

RESEARCH ARTICLE

Male Mating Strategies and Reproductive Constraints
in a Group of Wild Tufted Capuchin Monkeys
(*Cebus apella nigrinus*)

JESSICA W. LYNCH ALFARO*

Department of Anthropology, Center for Reproductive Biology, Washington State
University, Pullman, Washington

Tufted capuchin monkeys (*Cebus apella*) provide an extreme example of active female sexual solicitation of males. In spite of being targeted by females for sex, males may delay copulation for hours or days. Data were collected on the sexual interactions in one wild capuchin group at the Estação Biológica de Caratinga in Brazil from September 1996 to August 1997. All successful conceptions during this year occurred in the dry season, yet sexual behavior was observed during 9 months of the year. This study tested whether male sexual response to female proceptivity was seasonally-mediated. Male consortship participation, solicitation of females, latency to copulation, and copulation frequency were compared between fertile and nonconceptive females. Seasonal patterns in copulation interference, mating style, and alternative mating strategies were also examined. Thirty-two copulations were observed. The alpha male was solicited for significantly more consortship days per female, but his mating success, in terms of copulation frequency, did not differ from that of two other adult males in the group. In the dry season, when the females were fertile, the males showed increased contest competition for mates, a higher frequency of alternative mating strategies against copulation interference, and increased monitoring of the females' condition. However, contrary to expectations, the alpha male's latency to copulation was significantly longer in the fertile season than in the nonconceptive months, and no males were observed to mate more than one time per day, even at the conceptive peak. Male mating strategies were affected by both season and rank, and there was evidence for reproductive constraints on males throughout the year. Limited male ejaculatory capacity and male choice in the timing of copulations within

Contract grant sponsor: Fulbright/IEE; Contract grant sponsor: Wenner-Gren Foundation; Contract grant number: 6068; Contract grant sponsor: Tinker Foundation/Nave Fund; Contract grant sponsor: National Science Foundation.

*Correspondence to: Dr. Jessica W. Lynch Alfaro, Department of Anthropology, College Hall 208, Washington State University, Pullman, WA 99164. E-mail: jlynch-alfaro@wsu.edu

Received 22 November 2004; revised 23 February 2005; revision accepted 14 March 2005

DOI 10.1002/ajp.20188

Published online in Wiley InterScience (www.interscience.wiley.com).

female proceptive phases may both be important factors in driving the sexual dynamics of this species. *Am. J. Primatol.* 67:313–328, 2005.
© 2005 Wiley-Liss, Inc.

Key words: *Cebus apella nigritus*; mating strategies; consortships; proceptivity; sperm competition

INTRODUCTION

Tufted capuchin monkeys (*Cebus apella*) are considered an extreme example of active female proceptivity [Dixson, 1998; Manson, 1994; Smuts, 1987]. A typical female spends the first 3 or 4 days of her 4–6-day proceptive phase following a male and attempting to mate with him [Janson, 1984]. Generally, the male does not respond immediately with any receptive sexual signaling, but instead may delay copulation for hours or even days [Janson, 1984]. Females are aggressive and persistent in their solicitation of males [Janson, 1984, 1986; Phillips et al., 1994]. However, female initiation of sexual behavior is common to many primates [Small, 1988]. What appears to be truly unusual in *C. apella* is not the females' active solicitation of males, but the failure of the target male to respond readily to a female's sexual interest. Male mate choice in selecting particular females, or timing copulations to coincide with a female's proceptive phase, may be a key element in male capuchin reproductive strategies, as has been reported for male baboons [Bercovitch, 1987].

Although capuchin monkeys may copulate throughout the year, across much of the range of *Cebus apella* births are confined mainly to the early- to mid-wet season [Di Bitetti & Janson, 2000, 2001; Lynch & Rímoli, 2000]. Thus, most conceptions occur in the dry season, and copulations outside this period are frequently infertile. In *Cebus capucinus*, the majority of copulations occur with nonfertile females, such as those that are pregnant or lactating [Manson et al., 1997; Perry, 1997]. Perhaps *C. apella* males show decreased sexual interest when solicited by females in the wet season, at which time fertilization of females is unlikely. Testosterone concentrations in male tufted capuchins have been shown to increase significantly during the dry season, when females are experiencing conceptive cycles. This pattern holds true for both alpha and subordinate males [Lynch et al., 2002], even though sexual activity also occurs in the wet-season months [Janson, 1984; Lynch et al., 2002]. If male sexual interest is testosterone-mediated, and males are able to distinguish between solicitations from fertile vs. nonfertile females, one would predict a dramatic increase in male sexual response during the dry season. Males that are sexually solicited by females should show a shorter latency to copulation than they do in the nonconceptive season, and males might be expected to monitor the females' condition and actively solicit sex from receptive females in the dry season.

Cebus apella males have also been noted for their surprising lack of direct male–male competition over mates [Janson 1984, 1986]. However, if females are fertile only for a short period during the year, one might expect that male–male contest competition for females would be high only during that period. Robinson [1988] found that in *Cebus olivaceus*, many while males in the group mated in other months of the year, the alpha male controlled access to all fertile females, and was the only one that copulated during the conceptive period [Robinson, 1988]. One can expect (for *C. apella* males) that during the dry season, when conceptions are most likely, there will be a higher frequency of copulation

interference. The alpha male may be able to inhibit all subordinate male sexual activity [Robinson, 1988] in the dry season, or subordinate males may employ alternative mating strategies at that time, such as sneaky [Berard et al., 1994] or unimount [Janson, 1984] matings. In sum, the “seasonal hypothesis” is that males can distinguish between fertile and nonfertile females, and therefore show sexual interest and male–male mate competition in the conceptive season only.

An alternative hypothesis is that capuchin males are constrained throughout the year in the number of ejaculations they can perform per day. Janson [1984] reported that no males in his study copulated more than once a day. *Cebus olivaceus* males have a relatively long ejaculatory interval compared to other primates that live in multimale, multifemale groups [Dewsbury & Pierce, 1989]. If *C. apella* males are limited in the number of ejaculations they can perform, then alpha males (the recipients of the majority of female solicitations) may need to be choosy about when and with which female they mate. Subordinate males, which have far fewer opportunities to mate [Janson, 1984], may show a comparatively short latency to mounting behavior when solicited by a female. Subordinate males may also be more active than the alpha male in soliciting females themselves. If capuchin male sexual behavior is limited by physiological constraints on ejaculatory frequency, males may mate on more days or with more females during the conceptive season; however, the number of copulations per male per day will remain low throughout the year, despite increases in female sexual solicitations during the conceptive season.

