

CHAPTER FIFTEEN

Why Be Alpha Male?
Dominance and
Reproductive Success in
Wild White-Faced
Capuchins (*Cebus
capucinus*)

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INTRODUCTION

Most social mammals residing in multimale–multifemale groups display some sort of dominance hierarchy, although the stability and determinants of these hierarchies vary across species and according to sex. In species where females are philopatric, female dominance is usually based on kinship, whereas male dominance is determined by the outcome of male–male competition (Preuschoft and

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Paul, 2000; Walters and Seyfarth, 1987). Sexual selection theory predicts that males who win intrasexual competition will receive reproductive benefits and this prediction has led to the long-standing assumption that male dominance rank is positively correlated to reproductive success (Andersson, 1994). However, the distribution of reproduction is extremely variable in animal societies (Keller and Reeve, 1994), and it should be noted that in many species mating success is not synonymous with reproductive success (e.g. Inoue *et al.*, 1993).

The correlation between male dominance rank and reproductive success has a particularly long history of debate in primate studies (e.g. Fedigan, 1983; Cowlshaw and Dunbar, 1991; De Ruiter and van Hooff, 1993; Ellis, 1995). Although this issue has been more thoroughly investigated in the Order Primates than in any other taxon (see Berard, 1999 for review), the correlation between male dominance and reproductive success is less than straightforward, with results ranging from no correlation to a significant positive or negative correlation depending on the species, seasonality, and/or housing conditions (e.g. Altmann *et al.*, 1996; Paul, 1997). Here, we examine the relationships between male dominance rank and reproductive success in two groups of wild white-faced capuchins (*Cebus capucinus*) residing in Santa Rosa National Park, Costa Rica, between 1993 and 2000.

Social System of White-Faced Capuchins

White-faced capuchins are medium-sized, Neotropical primates (in our study population males weigh approximately 3.3 kg and females 2.3 kg; see Fedigan and Rose, 1995) and range throughout Latin America from Honduras through the northwest coast of Ecuador. In general, capuchins (*Cebus*) more closely resemble Old World monkeys than do other Neotropical genera in that *Cebus* species reside in groups comprised of multiple related females, immigrant males, and their immature offspring. However, unlike Old World monkeys, capuchin groups are composed of nearly equal ratios of adult males and females (Robinson and Janson, 1987). White-faced capuchin groups are comprised of approximately 17 individuals with, on average, four adult males and five adult females (Fedigan and Jack, 2001). This species is moderately sexually dimorphic, with males being 25–35% larger than females (Fedigan, 1993). Female white-faced capuchins give birth approximately every 27 months (Fedigan, 2003) and, although they engage in non-conceptive matings throughout the year (Manson *et al.*, 1997), they display a birth peak between January and April (Fedigan *et al.*,

1996). Males emigrate from their natal group at around 4 years of age and they continue to change groups throughout their lives approximately every 4 years (Jack and Fedigan, 2004a,b).

Within groups, both males and females form linear dominance hierarchies; however, they are determined through very different mechanisms. Female dominance is related to matrilineal kinship and the maintenance of coalition partners through reciprocal grooming and proximity (Perry, 1995; Fragaszy *et al.*, 2004), whereas male dominance appears to be largely determined by the outcome of intrasexual competition (Perry, 1998a,b; Fragaszy *et al.*, 2004), although overt aggression among co-resident males is rare (Jack, 2001b). Male dominance is relatively unstable over time due to the frequent dispersal of group males (i.e. males emigrating from or immigrating into the groups; see Jack and Fedigan, 2004b) or, less commonly, through rank reversals within groups (Perry, 1998a, pers. obs.).

Why be Alpha Male?

