multifemale groups consisting of natal females, immigrant males and immature offspring. Frequent park-wide censuses of all the monkeys in Sector Santa Rosa indicate an average capuchin group size of 17 and adult sex ratios approaching 1:1 (Fedigan and Jack, 2001). Males are approximately 25–35% larger than females and are usually dominant over them (Ford and Davis, 1992). White-faced capuchins are not seasonal breeders because copulations and births occur throughout the year (Manson et al., 1997; Fedigan, 2003). However, the Santa Rosa population does experience a birth peak during the dry season from January through mid-May, indicating a conception peak occurs during the wet season (Fedigan, 2003; Carnegie et al., 2005). Male white-faced capuchins are transient, dispersing from the natal group at about 4.5 years and continuing to disperse approximately every 4 years after that (Jack and Fedigan, 2004a,b). When immigrating into groups, young males may do so by peacefully joining the residents and taking up low-ranking positions in the male hierarchy. But adult males usually enter groups by force, challenging and driving the resident males from the group, and wounding group members in the process (Fedigan and Jack, 2004). Infants often die during or soon after takeovers, and these upheavals usually occur during the dry season birth peak (Fedigan, 2003). Preliminary analyses indicate that

TABLE 1. Adult female reproductive rates and infant survival

Adult female	No. of infants born during observation period	Mean IBI (years) ^a	Proportion of infants surviving to 1 year
1	10	1.94	0.89
2	9	1.42	0.50
3	8	2.00	0.88
4	7	1.34	0.50
5	5	2.46	1.00
6	5	2.00	1.00
7	5	1.38	0.40
8	4	2.33	0.33
9	4	2.56	1.00
10	4	1.61	0.50
11	4	1.67	0.75
12	3	3.66	0.33
13	3	2.90	0.33
14	3	2.60	0.00
15	3	2.23	1.00
16	3	1.79	1.00
17	3	1.96	0.67
18	3	0.90	0.00
19	2	1.81	0.50
20	2	2.35	0.50
21	2	2.00	1.00
22	2	0.90	0.50
23	2	1.29	0.50
24	2	0.82	0.50
25	1	—	1.00
26	1	—	1.00
27	1	—	1.00
28	1	—	1.00
29	1	—	0.00
30	0 ^b	—	—
31	0 ^b	—	—

^a Completed intervals.

^b These females did not give birth during our study but had infants at the start of our study.

resident alpha males sire the majority of the infants born into our study groups (Jack and Fedigan, 2006).

Study sample

The data used in this study come from tracking three contiguous social groups of capuchins. The Cerco de Piedra group has been followed from 1983 through the present and the data are taken from 1986 (when we first began to collect reliable dominance and reproductive data) through June 2007 (22 years of data). The Sendero group was followed from 1983 until 1993 when it became extinct; data are taken from 1986 through 1993 (8 years of data). The Los Valles group was first reliably tracked in 1990 and the data are taken from 1990 through June 2007 (18 years of data). From these three groups, we have tracked 31 adult females and 103 infants (Table 1).

We commenced biweekly observations of life history parameters and daily behavioral data collection in 1986 and these groups have been monitored continuously since then with the exception of six gaps of 2 to 6 months each. The birth dates of infants that were born during the “data gaps” were estimated based on their size when we first encountered them and our experience with infants of known age. Death dates of infants that disappeared during the periods when groups were not monitored were estimated as the mid-point of the period. It is possible that we missed some infants that were born and died during these short periods when groups were not monitored. When new investigators join the

research team, they are trained in the field to identify individual monkeys, ensuring accuracy and continuity of identity and age assignments. Using this method, individual monkeys have been tracked for the past 22 years and up to three generations of females have been observed in one of our long-term study groups.

Measures of reproductive success

In this article, we examined two measures of female reproductive success: IBI and infant survival. Our fecundity data were unavoidably censored by the arbitrary start and stop dates of our study, therefore we calculated completed IBIs as a measure of the pace of infant production. Infant survival was calculated as whether or not the infant survived its first 12 months of life, indicated as a yes/no measure. We used 1 year as a critical stage-marker of survival because the vast majority of immature mortality occurs during the first year of life (Fedigan et al., 1996). One year also marks the end of infancy for this species; after this age, immatures suckle infrequently and their deaths would not affect the mother's resumption of cycling (Carnegie, unpublished) or the length of their mother's subsequent IBI (Fedigan, 2003). If we were to extend our analyses of offspring survival to include the total number to reach adulthood, or even 2 years of age, our data would be necessarily biased toward female offspring since we have confirmed male white-faced capuchins can disperse from their natal groups as early as 20 months (emigration followed by a confirmed immigration: Jack and Fedigan, 2004a).