This study examined a group of wild tufted capuchin monkeys in Minas Gerais, Brazil. Male behavior was analyzed for the influence of season and rank on male sexual interest, as evidenced by the frequency of male solicitation of females, latency to copulation after sexual solicitation from females, copulation frequency, copulation type, and participation in postcopulatory display. Seasonal patterns in male–male competition, such as copulation interference and alternative mating strategies, were also examined.

MATERIALS AND METHODS

Study Site and Subjects

This study was carried out from September 1996 to August 1997 at the Estação Biológica de Caratinga (EBC), a highly seasonal, 1,000-ha fragment of Atlantic forest in Minas Gerais, Brazil. Tufted capuchins were previously studied at EBC [Lynch & Rímoli, 2000; Rímoli & Ferrari, 1997], and the main study group was well-habituated to observers at the onset of this project. This group ranged from 24 to 28 individuals during the study, including four adult males, two subadult males, six adult females, six subadult females, and several juveniles and infants, which were recognizable by their natural markings. Age and sex classes were determined using criteria defined by Izawa [1980]. Changes in group size were all due to births or disappearances of infants and juveniles [Lynch & Rímoli, 2000].

At the onset of the study (Fall 1996), all adult females were either pregnant (PT, PM, SO, and TE) or had infants less than 1 year of age (CE and HL). Using long-term data from Izawa’s site at La Macarena, Columbia [Lynch & Rímoli, 2000], the interbirth interval can be calculated for *C. apella* females with surviving infants as lasting a mean of 25.6 months, with a range of 21–35 months. Taking into account the average 153-day gestation length for *C. apella* [Wright & Bush, 1977], and conservatively using the briefest IBI from Izawa’s study (21 months), we can conclude that the period from birth to conception is at least

16 months in *C. apella* females. According to this calculation, all adult females in the study group were infertile until at least March 1997.

Behavioral Observations

Visual contact with the group was established on 201 days. A scan sample [Altmann, 1974] on social distance was taken once every hour for all observed individuals, and used to determine the degree of visibility for each individual within the group. The scan samples, and behavioral observations in general, were less frequent in the late wet season (January through March), when the group was more difficult to find and follow, and heavy rain hampered observations. In the wet season, 681 hourly scans were performed (56.75 scans=mean number of scans per 15-calendar-day observation period), compared to 433 hourly scans in the dry season (a mean of 61.86 scans per 15-calendar-day observation period). The alpha male is generally the most visible individual in *Cebus apella* groups [Defler, 1979; Izawa, 1980; Janson, 1984, 1986], so information on visibility is necessary to evaluate the frequency of sexual behavior noted for each male. Because of the dense vegetation throughout much of the study group's home range, and the dispersed nature of the group, 5 min were allotted for each scan sample to be completed [Altmann, 1974].

To determine the rank of the males within the group, I recorded data on both approach-retreat interactions and dyadic aggressive interactions, noting the individuals involved and the direction of signals [Lynch, 2001]. Approach-avoid interactions, collected through both focal-animal follows and ad libitum observations, were entered into a matrix to construct a dominance hierarchy (modified from Perry [1995]). An alternate dominance hierarchy was produced on the basis of the actors and recipients in dyadic aggressive interactions [Di Bitetti, 1997]. Since both methods of constructing the hierarchy produced similar and corroborative results, the two data sets were pooled.

All displays of proceptivity and the identities of individuals involved were recorded. A female was considered to be proceptive on days when she copulated or performed behaviors such as eyebrow-raises and grimaces toward males [Janson, 1984; Linn et al., 1995; Phillips et al., 1994]. Proceptivity is further characterized by frequent approaches and leaves directed at a target male, and the emission of a repetitive cry or squeal [Carosi & Visalberghi, 2002; Janson, 1984]. A male-female dyad was considered to be in "consortship" when a proceptive female was eyebrow-flashing, grimacing, and following a male that was not reciprocating with any signs of sexual behavior. Consortships, or female sexual pursuit of males, often (but not always) preceded mutual sexual interactions in which both individuals actively displayed sexual signaling toward one another. Consortships were counted by day and by dyad, so one individual could be scored with multiple consortships on a given day. The term "consortship" has been used in the capuchin literature to describe the female sexual pursuit of indifferent males [Dixson, 1998; Janson, 1984], and is used the same way here. Capuchin consortships, however, are not equivalent to the consortships described for many other primate taxa [Manson, 1997].

"All-occurrence" observations were made of all mutual sexual interactions, and the observer would stop other protocols to follow any signs of sex-related behavior or vocalizations. Once sexual activity was identified, the individuals involved were followed until completion of courtship, copulation, or postcopulatory display unless they were lost from view. The temporal sequence of sexual behavior in tufted capuchins begins with courtship behaviors of mutual

solicitation, including short chases, eyebrow raises, and grimaces by both individuals. Copulation may be single- or multimount, and the female and male may take turns mounting each other [Carosi & Visalberghi, 2002; Janson, 1984]. Only male-on-female mounts of adults or subadults were considered copulations. Ejaculation could not be consistently determined. Latency to copulation was calculated by the time (in minutes) from the onset of sexual solicitation by either the male or female until the onset of the first male-on-female mount. Latency to copulation was scored as 60 min long if the female sexual solicitations, in the form of a consortship, lasted for more than an hour before copulation occurred, because it was not possible to closely monitor consortships for hours at a time. If the onset of sexual activity was not observed for a particular dyad, latency to copulation was not calculated, unless solicitations continued for more than 1 hr prior to copulation.

Tufted capuchin copulations have been categorized into two types. Janson [1984, p 192] found that “copulations involving subordinate males are much less complex than those with the dominant male...A female usually solicits a subordinate without extensive chasing, simply by directing a grimace toward him, then runs up quickly, mounts [sic], thrusts for a few seconds to a minute, and leaves soon after dismounting.” In such “unimount” copulations, precopulatory courtship is minimal, and one or both of the participants departs quickly after the copulation without further sexual signaling. “Consortship” copulation, which Janson [1984] described as characteristic of the dominant male, includes hours or days spent by the mating pair in close proximity, as well as lengthy precopulatory courtship, multimount copulation, and postcopulatory display. A third copulation type, the “sneak,” was observed during the present study. Intermediate to the consort and the unimount, sneak copulations occur away from other group members and involve little precopulatory courtship but extended postcopulatory display.