We have often asked the question, “Why be alpha male?” As is the case in most primate species, alpha male white-faced capuchins work harder than other group members in that they spend more time engaged in vigilance, expend greater effort in deterring predators and extra-group males, and they are the most active participants during inter-group conflicts (Rose and Fedigan, 1995). What are the benefits of all these efforts? Enhanced mating and reproductive success has long been considered the major benefit of high status (reviewed in Berard, 1999). However, our observations of white-faced capuchins over the past two decades indicate that although alpha males may obtain a slightly greater proportion of copulations (see Rose, 1998), they are by no means exclusively selected as mates by females (Fedigan, 2003; Fragaszy *et al.*, 2004). Indeed the mating system of white-faced capuchins appears to be very egalitarian; subordinate males, including sub-adults, will mate in full view of alpha males and they make no effort to hide their mating activities. Copulations in this species are very conspicuous, involving a coordinated dance display performed by the male and the female, and accompanied by specific vocalizations and facial expressions (see Manson *et al.*, 1997 for a complete description). Thus far, we have no concrete evidence of overt mating competition occurring among co-resident males (Carnegie, unpublished data; Jack, 2003). To date, the reproductive system of this species has not been investigated and it remains

to be determined if the egalitarian mating system that we have observed among co-resident males equates to shared reproduction within the group.

Although initially developed to explain differences in the reproductive output of females in cooperative and highly social groups, models of reproductive skew and concession theory have also been used to determine the optimal amount of reproduction a dominant needs to concede to a subordinate in order to keep him/her in the group and peacefully cooperating (e.g. Vehrencamp, 1979; Emlen, 1982; Reeve and Ratnieks, 1993; Reeve and Emlen, 2000). High skew societies are those in which reproduction is dominated by one or a few breeders, whereas low skew societies are those in which reproduction is more equitably distributed among group members. Concession theory predicts that the differences in the reproductive output of dominants and subordinates will be lower when the presence of subordinates in a group increases the fitness of dominants (Clutton-Brock, 1998). That is, when subordinates provide fitness benefits to dominant males (i.e. cooperation in resource and/or mate defense), dominants will concede a portion of reproduction to subordinates as a “staying incentive” in order to keep them cooperating in the group.

The presence of subordinate males does impose some costs to dominants in white-faced capuchin groups (e.g. increased social vigilance: Jack, 2001a; Perry, 1998b; increased foraging competition: Rose and Fedigan, 1995). However, in this species, male cooperation is necessary to enter groups, which is most often achieved through aggressive takeovers (Fedigan and Jack, 2004), and to retain membership in these groups (Rose and Fedigan, 1995; Perry, 1998b; Jack, 2001b; Jack and Fedigan, 2004b). In all cases of successful group takeovers, invading males are of superior physical strength, or they form coalitions that out-number resident males (Fedigan and Jack, 2004). Given the necessity of male cooperation in this species, it is not surprising to find that male–male relationships within groups are very tolerant, with low levels of intragroup aggression (Jack, 2003; Perry, 1998b). We have also recorded high levels of affiliative interactions among some resident males and that the maintenance of these male–male bonds can persist through multiple emigrations (Jack, 2003; see also Jack and Fedigan, 2004b). We therefore interpret the relaxed mating system of white-faced capuchins as a means by which alpha males can maintain the cooperation of co-resident males.

This study examines male reproductive success in wild white-faced capuchins to determine if high dominance rank confers a reproductive advantage. We also address the issue of reproductive skew in this species, by examining whether or

not alpha males provide their co-resident males with staying incentives in terms of reproductive opportunities.

METHODS

Study Site

Data presented here are based on two of our long-term study groups of wild white-faced capuchins residing in the Santa Rosa Sector of the Area de Conservacion Guanacaste in Costa Rica. Formerly known as Santa Rosa National Park (SRNP), the sector lies 35 km northwest of Liberia and approximately 30 km south of the Nicaraguan border, in the Guanacaste Province. SRNP is comprised of approximately 108 km² of dry deciduous forest and reclaimed pasture in varying stages of regeneration, and ranges from sea level to 300 m in altitude (see Fedigan *et al.*, 1996; Fedigan and Jack, 2001 for additional site details).

