RESEARCH ARTICLE

Infanticide in Black Capuchin Monkeys (*Cebus apella nigritus*) in Iguazú National Park, Argentina

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We report here one observed and two potential cases of infanticide during a brief period of 1 month after a dominant male replacement in one group of black capuchin monkeys in Iguazú National Park, Argentina. We also compile infant disappearances and demographic data in seven groups followed from 1–14 years. Behavioral and molecular data showed that the probability that an infanticidal male would kill his own progeny is very low in this species. Females that lost infants less than 6 months old had shorter interbirth intervals than females whose infants survived (14.12 ± 5.32 months, $n = 17$ vs. 20.42 ± 5.65 months, $n = 34$). Females whose infants die shortly after takeovers mate with the presumed infanticidal male during the most fertile days of their subsequent estrous periods giving this male a high probability of siring the new progeny. We recorded 181 proceptive periods and 52 births from 18 adult females in two groups. Most proceptive periods were concentrated during a conception season, but there was an increase in sexual behavior after male takeovers. Seven females copulated while pregnant after the observed male takeover, an unusual behavior in this species in years of group stability. Of 24 infants born during takeover years, 62.5% did not survive the first year, whereas only 22.5% of 80 infants died in years without male replacements. We found a significant positive association between infant mortality and male takeovers, but not with food provisioning. The main cause of infant mortality in this population is associated with male takeovers. Our results suggest that infanticide can have an important effect on the behavior of this species, selecting for female behaviors that function to reduce infanticide risk. Am. J. Primatol. 70:473–484, 2008. © 2008 Wiley-Liss, Inc.

INTRODUCTION

Infanticide has been accepted recently as a strong selective force that can shape the behavior of many primate species [Janson & van Schaik, 2000]. Nevertheless, observed cases of infanticide are still relatively uncommon [for a review, see van Schaik, 2000a]. For capuchin monkeys, infanticide has been reported for white-faced capuchins, *Cebus capucinus* [Fedigan, 1993, 2003; MacKinnon, 2003; Manson et al., 2004; Rose, 1994], wedge-caped capuchins, *C. olivaceous* [Valderrama et al., 1990], and suggested for *C. apella* [Izawa, 1994].

Infanticide among wild primates may be explained by the sexual selection hypothesis, which states that males committing infanticide will on average increase their reproductive success by doing so [Janson & van Schaik, 2000; van Schaik, 2000a]. This hypothesis predicts that for infanticide to be an adaptive male reproductive strategy: (a) the probability that the infanticidal male sired the victim(s) is zero or close to zero; (b) the victim's mother can be impregnated earlier than if the infant(s) had lived; and (c) the infanticidal male is likely to sire the victim's mother's next infant. All these conditions must be met simultaneously. Other alternative hypotheses and their predictions are summarized in Table I.

Most cases of male infanticide in natural populations take place when a reproductive male becomes dominant either by rising in rank within his

TABLE I. Alternative Hypotheses to the Sexual Selection Hypothesis for Infanticide by Males

Hypothesis	Source	Description	Predictions
Social pathology	Boggess [1979]	Infanticide is a maladaptative behavior of males that are "psychologically" disturbed because of anthropogenic effects on the habitat	Males will not be selective in their attacks. Infanticide will occur only in disturbed habitats
Infanticide as a by-product of male aggression	Bartlett et al. [1993]	Infants are killed inadvertently as a consequence of generally increased aggression resulting from rank instability among males	Males will not be selective in their attacks. Females without infants will suffer as much aggression as females with infants
Cannibalism	van Schaik [2000a]	Infanticidal males obtain nutritional benefits by consuming the infant	Infanticidal males will consume the infants they kill
Resource competition	Rudran [1973] and Agoramoorthy and Rudran [1995]	Infanticide results in increased access to limiting resources for the killer and his descendants	Juveniles should also be killed, as they consume more resources and can be easily killed
Adoption avoidance	Sherman [1981] and Elwood and Ostermeyer [1984]	Infanticidal males avoid misdirecting parental care	Infanticide will be expected most often in species where males show extensive parental care
Elimination of future rivals	Hiraiwa-Hasegawa and Hasegawa [1994]	Infanticide eliminates future competitors for access to mates for the resident male or for his offspring	Male infants will be killed exclusively

Note: Extracted with citations from van Schaik, 2000a.

own group or by immigrating and defeating the resident male in a different group [van Schaik, 2000b]. Many infants survive periods of high infanticide risk, possibly owing to defense by mothers and allomothers (including attacking or avoiding potentially infanticidal males) or defense of infants by their fathers [van Schaik, 2000b]. In cases when the risk of infanticide comes mainly from inside the group, a plausible female anti-infanticide behavior is to mate promiscuously, which may confuse paternity, especially when coupled with extended periods of sexual activity and concealed ovulation [Heistermann et al., 2001]. However, the mere fact of having mated with a female is not enough for a male to avoid committing infanticide [Hasegawa, 1989], and both the relative frequency of mating and its timing may also play a role in the decision of the infanticidal males [van Schaik, 2000a]. Mating during pregnancy can also prevent infanticide [Hrdy, 1979; van Schaik et al., 1999].

Capuchin monkeys are distinguished among primates by having relatively slow development. Data on weaning ages in the wild are very limited. In captivity, the estimated time of weaning varies from 10.8 to 20.5 months depending on the criteria used to define weaning [Fragaszy & Adams-Curtis, 1998; Weaver, 1999; quoted in Fragaszy et al., 2004]. Gestation length in nature ranges from 149 to 158 days [Di Bitetti & Janson, 2001a; Robinson & Janson, 1987]. In general, females give birth once every 2 years if the previous progeny survives until the age of weaning, but a female can have infants in successive years, especially if its current offspring dies early [<3–9 months; Di Bitetti & Janson, 2001a]. Thus, infanticidal dominant males should

gain a reproductive advantage by killing unweaned infants before the breeding season, accelerating a female's conception of the new male's infant.