During my study, postcopulatory displays (also termed “post-ejaculatory courtship” by Carosi and Visalberghi [2002]) were characterized by male “chutter” vocalizations and female cries. The male and female stared at one another with eyebrows raised, and the female curled up and remained stationary while the male moved around her, approaching and leaving several times, intermittently sitting up on his haunches with one hand placed on his chest, and rotating his head from side to side. The duration of the postcopulatory display was calculated in minutes from the last male-on-female mount until either individual left the view of the other, or both individuals stopped showing any signs of sexual behavior. Female-on-male mounts and postcopulatory displays were considered as “partial mating sequences.” Both are highly contextualized behaviors that give a strong indication that a male-on-female mount has occurred [Janson, 1984].

Data were also collected on alternative mating strategies. “Furtive visual signaling” was scored if a female solicited a subordinate male with eyebrow raises and grimaces while hiding from alpha male’s view and emitting no vocalizations. “Volume modulation of copulatory vocalizations” was scored if a female’s sexual cries were noticeably quieter during copulations with subordinate males compared to those with the alpha male, despite equal intensities of the nonvocal sexual signals. “Deceptive vocal signaling” was scored when loud nonsexual vocalizations were emitted by individuals engaging in sexual activity away from the group. “Capitalization on alpha male distraction” was scored if a copulation between a subordinate male and a female occurred when the alpha male was defending a prized food item, in proximity to a predator, or copulating with another female. Males were scored as “monitoring female sexual activity” by

either olfactory means (smelling the female or sniffing branches where the female had been sitting), or visual means (following females in consort with other males). “Extragroup sexual interactions” were scored if any individual from the study group was observed in consorts, courtship, copulation, or postcopulatory display with nongroup members. “Incitement of the alpha male” was scored if a female mated with a subordinate male in full view of the alpha male and then immediately solicited the alpha male for sex. “Escape from the proximity of the alpha male” was scored if a female used deception to depart from a consortship with the alpha male.

Statistical Analyses

Nonparametric analyses were conducted because the data were not normally distributed. The wet season included September through mid-April, and the dry season was late April through August (following Strier et al. [1999] for this site during the same time period). The frequency of completed copulations and partial mating sequences per month per male were divided by the number of scan samples for that month for that male, to control for observability across males. Pairwise Wilson signed-ranks tests were performed on the converted frequencies to compare copulation frequency across all adult males. For statistical comparisons of the durations of sexual behaviors (i.e., latency to first mount and duration of postcopulatory display), only those cases were included in the analyses in which the observer had been present for the entirety of that phase of sexual behavior.

A male was scored as having a consort day on each day in which he was actively solicited by a female. Even if the consort pair was seen together for only a short period of time, the consort was scored as “1 day,” because it was difficult to stay with a consort pair for hours at a time. The use of consort “days” also served to adjust for differential visibility of males: an alpha male that was scored in consortship for several hours would be scored with one consort day, and another male, even if he was only briefly observed in consort, would also be scored as having one consort day.

RESULTS

Seasonal Distribution of Sexual Activity

Sexual activity was observed in 9 months out of the year (Fig. 1). Three adult males in the group (AC, NL, and ST) displayed sexual behavior in the wet season, and they and two additional males (FR and RO) were sexually active in the dry season. Five adult and five subadult females displayed sexual behavior in the course of the study. Throughout the wet season, only one female was sexually active on a given day. At the onset of the dry season, from late April through May, there was an increase in the number of days that adult females displayed proceptive behavior, and a substantial temporal overlap in proceptive phases among females. Two females were sexually active on 16 of the 34 days with sexual activity during the dry season, and on 1 day four adult females were proceptive simultaneously. In the dry season, each adult female’s sexual activity was clustered in 2–7-day periods, separated by 14–21 days without sexual activity, which was suggestive of ovarian cyclicity. Most of the subadult female mating activity occurred in late June and July, approximately 4–6 weeks after the adult female mating peak.