Study Groups

LF began studying the capuchins of SRNP in 1982 (Fedigan, 1986; Fedigan *et al.*, 1985; Chapman *et al.*, 1988) and research has been on-going since that time. Although numerous groups have been studied over the years, the data presented here focus on our two long-term study groups, Cerco de Piedra (CP) and Los Valles (LV). Data collected on these groups have included, but are not limited to, the recording of group demographics and dominance relationships (see Jack and Fedigan, 2004a,b; Fedigan and Jack, 2004, for additional details on long-term monitoring of these two groups). Here, we address the issue of male dominance and reproductive success by examining the paternity of infants born into the LV group over a 6.25-year period (November 1993 to January 2000) and infants born into the CP group over a 6.5-year period (October 1993 to April 2000).

Individual group members were identified by natural markings such as peak shape, scars, and missing or broken digits and according to their age-sex class. Our long-term observations of this species demonstrate that male white-faced capuchins do not reach full adult body size until they are 10 years of age (see Jack and Fedigan, 2004a,b), whereas sexual maturity occurs at approximately 8 years

of age (Freese and Oppenheimer, 1981). In general, juvenile males are not sexually active within our groups; and since we began our intensive observations in 1985, we have only once observed a single juvenile male (an immigrant male aged 6 or 7 years) copulate with group females (see Jack and Fedigan, 2004a). Therefore, in this study, we include only those males classified as adult (≥ 10 years) or subadult (7–10 years), all of whom were immigrants into the study groups. Male dominance rank was monitored continuously throughout the study period and determined by the direction of agonistic signals, supplantation, and approach/retreat interactions. Across all study years, multiple adult and/or subadult males (≥ 2 , maximum six) resided in each of the study groups and all males could be easily ranked in a linear hierarchy.

DNA Sample Collection and Analysis

We collected hair and/or fecal samples from all individuals present in the two study groups between 1997 and 2000. Additionally, we were able to collect samples from all former resident males, by following them after their transfer into other social groups. Fecal samples were collected immediately upon defecation and stored in vials containing 95% ethanol (see Gerloff *et al.*, 1995). Hair samples were collected using a modified blow darting technique (using a blunt dart with duct tape) and stored in paper in a dry location. Whenever possible, both hair and multiple fecal samples were collected for each individual. DNA extractions, using QIAGEN kits appropriate to sample types, and genotyping (PCR) were performed by Dr. David Paetkau, Wildlife Genetics International (unpublished data). Paternity exclusions detailed here are based on the use of three dinucleotide microsatellite markers with previously demonstrated utility in New World primates. One marker PEPL4 was developed for *Lagothrix* (Escobar-Parámo, 2000), while the remaining two markers (D3S1210 and D8S165) are human derived loci that have previously amplified well for *Saimiri boliviensis* (Witte and Rogers, 1999). Twenty-three additional markers were tested but were either found to be monomorphic in the Santa Rosa capuchins or the PCR was illegible (see Table 1 for details on additional markers tested). The three markers utilized here had either 3, 4, or 5 alleles, and DNA amplification (PCR) was independently repeated for each locus a minimum of two times, to combat the problems of false genotyping often associated with PCR products taken from non-invasive samples such as we use here (see Gerloff *et al.*, 1995).