Predictors of reproductive Success

Age of mother. All females residing in the three study groups either had infants at the start of the study in 1986 or gave birth to infants during the study period (Table 1, $N = 31$). The exact ages of 16 females in our sample were known, while the ages of the 15 females residing in our groups at the start of the study were estimated by extrapolating from juveniles and adult females of known age.

Rank of mother. In May of each year, we use behavioral data collected during the prior 5 months to develop a dominance hierarchy for the adult female members of each group. We construct a matrix based on all approach-retreat interactions (i.e., supplantations) and the direction of submissive signals in dyadic interactions (i.e., cower, bared teeth display). Individual females are arranged in the order that produces the fewest reversals. Although some relationships are less decided than others and triadic interactions are common, by focusing on dyadic conflicts, supplantations and submissive signals, it is possible to construct hierarchies for the adult females of each group in each year of study.

Because the number of adult females in a group at any one time can range from three to seven, and we sometimes need to make comparisons across groups and over time, we calculated an individual's rank as the proportion of their adult female cohort over which they are dominant (Cheney et al., 1981, 2004). For example, in a group of six adult females, the alpha female holds the rank of 100%, the beta female holds the rank of 80% (four of five other females dominated), and so forth.

Sex of the infant, group size, and number of close kin. We examined whether the sex of the infant affected its survival or the length of its mother's interbirth inter-

val. With experience, patience and steady binoculars, we can usually determine the sex of an infant white-faced capuchin within the first month following its birth. Although female capuchins have a pendulous clitoris that can be mistaken for a penis (Fragaszy et al., 2004), if the observer can get a clear look at the distal end of the structure, it is possible to differentiate between male and female genitalia. The tip of the penis is plunger or trumpet shaped, whereas the distal end of the clitoris is bulbous or rounded. To evaluate whether group size affects infant survivorship or the length of an interbirth interval, each IBI was assigned the number that was the current group size when the first infant in the interval was born. We record the size and membership/composition of each study group each month. Thus, we also calculated the number of the mother's close matrilineal kin (e.g., the mother's mother and the mother's grandmother and the mother's siblings and her other offspring—an r value of 0.25 to 0.50) living in the group at the time of her infants' births.

Resident male replacement. Replacement of the resident males in our study groups takes place approximately every 4 years (Fedigan and Jack, 2004). These changes in male membership usually occur when coalitions of outsider males aggressively enter our study groups and fight with the resident males. We refer to these aggressive replacements as male takeovers and they often result in severe wounding (especially of the alpha male) and eventual eviction of the resident males and coincide with the deaths and disappearances of infants (Fedigan, 2003). Another form of replacement occurs when the resident males emigrate without apparent provocation and leave the group without any adult males, at which time another male or coalition of males will immigrate into the group. We refer to the latter type of replacement as "waltz-ins". Although waltz-ins do not involve fighting between the outgoing and incoming sets of resident males, they are, like the aggressive takeovers, often followed by infant deaths and disappearances. Infant deaths are significantly more common in the 3 to 12 months immediately following the replacement of group males than they are during stable periods (Fedigan, 2003), indicating that these events may have a profound effect on female reproductive success. Thus, we investigated the 12-month period following the birth of each infant in our sample to determine if a male replacement (takeovers and waltz-ins) occurred and their effect on infant survivorship.

Resource availability. Resource availability is a notoriously difficult variable to measure; therefore rainfall is widely used as an indirect measure (Janson and Chapman, 2000). Studies have shown that the net primary productivity of tropical dry forest is positively correlated with the amount and timing of annual rainfall in Africa and the neotropics (see reviews by Murphy and Lugo, 1986; Chapman et al., 2000). For example, the net primary productivity of dry forest in southwestern Puerto Rico is correlated with annual rainfall, although soil types and topography introduce variability into the relationship (Murphy and Lugo, 1986). As noted by Janson and Chapman (2000), rainfall and productivity are broadly correlated except in those wet tropical forests that experience >2,500 mm per year (see Kay et al., 1997). However, rainfall can affect availability of primate food types differentially because fruit become more avail-

able as rainfall increases but digestible leaves may not (Janson and Chapman, 2000). Insect abundance per-area has been only rarely measured but peaks in insect abundance coincided with fruit peaks in at least one study (Terborgh et al., 1986). Since our study animals eat a fruit-and-insect diet, the productivity of which very likely increases with increasing rainfall levels and since annual rainfall levels in our dry forest site are only very rarely >2,500/annum (mean = 1,710/annum), we feel justified in using annual rainfall amounts as a proxy measure for resource availability.