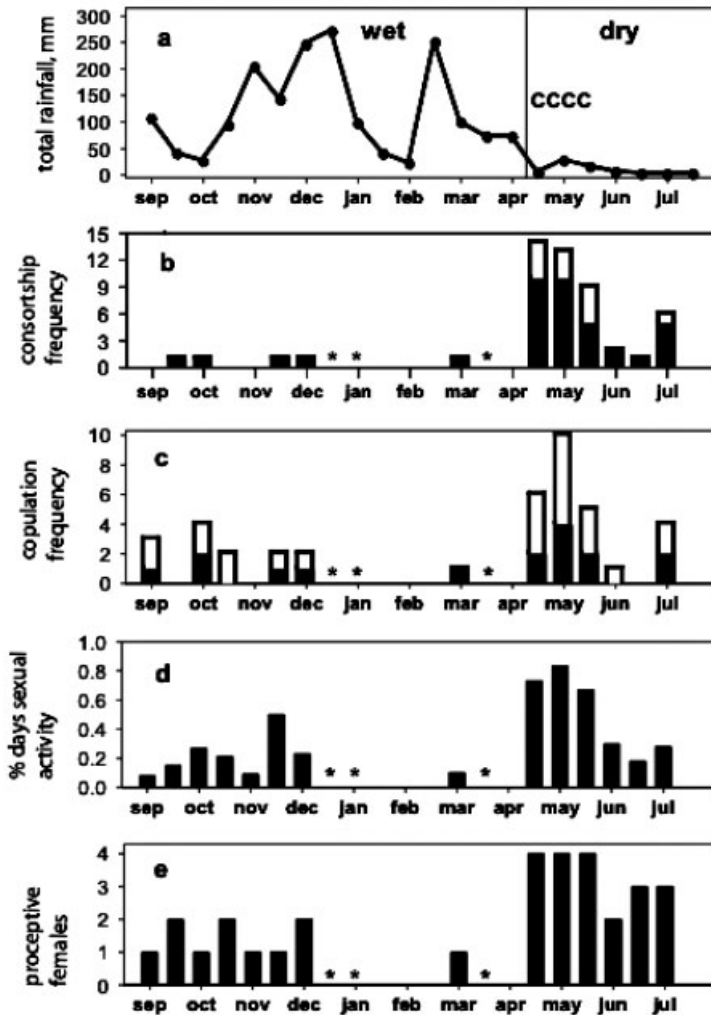


Fig. 1. (a) The total rainfall (in millimeters) at EBC, Minas Gerais, Brazil, from September 1996 to August 1997, shown in 15-day periods, is compared with the (b) frequency of female-initiated and maintained consortship days, (c) frequency of copulations and partial mating sequences (i.e., female mounts or postcopulatory displays, as explained in the text), (d) percentage of days of observation that included sexual activity within the group, and (e) number of different females scored as displaying proceptive behaviors, for each 15-day period of the study. Consortships were scored by day and by male-female dyad, so multiple consortships may have been scored on a given day. In part a, each C denotes a confirmed conception, based on birth records and a 153-day gestation length [Wright & Bush, 1977]. Asterisks in b-e indicate no behavioral data for those 15-day sampling intervals. In b and c, black bars indicate the alpha male, and white bars indicate subordinate males.

By calculating from the estimated age of infants during censuses of the same capuchin group in November 1997 and January 1998, and using a gestation length of 153 days (as reported for *Cebus apella* in captivity [Wright & Bush, 1977]), we can conclude that all conceptions during the study period ($n=4$) occurred during the dry season, as indicated in Fig. 1a.

Female Sexual Solicitations of Males

Proceptive females ($n=10$) spent significantly more consortship days with the alpha male (AC) than with any of the other adult males, as indicated by pairwise comparisons (Wilcoxon signed-ranks: AC-NL, $z=2.20$, $P=0.028$; AC-ST, $z=2.68$, $P=0.007$; AC-FR, $z=2.67$, $P=0.008$). In the wet season, the alpha male was the only male that females solicited for consortships (see Fig. 1b). On five different occasions during the dry season, two females solicited the alpha male simultaneously. In the dry season, nine of the 11 consortships that females directed at subordinate males occurred on days when the alpha male was already in a consortship with another female. No subadult males were ever solicited for consortships.

Male Copulation Frequency

All four adult males and one subadult male were seen participating in copulations or partial mating sequences. No male was ever seen copulating more than once a day in either the wet or dry season. The alpha male (AC) accounted for 16 of the 42 copulations and partial mating sequences observed. A subordinate adult male (NL) was responsible for 13, and a third adult male (ST) was responsible for nine copulations or partial mating sequences. The most peripheral adult male (FR) was seen mating once only, with an extragroup female, and the subadult RO mated three times, but only once to completion.

The three highest-ranking males (AC, NL, and ST) mated in both the wet season and the dry season. When the frequency of copulations by female mating partner ($n=10$ females) was compared among these three males, there were no differences in copulation frequency (Wilcoxon signed-ranks: AC-NL: $z=0.77$, $P=0.44$; AC-ST: $z=1.19$, $P=0.24$; NL-ST: $z=1.36$, $P=0.17$). FR and RO were sexually active in the dry season only. A young subadult male (FF) was mounted once by an adult female, but did not respond sexually.

Male-Male Contest Competition

The alpha male was never interrupted during mounting behavior. Four out of 21 copulations (19%) by non-alpha males were interrupted by other males. All interruptions occurred during the dry season mating peak. The alpha male was responsible for two of these interruptions; in one case, the arrival of the alpha male into view inhibited RO's sexual behavior. RO was interrupted in two out of three copulations.

On five different days, more than one male mated with the same female. In rapid sequential matings, the mean interval between the last mount for one male and the first mount by another male on the same female was 14.0 ± 13.0 min, with a range of 2–33 min ($n=6$). These rapid sequential matings occurred three times in the wet season without overt male-male aggression. However, in the dry season both RO and ST attempted to copulate with HL in rapid succession, but neither mating sequence was completed because each male interrupted the other male's copulation.

Copulation by Type

The alpha male always had consort copulations, whereas only subordinate males engaged in sneak and unimount copulations. Of the 28 copulations or partial mating sequences that could be categorized by type, the dominant male

was responsible for 11 of the 13 consort copulations (85%), and subordinate males performed 100% of both the sneak ($n=7$) and unimount ($n=8$) copulations. All subordinate male copulations during the wet season were unimount ($n=7$). In contrast, all completed subordinate adult male copulations in the dry season were either sneak ($n=7$) or consort ($n=2$) copulations. The consort copulations by subordinate males always occurred on days when more than one female was proceptive.

Mount Latency

When the means for all male–female pairs ($n=5$) that mated in both the dry and wet seasons were compared, male latency to mount after the onset of sexual behavior showed a trend toward being longer in the dry season than in the wet season (Wilcoxon signed-ranks, $z=1.75$, $P=0.08$). A comparison of the mean latency across females revealed that the alpha male took significantly longer than NL to mount a female after the onset of sexual behavior, in both the wet season (Mann-Whitney U-test, $n=3$ females, $z=-2.2$, $P=0.028$) and the dry season (U-test, $n=5$ females, $z=-2.63$, $P=0.009$). When considered individually, the alpha male (but not the other males) showed a significantly longer latency to mount during the dry season compared to the wet season (AC: Mann-Whitney U-test, $n_1=3$ females, $n_2=5$ females; $z=-2.25$, $P=0.024$).

Male Initiation of Sexual Interactions

One adult male (NL) initiated the sexual interactions preceding six of his 11 copulations. NL initiated sexual interactions in both the wet and dry seasons. In contrast, neither the alpha male nor ST initiated sexual interactions prior to female solicitations (AC initiated zero of 10, and ST initiated zero of three). No data are available for FR or RO regarding the initiation of sexual interactions.

Duration of Postcopulatory Display

When the means for all male–female pairs with postcopulatory data in both seasons ($n=6$) were compared, the duration of postcopulatory display per pair showed a trend to be longer in the dry season than in the wet season (Wilcoxon signed-ranks: $z=1.826$, $P=0.068$). There was no difference in postcopulatory duration across sexually active males in either the wet or dry season. While each male had a higher mean duration of postcopulatory display in the dry season than in the wet season, when considered individually the difference reached significance only for the alpha male (AC: Mann-Whitney U-test, $n_1=5$ females, $n_2=5$ females, $z=-2.46$, $P=0.014$).