Table 1. Microsatellite markers tested in two groups of *Cebus capucinus*

Marker	Repeat length	Amplification?	Legible?	Variable?
PEPL4	2	Yes	Yes	Yes; 5 alleles
D8S165	2	Yes	Yes	Yes; 3 alleles
D3S1210	2	Yes	Yes	Yes; 4 alleles
D6S260	2	Yes	Yes	2 alleles, 1 rare
D14S51	2	Yes	Yes	2 alleles, 1 rare
Ap6	2	Yes	Yes	Monomorphic
PEPC40	2	Yes	Yes	Monomorphic
PEPC59	2	Yes	Yes	Monomorphic
PEPC8	2	Yes	Yes	Monomorphic
PEPC3	2	Yes	No	3 alleles?
D3S1229	2	Yes	No	Yes?
D5S117	2	Yes	Marginal	Monomorphic?
Ap20	2	No		
Sw21F	2	No		
Sw65B	2	No		
CYP19	4	Yes	Yes	2 alleles, 1 rare
D21S1443	4	Yes	Yes	Monomorphic
THO1	4	Yes	Marginal	2 alleles
D1S518	4	Yes	Marginal	2 or 3 alleles?
D14S118	4	Yes	No	Monomorphic?
D8S588	4	Yes	No	3 alleles?
D9S746	4	Yes	No	Unknown
D12S1025	4	No		
D4S1628	4	No		
D8S373	4	No		
VWF-TNR	4	No		

Paternity Determination

By comparing the genotypes of infants and mothers, we were able to deduce paternal genotypes. We then examined the genotypes of all non-natal males, both adult and subadult, present in the group when the infant was conceived. Conception dates were determined by counting back 164 days from the birth date of each infant (see Fedigan and Rose, 1995; Robinson and Janson, 1987), although all males present in the month before and after the possible conception dates were also investigated for possession of the paternal alleles. Each male who did not possess the paternal alleles was excluded as a possible sire of the offspring. A male was considered the likely sire of an infant only if all other males could be excluded and the particular male in question possessed the paternal genotype at all three loci (e.g. Borries *et al.*, 1999; Soltis *et al.*, 2001).

Although four males in our sample resided first in one study group and then in the other, they are considered here as distinct males within each group and

their reproductive success (and dominance rank) within each of the groups is treated independently.

RESULTS

Los Valles Group

Between November 1993 and January 2000, nine immigrant males (adults and subadults) resided in LV. Six of these males were adults (BU, MO, NO, DI, PI, and SI) and three were subadults (SP, LE, and TR). Several of the males present in the group occupied more than one rank during their tenure, and each is considered according to his rank at the particular time that a conception was estimated to occur. Therefore, throughout the study period, the nine immigrant males occupied ranks as follows: three alpha males (BU, NO, and DI) and nine subordinates (BU, MO, LE, SP, DI, PI, SI, NO, and TR; see Table 2). A total of 15 infants were born into the group during the study period. Three of these infants disappeared from the group prior to being sampled; two disappeared together, accompanied by their mothers and one subadult male (group fission was suspected); while the third infant disappeared at 6 months of age and was presumed dead. These three infants are excluded from our analyses. Of the 12 remaining infants in our LV sample, three of the paternity exclusions (HE, SA, and CH) were incomplete as we were unable to type the infant's mothers (they died or disappeared prior to sampling). Finally, we could not exclude multiple possible sires from two additional LV infants, LZ and SA, who were siblings.

Table 2 lists these 12 infants born into LV during the study period, as well as adult and subadult males present (possible sires listed in descending order of rank), and the identity of males not excluded as possible sires. Of the seven infants for whom only one male could not be excluded, the alpha male was the sole non-excluded male for six (85.7%), while the beta male could not be excluded for the one remaining infant (14.3%; Table 2). In the case where the beta male was the probable sire of the infant, he was the only other adult male present in the group at the time of conception. In addition, this male (SI) had been the alpha male of the neighboring BH group where he and the infant's mother had resided prior to transferring together into LV 2 years earlier.

Paternity exclusions were incomplete for 5 of the 12 infants in our sample (i.e. multiple males could not be excluded as possible sires). The alpha male was included among the possible sires in four of these cases (infants LZ, ST, SA,