In addition to serving as an indicator of food availability, water is important to white-faced capuchins as a resource in its own right. In the tropical dry forests of Santa Rosa, virtually no rain falls during the 6-month dry period and, as the dry season progresses, there is a gradual disappearance of waterholes. Our study animals attempt to drink water every day and modify their ranges in the dry season to facilitate daily access to waterholes (Fedigan and Jack, 2001). Lack of water can affect infant survival directly via dehydration or indirectly via the mother's health and ability to lactate. Like infant survival, the length of a female's interbirth interval may be affected by the resources available to her as she lactates and then transitions into the cycling and gestation phases of her IBI. Therefore, we used annual rainfall as an indicator of resource availability (both food and water) and examined the effects of rainfall abundance on IBI and infant survivorship. For each infant in the sample, we calculated the total amount of rainfall that occurred in the 12 months subsequent to its birth.

Analyses

IBIs were analyzed as a repeated measures analysis using the MIXED procedure in SPSS 15.0. The MIXED procedure accounts for the effects of repeated measures on individuals, allowing the inclusion of all observations on every individual, but adjusting the degrees of freedom in hypothesis tests to account for the lack of independence of observations within individuals. All analyses were run with the assumption of compound symmetry. Repeated measures on individual mothers were identified by using the mother's age at the start of each interval.

IBIs were included only if the interval was complete. Therefore, the interval between a female's last known birth and her death or disappearance was excluded from the analyses. Similarly, for individuals still alive, the interval between her last birth and the present time was excluded. This resulted in a total of 74 complete IBIs for a total of 24 individuals.

The duration of the IBI in years was assessed as a function of seven variables: 1) whether the first infant in the interval survived to at least 1 year of age; 2) age of the mother in years at the start of the interval; 3) rank of the mother (0 to 100) within the group at the start of the interval; 4) sex of the first infant in the interval; 5) size of the group to which the female belonged at the birth of the infant; 6) number of close matrilineal kin of the mother alive in the group at the start of the interval; and 7) total rainfall in the year following the birth of an infant. In this analysis, the predictor variable of infant sex had three categories: female, male, and unknown. The infants of unknown sex were those that died/disappeared in early infancy before the sex of the individual could be ascertained. To test specifically for differences

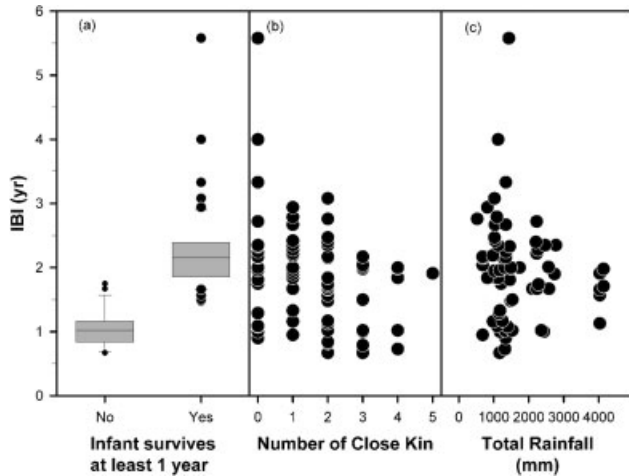


Fig. 1. Interbirth interval in years for *Cebus capucinus* as a function of (a) whether the 1st infant in the interval survived at least 1 year, (b) the number of close kin of the mother in the group at the time of birth of the first infant, and (c) total rainfall (mm) in the year following the birth of the 1st infant. In the box and whisker plots of (a), the shaded box represents extent of 25th and 75th percentiles; the line in the shaded box represents the median, the whiskers represent 10th and 90th percentiles, and dots represent observations beyond 10th or 90th percentiles.

between male and female infants in the length of IBI, we decomposed the two degrees of freedom for the SEX effect with two orthogonal planned comparisons: females vs. males, and known sexed individuals vs. unknowns. Analysis of the model began with the inclusion of all main effects. Model simplification proceeded by backward elimination of nonsignificant terms, using the likelihood ratio test to determine whether a particular term could be eliminated from the model. For reporting purposes the significance of main effects excluded from the model were tested with likelihood ratio tests comparing the final model with the final model plus the excluded effect.