Alternative Mating Tactics

The majority of the records for alternative mating tactics (28 of 37), and the most diversity in alternative mating tactics occurred during the dry season, when females were most fertile. The only alternative strategies employed in the wet season were volume modulation of copulatory vocalizations, capitalization on alpha male distraction, and approaching and mating with the alpha male immediately after mating with a subordinate male. All other tactics occurred in the dry season only.

“Capitalization on alpha male distraction” included a unimount copulation in the wet season as the alpha male retrieved a papaya (a highly prized food item)

from a garden, a unimount copulation in the wet season after a tayra (*Eira barbara*) passed beneath the group, and a sneaky copulation in the dry season while the alpha male copulated with another female.

Females attempted to incite the alpha male to perform sexual behavior in both seasons. On three occasions during the wet season, a female mated with the alpha male immediately following a mount by a subordinate male. During the dry season, females (n=5) also approached and pursued the alpha male with sexual solicitations immediately after subordinate male copulations, but these solicitations were never observed to result in subsequent mounting behavior by the alpha male.

Examples of “deceptive vocal signaling” were limited to the dry season. They included a female screaming as if injured as she actively solicited and copulated with a subordinate male, a subordinate male and female giving “lost” calls while mating away from the group, and a subordinate male giving “lost” calls as he solicited a distant female (in proximity to the alpha male) with eyebrow flashes and a curl-up posture.

During the dry season, one proceptive female escaped the proximity of the alpha male. She descended a cliff in an attempt to leave him, and as he pursued her she was simultaneously receiving covert solicitations from a subordinate male. Minutes later this female was observed to backtrack in the opposite direction, while the subordinate male followed in that female’s path and sniffed the branches on which she had traveled. Soon the alpha male reemerged from below the cliff and followed the same path. However, the female had disappeared, along with a third adult male, and was absent from the group for most of the day.

Subordinate males monitored female sexual activity in the dry season only. One male “trailed” the alpha male and his two consort females for at least 30 min, from a distance of about 50 m, sniffing branches on which both females had been lying, and avoiding the alpha male’s view. Subordinate males found in proximity to copulating pairs were observed to watch the pair (sometimes while displaying an erect penis), perform branch-breaking displays, and/or emit distressed vocalizations. Extragroup sexual interactions occurred in the dry season only, and included a female entering the group to engage in a sexual consortship with the alpha male for 2 days, and a mounting of FR by a female from another group, out of sight from other members of both groups.

DISCUSSION

Female Consort Choice

As found in other *Cebus apella* populations, the alpha male was the most solicited consort partner, receiving significantly more frequent, longer-lasting consortships from females than did the other males in the group. The alpha male was solicited for consortships throughout the year, while other males were solicited during the dry season only. Most consortships for subordinate males occurred on days when the alpha male was already engaged in a consortship with a different female. As found in other studies of tufted capuchins [Janson, 1984; Linn et al., 1995; Phillips et al., 1994; Welker et al., 1990], the alpha male was clearly the preferred consort partner for most females, and he had significantly longer and more consistent access to proceptive females than did any of the subordinate males.

Seasonal Variation in Male Mating Competition

Male sexual behavior showed significant seasonal variation. During the dry season mating peak, there was an increase in the number of sexually active males,

copulation interference, and alternative mating tactics. Together, these data suggest that males engaged in more sexual competition (both aggressive and scramble) during the dry season when females were more likely to be fertile.

All copulation interferences occurred during the dry season. Direct copulation interference between adult males was rare ($n=1$ of 28 copulations), but adult males interrupted two of three copulations by the subadult male. Most of the successful copulations by subordinate males during the dry season occurred away from the group, as either sneak or extragroup copulations. In contrast, in the wet season subordinate males were more likely to perform rapid, unimount matings in the presence of other group members (as described by Janson [1984]), and on three separate occasions, multiple males mounted the same female in rapid succession without intermale aggression. Capuchin females at both Manu National Park, Peru, and Iguazú National Park, Argentina, were also observed to engage in promiscuous mating with multiple males on a given day, although the seasonality of these occurrences was not reported [Janson, 1984, 1998].

In the dry season, low-ranking males appeared to be inhibited from expressing sexual behaviors in the presence of the dominant male, as seen in captive tufted capuchins [Linn et al., 1995]. Alternative mating tactics, such as furtive visual signaling, deceptive vocal signaling, and escaping from the proximity of the alpha male occurred in the dry season only. The subordinate adult males' alternate mating strategies of sneaky or and unimount copulations may function to decrease the likelihood of copulation interference (e.g., in *Presbytis entellus* [Blaffer Hrdy, 1977] and *Macaca mulatta* [Berard et al., 1994]). Male monitoring of female proceptive behavior and condition was noted in the dry season only.

Male Rank, Mating Style, and Reproductive Constraints

No males were observed to mate more than one time per day, in either the wet or the dry season. This suggests that males may be reproductively constrained throughout the year. Male latency to mount showed a tendency to increase in the dry season, when females were most fertile. This is in direct opposition to expectations based on the increase in male testosterone seen in the dry season [Lynch et al., 2002], because a longer latency to mount is considered an indication of low sexual motivation by the male [Meisel & Sachs, 1994]. Busey and Estep [1984] found that the sight of other males copulating acted as a sexual stimulus for male pigtail macaques (*Macaca nemestrina*) and shortened the refractory period that follows ejaculation in these monkeys. In the present study, on three occasions in the wet season, a capuchin female mounting with a subordinate male in the presence of the alpha male rapidly resulted in the alpha male mounting the same female. However, during the dry season, a female's approach and sexual pursuit of the alpha male after a mount with a subordinate male never resulted in an alpha male mount of that female ($n=5$). On two of these occasions, the alpha male was already in consortship with another female, and on two others it was the female in consort with the alpha male that left him, copulated with another male, and then returned directly to him. This further suggests limitations to the number of ejaculations a male can perform.

The mating success of the alpha male, in terms of copulation frequency, was no different from that of two other adult males in the group, in either the dry or wet season, despite overwhelming bias toward the alpha male in the number and duration of consortships received from females. The alpha male rarely initiated sexual interaction with females, showed a significantly longer latency to first

mount once sexual behavior had been initiated, copulated exclusively in the context of a lengthy consortship, and usually had a multimount style of copulation. In contrast, some subordinate males showed more initiative in soliciting females, were faster to mount, and employed a variety of alternative mating strategies and more variable copulatory behavior, using both single- and multimount series. A similar pattern was found in guinea pigs (*Cavia* spp.) [Rood, 1972], in which the alpha male was a multimount ejaculator but subordinate males ejaculated during the first mount. Rood [1972] argued that subordinate guinea pig males were able to ejaculate much more quickly both because they were more highly aroused and because they had fewer opportunities to copulate than the alpha male. As predicted in the reproductive constraint model, the subordinate male capuchins, which received significantly less frequent solicitations by proceptive females, were ready to act sexually at any given opportunity, and in some cases even solicited females directly.