Table 2. Paternity exclusions for infants born into study groups

Los Valles: November 1993 to January 2000				
Infant	Mother	Conception date	Males present and rank ^a	Males not excluded
LZ	BL	20-Nov-1993	BU, MO	BU, MO
HE	BO ^c	22-Jul-1994	BU, MO, SP ^b , LE ^b	MO and LE ^b
AL	KL	27-Aug-1995	BU, SP ^b , LE ^b	BU
ST	CA ^c	13-Aug-1995	BU, SP ^b , LE ^b	BU, SP ^b , LE ^b
SA	BL	20-Sep-1995	BU, SP ^b , LE ^b	BU, SP ^b
CH	BO ^c	23-Mar-1996	BU, SP ^b , LE ^b	BU, SP ^b
PP	FE	21-Oct-1997	NO, DI, BU, PI, SI, TR ^b	NO
MA	KL	21-Nov-1997	DI, NO, PI, SI, TR ^b	DI
SO	DL	27-Nov-1998	DI, SI, PI	DI
CY	BL	21-Feb-1999	DI, SI	DI
DJ	FE	22-Jun-1999	DI, SI	SI
Y2K	KL	22-Jul-1999	DI, SI	DI
Cerro de Piedra: October 1993 to April 2000				
Name	Mother	Concept	Males present	Males not excluded
NY	LI	30-Jul-1993	NO, PI, DI	NO
PU	TU ^c	22-Apr-1993	NO, PI, DI	NO
RA	LI	5-Dec-1995	NO, PI, DI	NO
TI	SE	5-Dec-1995	NO, PI, DI	NO
SI2	LI	24-Feb-1998	NO, TR ^b	NO
ZA	SE	23-Aug-1998	NO, TR ^b	NO
BA	LI	19-Nov-1999	NO, TR ^b	NO

All infant names listed in bold indicate incomplete paternity exclusions.

^a All males are listed in descending order of their rank at time of infant's conception.

^b Subadult male.

^c Mother not typed.

and CH in Table 1). The last case of unsuccessful exclusion (see infant HE in Table 2) involved a beta male and one subadult male, indicating that this infant was sired by a subordinate male.

In summary, of the 15 infants born into the LV study group, three were untyped, paternity exclusions were incomplete for five and complete for the seven remaining infants. However, if we consider the infants sired by males according to rank-class (alpha or subordinate), which enables us to include the infant HE as we were able to exclude the alpha as a possible sire, six of eight (75%) were sired by alphas, and two of eight (25%; including HE) were sired by subordinate males.

Cerco de Piedra Group

Four immigrant males (one alpha and three subordinates) resided in the CP group between October 1993 and April 2000. The same adult male (NO) was alpha throughout this entire period, with the exception of 9 months during which time he took up residence as alpha male in the LV group. He followed his two subordinate males (PI and DI) who had aggressively taken over the neighboring LV group 1 month prior. During his 9 month absence, no new males entered the CP group, which remained without a resident male. This enabled NO to return to CP after being ousted from LV by his two former subordinates, at which time he returned to his position of alpha male accompanied by a subadult male from LV (TR). Note that these two males, and others who resided in both of our study groups (see below), are treated as different individuals in each group (e.g. NO/CP and NO/LV).

Nine infants were born in CP during the study period (Table 2). Samples were not obtained from two of these infants, as one died of apparently natural causes at 3 months of age and the other disappeared at 26 months with his mother, another adult female and an older brother (group fission suspected). Paternity exclusions were performed for the remaining seven infants; and in every case only the alpha male, NO, was the sole male that could not be excluded as a possible sire.

Dominance and Reproductive Success (Combined Group Data)

Over the course of our study, four males resided in each of the LV and CP groups. In addition, several males in LV occupied a different rank at varying points throughout the study. Given that our interest here is not in individual reproductive success, but rather reproductive success according to male rank, each of these males is considered according to his rank at the estimated time of each conception (see Curie-Cohen *et al.*, 1983 for similar treatment of male rank changes in rhesus macaques). For example, Table 2 shows that DI was beta male in LV when PP was conceived in October 1997, and the alpha male when the remainder of the LV infants were conceived. Such rank change can occur due to reversals within the group (i.e. a low ranking male moving up, which only rarely occurs), through the immigration of new males into the group, or through the emigration of resident males out of the group (see Fedigan and Jack, 2004; Jack and Fedigan, 2004b). Given the frequent fluctuation of rank