In the analysis of infant survival, the dependent variable was whether the infant survived to at least 1 year of age. The predictor variables were 1) age of the mother in years at the birth of the infant; 2) the rank of the mother (0 to 100) within the group when the infant was born; 3) sex of the infant (male, female and unknown); 4) size of the group to which the female belonged at the birth of the infant; 5) the number of close matrilineal kin of the mother alive in the group at the birth of the infant; 6) whether there was a male replacement event during the 12 months following the birth of the infant; and 7) total rainfall in the year following the birth of the infant.

We analyzed infant survival via a logistic regression on the seven predictor variables, using a step-wise, backward elimination of insignificant terms to arrive at the final model. There were 95 records of infants used in the analysis. The data for eight infants in our sample were not utilized because these infants were born in the most recent year of the study (i.e. they are <12 months of age and still alive). We applied the Hosmer and Lemeshow Goodness of Fit test, to establish that the final model was an appropriate fit to the data.

RESULTS

Interbirth intervals

The 74 completed IBIs in our study population ranged from 0.67 to 5.58 years with a mean of 1.89 years (median = 1.93 years, SD = 0.80 years). The average IBI across all females when the first infant in the interval survived to at least a year was 2.25 years. If the first infant died before reaching 1 year of age, then the average IBI for mothers was 1.05 years (Fig. 1a). The best predictor of the length of IBI was survival of the first infant in the interval ($F_{1, 57.09} = 140.5$, $P < 0.001$).

The number of close matrilineal kin of the mother in the group also had a significant effect on IBI ($F_{1, 58.5} = 12.4$, $P = 0.001$), with IBI decreasing by about 0.121 years for each close kin member in the group (Fig. 1b). Since the maximum number of living close matrilineal kin for any given adult female in our sample was five, this factor amounted to a maximum predicted decrease of about 7 months in IBI. Finally, rainfall in the year following the birth of the first infant in the interval influenced IBI ($F_{1, 47.6} = 6.4$, $P = 0.014$) (Fig. 1c). Total yearly rainfall varied from a low of 0.52 m during a period of relative drought in 2001 to a high of 4.13 m in a period encompassing the extreme wet season of 2005. Our results showed IBI decreasing by 0.0935 years per meter of rainfall, which results in a prediction of IBIs being ~3 months shorter in very wet periods than in very dry periods.

None of the other main effects were significant. That is, age and rank of the mother (Fig. 2a), sex of the infant, and group size did not have significant effects on the length of the IBI. We also explored a series of models that included two-way interactions. There were no indications that there were any interactions. The absence of significant interactions between survival of the first infant in the interval and any other variables suggests that the effects of rainfall and number of close matrilineal kin are the same regardless of whether the first infant in the interval dies within the first year or lives to be at least 1 year old.

Infant survival

The probability of infants surviving to 1 year of age was a function primarily of whether there had been a male replacement in the group during that year ($b = -2.19$, $\chi^2 = 10.9$, $df = 1$, $P = 0.001$) (Fig. 3a). There was also a significant effect of the sex of the infant ($\chi^2 = 10.1$, $df = 2$, $P = 0.006$). There was a significant difference in the probability of survival between individuals of known sex (female and male) and individuals whose sex could not be determined ($\chi^2 = 5.95$, $df = 1$, $P = 0.015$) (Fig. 3b). This is not surprising, given that most infants that we failed to sex before their death died very early in life. However, there was also a significant difference in the probability of survival of females and males ($\chi^2 = 10.05$, $df = 1$, $P = 0.002$), with female infants surviving better than male infants. None of the other variables, including rank of the mother (Fig. 2b) were significant predictors of whether an infant survived to 1 year and there were no significant interaction effects.