Some other primates also show variation in copulation type based on rank. Tibetan macaques (*Macaca thibetana*) are characterized by a multiple mount-to-ejaculation pattern, but in hidden matings (usually by low-ranking males), ejaculation normally occurs in a single mount [Zhao, 1993]. Although the rhesus macaque (*Macaca mulatta*) is a multimount ejaculator [Shively et al., 1982], field observations have shown that subordinate males employ a sneaky strategy characterized by brief matings out of sight of other group members [Berard et al., 1994; Manson, 1996]. Subordinate rhesus males employ this tactic as a form of indirect mating competition against the more-dominant males, and DNA fingerprinting has revealed that these sneaky matings can be successful [Berard et al., 1990, 1994]. It remains unknown whether capuchin monkey single-mount matings are fertile, or how frequently subordinate males sire offspring. Preliminary evidence from captivity shows that in at least one case, the lightest and least dominant *C. apella* male (n=3) was the most potent, with the highest spermatozoa concentration and motility reading [Bush et al., 1975]. However, paternity data from wild *Cebus capucinus* suggest that alpha males in that species have a substantial (but not complete) reproductive advantage [Jack & Fedigan, 2003; Muniz et al., 2004].

Male Reproductive Constraints on Ejaculatory Frequency: Phylogenetic Inertia?

Some characteristics of male capuchin sexual activity suggest limited male sexual response throughout the year. The alpha male's reluctance to mate during consortship, and the alpha male's tolerance of other males mating in his presence on days with more than one proceptive female may be related to sperm depletion [Small, 1988]. If males are constrained in the number of ejaculations they can perform per day [Dewsbury 1982; Dixson, 1995], they may need to time their copulations carefully.

Interestingly, not only *Cebus apella* [Carosi & Visalberghi, 2002], but also *Cebus olivaceus* (Robinson, personal communication, in Dewsbury and Pierce [1989]) and the sister taxon to *Cebus* [Rylands et al., 2000], the squirrel monkey (*Saimiri sciureus* [Clewe & DuVall, 1966; Wilson, 1977]), have unusually long ejaculatory intervals for primates. *Cebus capucinus* is also reported to have low rates of sexual activity. Only 15 copulations by adult males in a group with four sexually active females were noted in 220 focal observation hours at Lomas Barbudal Biological Reserve, Costa Rica [Manson et al., 1997; Perry, 1997], and only 30 copulations from April 1995 to January 1996 in one 14–17-individual

group with four sexually active females, and four adult and three subadult males were observed at Palo Verde, Costa Rica [Panger, 1997]. According to Dixon [1998], the vast majority of primates are able to have more than one ejaculation per hour, but the *Cebus/Saimiri* clade appears to be an exception to this rule (see Carosi and Visalberghi [2002] for captive data on *C. apella*). The *Cebus/Saimiri* clade is placed taxonomically with the owl monkey (*Aotus*) [Fleagle, 1999; Schneider et al., 1996]. This genus is considered to be strictly monogamous, and, as expected, *Aotus* males have relatively long ejaculatory intervals and a very low rate of spermatogenesis [Dixon, 1998]. Perhaps there are phylogenetic constraints on copulatory rates in the *Cebus/Saimiri* clade. Although they live in multimale groups, *C. olivaceus* [Robinson & Janson, 1987] and the Peruvian *C. apella* [Janson, 1984] behave de facto like unimale groups, with one male receiving overwhelming female preference and a high percentage (if not all) of the copulations. In large squirrel monkey (*Saimiri oerstedii*) groups, adult females also show a significant preference for one dominant male [Boinski, 1987]. A low ejaculatory frequency is expected for unimale groups, in which males are not faced with sperm competition [Dixon, 1995]. Even Perry's [1997] study of the promiscuous *C. capucinus* found a very low rate of potentially fertile copulations, and a high rate of nonconceptive sex [see Manson et al., 1997]. Paternity tests and specific studies on sexual behavior in wild capuchin groups are needed to determine, for example, whether *C. olivaceus* troops with large group sizes are in fact strictly unimale in terms of reproduction (as suggested by Robinson and Janson [1987]), and whether the mounts by subordinate or subadult males are indeed fertile in *C. apella*.

Male Mate Choice in the Timing of Copulations

If capuchin males are constrained in the number of ejaculations they can produce each day, then timing in response to sperm competition may be crucial. In many animal species, there is an order effect (i.e., either the first ejaculation or the last ejaculation in a series is the most likely to produce offspring) [Dewsbury, 1982]. Compared to other mammalian sperm, capuchin semen is unusual in that virtually all of it is ejaculated into a coagulated mass, and all spermatozoa are contained within that coagulum [Bush et al., 1975; Nagle & Denari, 1982]. Females can retain this vaginal plug for up to 12 hr if it is not disturbed, and the coagulum appears to liquefy slowly and release sperm gradually [Bush et al., 1975]. In the present study, coagulated pieces of ejaculate were observed coming out of a female's vagina during rapid sequential matings. The second male's mount series may dislodge prior ejaculate from the female's vagina. An evolutionary advantage to multimount mating may be that these repeated intromissions facilitate the breakup and expulsion of prior ejaculates [Sauther et al., 1999]. Thus, the order of male copulations may be a crucial determinant of reproductive success in this genus. If in fact "last is best" for capuchin males, then consortship may be a complex "waiting game" from the alpha male's perspective. He may monitor other male's sexual behavior and prefer to mate with the females after the other males have ejaculated for that day. Alternatively, once the alpha male ejaculates, there may be a lengthy and compulsory refractory period in which he is unable to perform more copulations, despite female solicitation. In this context, it is relevant to note that while alpha males have been labeled as "choosy," they eventually mate with virtually all females that solicit them. The choosiness, then, may be more related to timing, and male reproductive constraints, than to a preference for individual females. In light of

the nonfertile proceptive displays exhibited by females during much of the year, the alpha male's choosiness may also be a means of testing how fertile a female is by assessing her persistence at sexual solicitations.