among subordinate males, and so as not to artificially inflate our sample size, we have opted to consider each male as either alpha or subordinate rather than by his linear rank. Calculated in this way, there was a total of 16 “ranked males” residing in our groups during the study period, and each is assigned a status of either alpha ($n = 4$) or subordinate ($n = 12$) according to his particular rank-class at the estimated time of conception. At no time during the course of our study was there only one male (i.e. the alpha male) present in the group when a conception was estimated to have taken place. We follow Smith (1981) and Curie-Cohen (1983) and assume that each male has an equal opportunity of siring each of the infants whose paternity was not determined. In this way, we were able to include incomplete paternity exclusions, and assign each male a reproductive success score (RS, Equation (1)) for each rank category he occupied in the group.

$$RS = \text{Infants sired} + \frac{\text{Possible infants sired}}{\text{Total no. of males not excluded}} \quad (1)$$

We also calculated an adjusted RS score (RSA, Equation (2)), which takes into account the total number of infants conceived within the group while each male was at a particular rank.

$$RSA = \frac{RS}{\text{No. of infants conceived during tenure}} \quad (2)$$

This score represents the total proportion of infants that were born into the group that the male was likely to have sired. The closer this number is to 1, the higher that male’s reproductive success. The RS and RSA for each male at each rank-class he occupied are given in Table 3, as are the minimum and maximum number of infants that each male sired. Although we have previously demonstrated that alpha and subordinate males do not differ significantly from one another in terms of tenure lengths within our study groups (Jack and Fedigan, 2004b), this adjusted reproductive success score enables us to control any bias that may be present in the number of offspring that each male had the opportunity to sire.

Of the 19 infants that were genotyped, alpha males ($n = 4$) sired a minimum of 13 (complete exclusions only) and a maximum of 17 infants (including the four incomplete exclusions; 68.4–89.5%), whereas subordinates ($n = 12$) were possible sires for a minimum of two and a maximum of six infants (10.5–31.6%; Table 4). Within our two groups, both RS and RSA were significantly correlated with male dominance rank-class over the course of the study period (RS:

Table 3. Male dominance rank and reproductive success

	Dominance rank(s)	No. of Infants born/typed ^a	Min. and Max ^b No. of infants sired	Reproductive success (RS ^c)	Reproductive success—adjusted (RSA ^d)
BU (LV)	1	6	1–5	2.84	0.473
BU (LV)	2	1	0	0.00	0.00
MO (LV)	2	1	0–2	1.00	0.50
SP (LV)	3 and 2	5	0–3	1.33	0.266
LE (LV)	3 and 4	5	0–2	0.83	0.166
NO (LV)	1	1	1	1.00	1.00
DI (LV)	2	1	0	0.00	0.00
DI (LV)	1	5	4	4.00	0.80
NO (LV)	2	1	0	0.00	0.00
TR (LV)	5 and 6	5	0	0.00	0.00
PI (LV)	3	3	0	0.00	0.00
SI (LV)	2, 4, and 5	6	1	1.00	0.167
NO (CP)	1	7	7	7.00	1.00
DI (CP)	2	4	0	0.00	0.00
PI (CP)	3	4	0	0.00	0.00
TR (CP)	2	3	0	0.00	0.00
Alpha total (mean)			13–17	14.84	Mean = 0.82 (<i>n</i> = 4)
Subordinate total (mean)			2 ^e –6	4.16	Mean = 0.06 (<i>n</i> = 12)

^a Excludes five infants that were not genotyped.

^b Minimum represents the number of offspring assigned to that male, while maximum is the minimum plus all additional infants for which that male could not be excluded as a possible sire.

^c $RS = \text{Infants sired} + \frac{\text{Possible infants sired}}{\text{Total no. of males not excluded}}$.

^d $RSA = \frac{RS}{\text{No. of infants conceived during tenure}}$.