DISCUSSION

It has now been determined for many species of non-human primates that the length of a female's interbirth

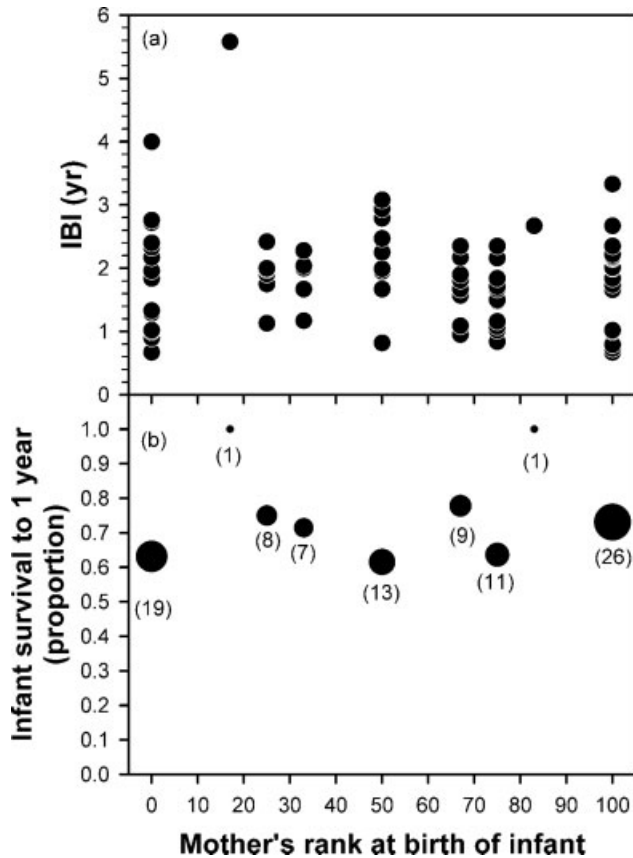


Fig. 2. (a) Interbirth interval in years for *Cebus capucinus* as a function of the mother's rank at the birth of the 1st infant. (b) Proportion of infants surviving at least 1 year as a function of the mother's rank at the birth of the 1st infant. The area of each point is proportional to the sample size for each rank category and the sample size for each rank category (e.g., 100, 75, etc.) is also indicated by the number in parentheses below the point. The mother's rank is calculated as the proportion of her adult female cohort over which she is dominant. For example, in a group of six adult females, the alpha female holds the rank of 100 (she dominates 100% of her cohort), the beta female holds the rank of 80 (she dominates four of five other adult females), and so forth.

interval is shorter following the early death of the first infant in the interval than it would have been had the first infant survived (e.g., see review in van Schaik, 2000; *Brachyteles hypoxanthus*: Strier, 2004). By far the greatest predictor of the length of IBI in our study females was the survival time of the first infant—if the infant died before 1 year of age, then the IBI was 1 year shorter than had it survived.

The length of a female's interbirth interval was also affected by the number of matrilineal kin present in the group—the more living matrilineal kin the shorter the interval. In Santa Rosa, the average capuchin group size is 17 and the maximum number of close matrilineal kin (mother, siblings, grandmother, offspring) alive and resident in the group at any given time for any given female is seven. The degree to which capuchins structure their relationships around multigenerational matrilineal kin, as do macaques (*Macaca* spp.) and baboons (*Papio* spp.), is still uncertain (Fragaszy et al., 2004). Nonetheless, capuchin social systems are female philopatric and there is some evidence from both captive and field studies that affilia-



Fig. 3. Proportion of infants surviving at least 1 year as a function of (a) whether there was turnover of the group's alpha male(s) within 1 year of the infant's birth, and (b) the sex of the infant. The numbers above each bar represent the number of infants in each category.

tive female–female relationships are relatively stable, and often made up of siblings or mother–daughter pairs. Capuchin females readily engage in allonursing and mother–daughter pairs often exhibit reduced rates of agonism and enhanced rates of grooming, proximity, and coalitional support (O'Brien and Robinson, 1991; Perry, 1996; Fragaszy et al., 2004; Perry et al., 2004). All of these benefits, due to the presence of matrilineal kin, could contribute to an acceleration of reproductive rates in females who have more close kin in their groups. Even in a species like red howlers (*Alouatta seniculus*) where the females typically disperse, Pope (2000) showed that established females recruit their migrant matrilineal kin into their new groups and experience higher reproductive success in groups that include greater numbers of kin. Pope suggested that allomothering behavior may have contributed to greater female reproductive success in some females.