Postcopulatory Display as Sperm Competition

The duration of postcopulatory display was significantly longer in the dry season, when females were most fertile. Postcopulatory display may be a form of sperm competition, as a male strategy to delay females from soliciting or copulating with other males [Parker, 1974]. In contrast to their reluctant participation in consortships, the males were very active in postcopulatory displays, which may ensure that their sperm is not quickly displaced by other males after copulation. Matthews and Adler [1977] found that transcervical sperm transport in rats required 6–10 min after ejaculation for completion, and that even a single intromission 2 min after ejaculation could dislodge the vaginal plug and disrupt sperm transport. Busey and Estep [1984] speculated that male pigtail macaques may interfere with one another's sperm in much the same way. Ring-tailed lemurs (*Lemur catta*) form consort pairs *after* copulation [Jolly, 1967], and male postcopulatory guarding of females may last for up to an hour [Sauther & Sussman, 1993; Sauther et al., 1999]. Lemur males cease to mount females after a single ejaculation, and postcopulatory guarding is thought to be a strategy to keep the copulatory plug intact [Sauther et al., 1999]. Postcopulatory display may be a mate-guarding behavior that protects sperm from displacement by other males in capuchin monkeys as well.

ACKNOWLEDGMENTS

I thank K.B. Strier (University of Wisconsin–Madison), J. Rímoli (Universidade Católica Dom Bosco), D. Morales Torres (Universidad Veracruzana), and S. Lucena Mendes (Museo de Biología Mello Leitão and Universidad Federal do Espírito Santo). Work at Caratinga was made a pleasure by A. Guimarães, A. Silene Oliva, L. Teixeira Dib, R. Ribeiro dos Santos, J. Gomez, E. Veado, and the EBC staff. The presentation of an earlier version of this paper at the 1998 American Association of Physical Anthropology meetings was funded by the University of Wisconsin–Madison's Department of Anthropology. I am grateful for comments on the manuscript by D. Abbott, H. Bunn, M. Carosi, L.M. Fedigan, G. Linn, J.H. Manson, R. Sherwood, C. Snowdon, K.B. Strier, T.E. Ziegler, and one anonymous reviewer.

REFERENCES

- Altmann J. 1974. Observational study of behaviour: sampling methods. *Behaviour* 49:227–265.
- Berard J, Schmidtke G, McGeehan L. 1990. Male reproductive success in a free-ranging colony of rhesus macaques. *Am J Primatol* 20:173.
- Berard JD, Nurnberg P, Eppelen JT, Schmidtke J. 1994. Alternative reproductive tactics and reproductive success in male rhesus macaques. *Behaviour* 129:177–201.
- Bercovitch F. 1987. Reproductive success in male savanna baboons. *Behav Ecol Sociobiol* 21:163–172.
- Blaffer Hrdy S. 1977. *The langurs of Abu*. Cambridge: Harvard University Press. 361p.
- Boinski S. 1987. Mating patterns in squirrel monkeys (*Saimiri oerstedii*): implications for seasonal sexual dimorphism. *Behav Ecol Sociobiol* 21:13–21.
- Busey CD, Estep DQ. 1984. Sexual arousal in male pigtailed monkeys (*Macaca*

- nemestrina*): effects of serial matings by two males. *J Comp Psychol* 98:227–231.
- Bush DE, Russell Jr LH, Flowers AI, Sorensen Jr AM. 1975. Semen evaluation in capuchin monkeys (*Cebus apella*). *Lab Anim Sci* 25: 588–593.
- Carosi M, Visalberghi E. 2002. Analysis of tufted capuchin (*Cebus apella*) courtship and sexual behavior repertoire: changes throughout the female cycle and female interindividual differences. *Am J Phys Anthropol* 118:11–24.
- Clewe TH, DuVall WM. 1966. Observations on frequency of ejaculation of squirrel monkeys, *Saimiri sciureus*. *Am Zool* 6:411.
- Defler TR. 1979. On the ecology and behavior of *Cebus albifrons* in eastern Colombia. *Primates* 20:475–502.
- Dewsbury DA. 1982. Ejaculate cost and male choice. *Am Nat* 119:601–610.
- Dewsbury DA, Pierce JD. 1989. Copulatory patterns of primates as viewed in broad mammalian perspective. *Am J Primatol* 17: 51–72.
- Di Bitetti MS. 1997. Evidence for an important social role of allogrooming in a platyrrhine primate. *Anim Behav* 54:199–211.
- Di Bitetti MS, Janson CH. 2000. When will the stork arrive? Patterns of birth seasonality in neotropical primates. *Am J Primatol* 50: 109–130.
- Di Bitetti MS, Janson CH. 2001. Reproductive socioecology of tufted capuchins (*Cebus apella nigrinus*) in northeastern Argentina. *Int J Primatol* 22:127–142.
- Dixon AF. 1995. Sexual selection and ejaculatory frequencies in primates. *Folia Primatol* 64:146–152.
- Dixon AF. 1998. Primate sexuality: comparative studies of the prosimians, monkeys, apes and human beings. Oxford: Oxford University Press. 546p.
- Fleagle JG. 1999. Primate adaptation and evolution. San Diego: Academic Press. 596p.
- Izawa K. 1980. Social behavior of the wild black-capped capuchin (*Cebus apella*). *Primates* 21:443–467.
- Jack K, Fedigan L. 2003. Male dominance and reproductive success in white-faced capuchins (*Cebus capucinus*). *Am J Phys Anthropol Suppl* 36:121–122.
- Janson C. 1984. Female choice and mating system of the brown capuchin monkey *Cebus apella*. *Z Tierpsychol* 65: 177–200.
- Janson C. 1986. The mating system as a determinant of social evolution in capuchin monkeys (*Cebus apella*). In: Else JG, Lee PC, editors. Primate ecology and conservation. New York: Cambridge University Press. p 169–179.
- Janson C. 1998. Capuchin counterpoint. In: Ciochon RL, Nisbett RA, editors. The primate anthology. Upper Saddle River, NJ: Prentice Hall. p 153–160.
- Jolly A. 1967. Breeding synchrony in wild *Lemur catta*. In: Altmann SA, editor. Social communication among primates. Chicago: University of Chicago Press. p 3–14.
- Linn G, Mase D, LaFrancois D, O'Keefe R, Lifshitz K. 1995. Social and menstrual cycle phase influences on the behavior of group-housed *Cebus apella*. *Am J Primatol* 35:41–57.
- Lynch JW, Rimoli J. 2000. Demography of a group of tufted capuchin monkeys (*Cebus apella nigrinus*) at the Estação Biológica de Caratinga, Minas Gerais, Brazil. *Neotrop Primates* 8:44–49.
- Lynch JW. 2001. Male social behavior and endocrinology in wild tufted capuchin monkeys, *Cebus apella nigrinus*. Ph.D. thesis, University of Wisconsin–Madison, Madison, WI.
- Lynch JW, Ziegler TE, Strier KB. 2002. Individual and seasonal variation in fecal testosterone and cortisol levels of wild male tufted capuchin monkeys, *Cebus apella nigrinus*. *Horm Behav* 41:275–287.
- Manson JH. 1994. Female mate choice in primates. *Evol Anthropol* 3:192–195.
- Manson JH. 1996. Male dominance and mount series duration in Cayo Santiago rhesus macaques. *Anim Behav* 51:1219–1231.
- Manson JH. 1997. Primate consortships: a critical review. *Curr Anthropol* 38:353–374.
- Manson JH, Perry S, Parish A. 1997. Non-conceptive sexual behavior in bonobos and capuchins. *Int J Primatol* 18:767–786.
- Matthews M, Adler NT. 1977. Facilitative and inhibitory influences of reproductive behavior on sperm transport in rats. *J Comp Physiol Psychol* 91:727–741.
- Meisel RL, Sachs BD. 1994. The physiology of male sexual behavior. In: Knobil E, Neill JD, editors. The physiology of reproduction. 2nd ed. New York: Raven Press. p 3–105.
- Muniz LSB, Perry S, Manson JH, Gros-Louis J, Vigilant L. 2004. Genetic assessment of male reproductive success in wild white-faced capuchin monkeys. *Folia Primatol* 75(suppl 1):310.
- Nagle CA, Denari JH. 1982. The reproductive biology of capuchin monkeys. *Int Zoo Yearb* 22:143–150.
- Panger MA. 1997. Hand preference and object-use in free-ranging white faced capuchin monkeys (*Cebus capucinus*) in Costa Rica. Ph.D. dissertation, University of California–Berkeley, Berkeley, CA.
- Parker GA. 1974. Courtship persistence and female-guarding as male time investment strategies. *Behaviour* 48:157–184.
- Perry S. 1995. Social relationships in wild white-faced capuchin monkeys, *Cebus capucinus*. Ph.D. dissertation, University of Michigan, Ann Arbor, MI.