^e Includes one case where two subordinate males were the only group males not excluded as a possible sire.

Table 4. Possible reproductive success according to male rank status (alpha versus subordinate)

Group	No. infants born	Total no. sampled ^a	Likely no. of infants sired (single non-excluded male)		Possible additional infants sired (multiple non-excluded male)	
			Alpha	Subordinate ^b	Alpha	Subordinate
Los Valles	15	12	6	2	4	4
Cerco de Piedra	9	7	7	0	0	0
Total	24	19	13	2	4	4

^a Excludes those infants that died before sampling.

^b Includes one case where two subordinate males were the only group males not excluded as a possible sire.

$r_s = 0.738$, $n = 16$, $p = 0.001$; RSA: $r_s = .770$, $n = 16$, $p < 0.001$), with alphas siring significantly more offspring than subordinates.

DISCUSSION

The data presented here cover a combined total of 12.75 years (1993–2000), during which time 4 alpha males and 12 subordinate males resided in our two study groups, and a total of 24 infants were born. Due to deaths or disappearances of 5 infants prior to sampling, only 19 of those infants were included in this study. Our examination of male reproductive success in these two groups of white-faced capuchins found a significant positive correlation between male rank-class (alpha or subordinate) and reproductive success, with alpha males siring most (68.4–89.4%) infants born into our study groups. These data show that being the top-ranked male within a group has definite reproductive benefits and that, although dominant males are providing subordinates with mating opportunities (see Rose, 1998), reproductive opportunities (i.e. paternity) are not truly being shared. Paul (2002) correctly points out that even if a female engages in multiple matings, as is the case with female white-faced capuchins, this does not necessarily mean that matings are random across female reproductive states (also see Carnegie *et al.*, this volume). Our finding that alpha males are fathering the majority of infants within our study groups may indicate that females are choosing to mate with alpha males during their conceptive periods or that fertile females are being monopolized by alpha males. Although we have not observed active mate guarding within our groups, it is possible that a more subtle form of competition is occurring, and subordinate males may avoid mating with females when dominants are showing interest in them. In a later study of the same groups, Carnegie (2004; Carnegie *et al.*, this volume) found that alpha males were more likely to mate with cycling, periovulatory females, whereas subordinate males were more likely to mate with pregnant females. Whatever the explanation, it is obvious that subordinates are not being rewarded with reproductive opportunities, by either group females or alpha males, in exchange for their cooperation in group defense.

Given the benefits that subordinates provide to dominants in terms of group defense from the possibility of takeovers by outsiders, we predicted that this species would display low reproductive skew (i.e. paternity would be shared by group males). In contrast to our expectations, and despite their very egalitarian mating system, white-faced capuchins exhibit high reproductive skew

(i.e. paternity is dominated by one or a few breeders). According to concession theory (e.g. Reeve and Ratnieks, 1993; Reeve *et al.*, 1998), high reproductive skew is predicted if (1) there are ecological constraints on dispersal (e.g. habitat saturation) or (2) dominants and subordinates are related (in which case both alphas and subordinates would receive inclusive fitness benefits). Our long-term studies of the white-faced capuchin population within SRNP have shown that the population has increased significantly in the past two decades; however, it has done so through increased group size rather than through an increase in the number of groups (Fedigan and Jack, 2001). There appears to be strong ecological constraints on the number of groups that the habitat can support, because during the 6-month dry season these monkeys become central-place foragers, focusing their activities around locally available water sources from which they drink on a daily basis. These water sources are very limited and the distribution of groups throughout the park is dictated by the location of these water sources and the number (and size) of groups sharing them. In addition, sex ratios at birth are skewed towards males (Fedigan, 2003), and adult sex ratios within groups of white-faced capuchins are nearly one to one (Fedigan and Jack, 2001); both factors potentially leading to increased male–male competition. Such ecological and demographic factors, either individually or combined, may necessitate that, after joining a group, males must bide their time at a low rank and tolerate low reproductive success. If this is the case, the “staying incentive” that dominants are providing their subordinates may merely be their tolerance of these males within the group.