Finally, we found an effect of rainfall on the length of an average interbirth interval—the more rain the shorter the IBI. As noted above, rainfall is an indirect indicator of resource availability in tropical dry forests. In addition to the influence of rain water on the availability of the plants and insects that make up the capuchin diet, the amount of rain that falls in the rainy season also affects the endurance of the waterholes during the dry season. It is not surprising that the more food and water available to a female the better able she is to reproduce, and especially in a highly seasonal environment such as Santa Rosa where standing water becomes very scarce during the late dry season. However, rainfall was not a significant predictor of infant survival. This may be because infants nurse during the first year of life and the critical relationship is between resource availability and the mother's needs; that is whether the mother has enough nutrients and fluids to support her reproductive functions (lactation, cycling and gestation) (e.g., Barrett et al., 2006). Although it is often assumed that infant survival will be enhanced if there are adequate resources, these may only directly affect white-faced capuchin immatures who have reached the age of weaning. Pertinent to this point, Altmann (1998) demonstrated in a study of for-

aging behavior in weanling baboons that nutrition and energy uptake in the juvenile stage affects not only survival but also lifetime reproductive success.

The greatest predictor of infant mortality before 1 year of age was the occurrence of a male replacement in the year following the infant's birth. These results substantiate our earlier findings on a smaller sample, which showed that infants often perish during or soon after changeovers in adult male membership within groups (Fedigan, 2003; Fedigan and Jack, 2004). Of the early infant deaths we have documented, 59% occurred in association with male replacements.

Since we also found that male infants are less likely to survive to the age of one than are females (male infant mortality rate was 32% vs. 10% for females; Fig. 3b), we examined the possibility that male infants are differentially targeted for aggression by newly resident adult males. However, infant mortality for males born during replacement years was only slightly higher than that for females (63% vs. 60%). If the lower survival rates of male infants is not due to higher rates of aggression from invading males, what other factors might be involved? A number of early theorists (e.g., Daly and Wilson, 1978; Clutton-Brock et al., 1985; Trivers, 1985) have argued that male mammals in general have lower survival rates than females. However, these theories usually focus on the juvenile stage a time when sexual size dimorphism begins to establish itself and renders the larger sex, usually males, more susceptible to poor environmental conditions (Clutton-Brock et al., 1985; Teather and Weatherhead, 1989). Several additional theories have been put forward to explain differential male mortality at all stages of life, from gestation through adulthood, and some of these may apply to capuchin male infants. A commonly cited theory posits that males are more vulnerable than females to lethal genetic problems due to heterogamety (e.g., Trivers and Willard, 1973; Myers, 1978; Kraemer, 2000), while others link high male infant mortality to their slower developmental rate. For example, Waldron (1987) found that infant male humans experience higher mortality from infectious diseases during their first year of life because they are born with lower immune resistance than females. Lower immune resistance in males may be tied to the immunodepressive effects of male sex steroids, which may in turn render males more susceptible to parasitic infections (e.g., Grossman, 1985; Zuk, 1990). Indeed, a recent meta-analysis by Moore and Wilson (2002) found a significant correlation between parasitic infections and differential male mortality in many species of birds and mammals. Since our sample size of infant deaths is still relatively small and sex ratios are highly subject to sample size effects (Brown and Silk, 2002), we may need to wait for more years of study to see if this pattern of lower infant survivorship in males continues.

Perhaps one of our more surprising findings is that the dominance rank of the mother at the time of the infant's birth does not predict either the infant's survival or the pace of the mother's parturition events. While not all studies of primates demonstrate a relationship between female dominance rank and reproductive success, it is nonetheless a widespread pattern (Ellis, 1995) and it has been shown for white-faced capuchins at a neighboring site that high ranking females have greater access to resources, enhanced nutrient intake and that they receive lower rates of agonistic signals such as supplantation (Vogel, 2004). Thus, we might have predicted

that enhanced nutrient intake would translate into higher rates of infant production through decreased IBI and better survival. But our analyses showed no effect of the mother's rank on her reproductive patterns. Our many other attempts at univariate analyses of these relationships (Fedigan, unpublished) have also failed to turn up any relationship between rank and reproduction in our study females.

In sum, we have found that the pace of a female white-faced capuchin's reproduction can be predicted by the number of close matrilineal kin she has in the group (sources of supportive allomothering and coalitions) and by the availability of resources (sources of needed nutrient intake). However, the best and strongest predictor of the length of her interbirth interval is whether or not the first infant in the interval survives. In turn, infant survival is most strongly predicted by whether male membership within the group is stable or whether there is a replacement event. We therefore suggest that sexual competition for control of reproduction is exerting a major impact on female reproductive success in the Santa Rosa capuchins.

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