- Perry S. 1997. Male-female social relationships in wild white-faced capuchins (*Cebus capucinus*). *Behaviour* 134:477-510.
- Phillips K, Bernstein I, Dettmer E, Devermann H, Powers M. 1994. Sexual behavior in brown capuchins (*Cebus apella*). *Int J Primatol* 15:907-917.
- Rímoli J, Ferrari SF. 1997. Comportamento e ecologia de macacos-prego (*Cebus apella nigrilus*, Goldfuss, 1809) na Estação Biológica de Caratinga (MG). Programa e Resumos, VIII Congresso Brasileiro de Primatologia, João Pessoa, Paraíba. 231p.
- Robinson JG, Janson CH. 1987. Capuchins, squirrel monkeys, and atelines: socioecological convergence with Old World primates. In: Smuts B, Cheney D, Seyfarth R, Wrangham R, Struhsaker T, editors. *Primate societies*. Chicago: University of Chicago Press. p 69-82.
- Robinson JG. 1988. Group size in wedge-capped capuchin monkeys *Cebus olivaceus* and the reproductive success of males and females. *Behav Ecol Sociobiol* 23:187-197.
- Rood JP. 1972. Ecological and behavioral comparisons of three genera of Argentine caviés. *Anim Behav Monogr* 5:1-82.
- Rylands AB, Schneider H, Langguth A, Mittermeier RA, Groves CP, Rodríguez-Luna E. 2000. An assessment of the diversity of New World primates. *Neotrop Primates* 8:61-93.
- Sauther ML, Sussman RW. 1993. A new interpretation of the social organization and mating system of the ringtailed lemur (*Lemur catta*). In: Kappeler PM, Ganzhorn JU, editors. *Lemur social systems and their ecological basis*. New York: Plenum Press. p 111-121.
- Sauther ML, Sussman RW, Gould L. 1999. The socioecology of the ringtailed lemur: thirty-five years of research. *Evol Anthropol* 8:120-132.
- Schneider H, Sampaio I, Harada ML, Barroso CML, Schneider MPC, Czelusniak J, Goodman M. 1996. Molecular phylogeny of the New World monkeys (Platyrrhini, Primates) based on two unlinked nuclear genes: IRBP Intron 1 and ϵ -globin sequences. *Am J Phys Anthropol* 100:153-179.
- Shively C, Clarke S, King N, Schapiro S, Mitchell G. 1982. Patterns of sexual behavior in male macaques. *Am J Primatol* 2: 373-384.
- Small M. 1988. Female primate sexual behavior and conception: are there really sperm to spare? *Curr Anthropol* 29:81-100.
- Smuts B. 1987. Sexual competition and mate choice. In: Smuts B, Cheney D, Seyfarth R, Wrangham R, Struhsaker T, editors. *Primate societies*. Chicago: University of Chicago Press. p 385-399.
- Strier KB, Ziegler TE, Wittwer DJ. 1999. Seasonal and social correlates of fecal testosterone and cortisol levels in wild male muriquis (*Brachyteles arachnoides*). *Horm Behav* 35:125-134.
- Welker C, Höhmann H, Schäfer-Witt C. 1990. Significance of kin relations and individual preferences in the social behaviour of *Cebus apella*. *Folia Primatol* 54:166-170.
- Wilson MI. 1977. Characterization of the oestrous cycle and mating season of squirrel monkeys from copulatory behaviour. *J Reprod Fertil* 51:57-63.
- Wright EM, Bush DE. 1977. The reproductive cycle of the capuchin (*Cebus apella*). *Lab Anim Sci* 27:651-654.
- Zhao Q. 1993. Sexual behavior of Tibetan macaques at Mt. Emei, China. *Primates* 34:431-444.