Johnstone and Cant (1999) recently suggested that in some species, where dispersal patterns are largely influenced by ecological constraints, such as those described here, subordinates may keep their mating and reproduction to a minimum so as not to risk eviction from the group by dominants. However, we have yet to see a dominant male harass a subordinate male engaged in copulation or forcibly evict a subordinate co-resident male from the group. Indeed, when subordinates are away from the group, alpha males go to great lengths to locate them. In such cases, alpha males will emit lost-calls (specialized long-distance vocalizations used to locate individuals who are lost or away from the group). When subordinates are reunited with the group, the alpha male often initiates a reunion display to welcome them back and ease social tension (see Fedigan and Jack, 2004). An analysis of our long-term data on male dispersal patterns showed that subordinates are more likely to disperse from the group

voluntarily (i.e. they are not aggressively evicted by dominant males), perhaps in response to an alpha's unwillingness to yield sufficient reproductive incentives (Jack and Fedigan, 2004c). These factors (alphas actively trying to keep subordinates in the group and subordinates voluntarily emigrating) provide strong evidence against the suggestion that subordinates keep their mating to a minimum to avoid eviction, and that ecological constraints on dispersal cause the high reproductive skew that we see in white-faced capuchins.

High-skew societies are also thought to occur when dominants and subordinates are related. White-faced capuchins are a male dispersed species, which generally implies that co-resident males are unrelated. However, in the absence of male philopatry, kinship among males can be maintained through parallel dispersal (Van Hooff, 2000). Parallel dispersal occurs when male siblings emigrate together, or when males preferentially disperse into groups containing familiar, previously dispersed, males. Male white-faced capuchins engage in parallel dispersal at very high rates, and this pattern of coordinated emigration and immigration remains high even in adulthood (Jack and Fedigan, 2004a,b). Moore (1992) suggests that natal individuals dispersing together and subsequently joining the same group, as has been observed among white-faced capuchins, may result in a level of relatedness within the new group that is comparable to that found in groups made up of philopatric individuals. Indeed, we have seen several cohorts of males reside in consecutive groups together, and we have also observed males reuniting with previously familiar males after more than 5 years of separation. Given these observations, it is possible that white-faced capuchins display high reproductive skew within groups because co-resident males are related. That is, even when they do not directly sire infants, subordinate males may achieve inclusive fitness benefits via the enhanced reproductive success of the related alpha males with whom they have cooperated. However, we await additional kinship analysis as further support for this interpretation.

SUMMARY

The relationship between male dominance rank and reproductive success has been a long-debated topic in primate behavior. While most early studies looked at mating success as a proxy measure of reproductive success, recent advances in using small quantities of DNA obtained from hair and feces have enabled

paternity testing even in a field setting. In this study, we examine the relationship between male dominance rank and reproductive success in two groups of wild white-faced capuchin monkeys (*Cebus capucinus*) residing in Santa Rosa National Park between October 1993 and January 2000. A total of four alpha males and 12 subordinates resided within the two groups during the study period and 25 infants were born. Of these infants, only 19 were genotyped due to the deaths or disappearances of six infants prior to sampling. Paternity was determined using DNA extracted from non-invasively obtained hair and fecal samples and amplified using PCR. Using this method, we were able to perform complete exclusions on 15 of the 19 infants genotyped. Our analysis revealed that alpha males in the two study groups sired significantly more offspring than did subordinates; alphas sired a minimum of 13 infants and a maximum of 17, while subordinates sired between two and six of the infants born in our groups. This multimale–multifemale species displays an extremely egalitarian mating system and overt mate guarding by dominant males has not been observed. However, the data presented here indicate that there is a definite advantage to being an alpha male in this species. This finding may explain the high rate of male secondary dispersal and, in particular, the voluntary dispersal of subordinate males observed in our long-term study groups.

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