Here we report one observed and one inferred case of infanticide, and an additional healthy infant disappearance, during a brief period of 1 month in one group of black capuchin monkeys in Iguazú National Park, Argentina. We also report infant disappearances associated with male takeovers in eight groups and some associated changes in the behavior of adult females (AdF) that could be interpreted as infanticide avoidance. We present demographic data to assess the importance of male takeovers on infant mortality.

METHODS

Study Area

The study took place in Iguazú National Park, Argentina (25°40′43″S, 54°26′57″W). The region is part of the Upper Paraná Atlantic Forest [Giraudo et al., 2003] and has a humid subtropical climate. There is a marked seasonal pattern in the abundance of leaves, flowers, fruit and arthropods. Fleshy fruits and arthropods, the most important resources for capuchin monkeys, are most scarce in winter (July–August) and reach a peak of abundance during spring and early summer [September–December; Di Bitetti, 2001a,b; Di Bitetti & Janson, 2001a; Janson, 1996; Placci et al., 1994]. For further details about the site, see Crespo [1982], Placci et al. [1994], Janson and Di Bitetti [1997], Di Bitetti [2001a] and Di Bitetti and Janson [2001a].

Possible monkey predators at the study site are crested eagles (*Morphnus guianensis*), black hawk-

eagles (*Spizaetus tyrannus*), ornate hawk-eagles (*S. ornatus*), jaguarundis (*Puma yaguarondi*), oncillas (*Leopardus tigrinus*), margays (*L. wiedii*), ocelots (*L. pardalis*), pumas (*P. concolor*), jaguars (*Panthera onca*) and tayras (*Eira barbara*). No large boas are present at this site. Possible anthropogenic habitat disturbances inside the study area are visits by tourists, noise from a road in the border of the territory and helicopter flights at 500 m height.

Study Subjects

Black capuchin monkeys (*C. apella nigritus*) are omnivorous primates, with a diet consisting mainly of fruits and arthropods [Brown & Zunino, 1990; Robinson & Janson, 1987]. The most recent classifications of the genus *Cebus* have raised this subspecies to the species *C. nigritus* [Groves, 2001; Rylands et al., 2000]. They live in multimale–multifemale polygamous groups, typically consisting of between seven and 40 individuals [Agostini & Visalberghi, 2005; Di Bitetti, 2001a]. There are generally two or more adult males (AdM) in a group, but a single male occupies a central role and can control access to food sources through aggression [Janson, 1985]. Females are philopatric, with linear dominance hierarchies [Di Bitetti, 1997; Janson, 1985]. The mating system of wild capuchin monkeys (*C. apella*) was studied by Janson [1984] in a Peruvian rainforest. In eight completely observed cases in two social groups, estrous periods last from 5 to 6 days. During the first 3–4 days, the female continuously follows the dominant male of the group, while conspicuously soliciting copulation by approaching him with grimaces, distinctive vocalizations and submissive like postures. On the next day, the female begins to solicit copulations from subordinate males, but the dominant male aggressively prevents other males from approaching her. During the remainder of the estrous period the dominant male stops following the female, who then copulates with up to six subordinate males in a single day. Ovulation occurs on the last day (± 1 day) of proceptive behavior [Carosi et al., 1999] and it can be assumed that, as in humans [Barrett & Marshall, 1969], the peak of fertility in capuchins precedes ovulation. Thus, the probability that the dominant male fertilizes the female is not only enhanced by his higher frequency and duration of copulations, but also by their timing, as he has almost exclusive access to females during the period of maximum fertility. Genetic evidence confirmed the inferences derived from these behavioral observations. Escobar-Páramo [1999] established paternity relationships in *C. apella* using microsatellite markers on DNA extracted from feces. She sampled a wild group (MC-1 from Macarena—Colombia) with four adult males and three adult females, another wild group (Macuco from Iguazú—Argentina) with three AdM and six AdF and one captive group (from the colony of the animal center at National Institute of Health—USA) with four AdM and four AdF. Her results support the assumption that the α male fathered all of the infants in a group, except for those born to his daughters. The Macuco group studied by Escobar-Páramo is the same group about which this report is written, studied several years before the specific events described below. Studies in captivity also show that female mate choice in *C. apella* is oriented toward the dominant male of a group and that the species has reproductive mechanisms (such as higher copulation and ejaculation rates, greater mating duration, longer post-copulatory courtships, ejaculations concentrated in the periovulatory period for dominant than subordinate males) to enhance reproduction by him [Nagle & Denari, 1982; Welker et al., 1990; unpublished work by Carosi, Dal Secco, Moltedo and Visalberghi in Fragaszy et al., 2004].

Females typically remain in their natal groups, whereas males disperse between 5 and 9 years of age [Di Bitetti & Janson, unpublished]. Females begin their estrous cycles in February–March, and few females are receptive after August. Births are very seasonal in Iguazú, occurring between the beginning of October and the end of February, during the peak availability of fruits and insects [Di Bitetti & Janson, 2001a]. Unlike several described populations of brown capuchin monkeys, females in Iguazú sometimes give birth in consecutive years even if their previous infant survives. This pattern results in a relatively short (compared with other capuchin populations) interbirth interval (IBI) of 19.35 months.

Data Collection and Analysis

We focused our observations on eight groups that ranged in an area of *ca.* 6 km^2 (see Fig. 1 for information on the schedule and intensity of the followings). We recognized individuals by their size, tuft shape, color patterns, scars and behavior. This allowed us to follow individuals through time and to recognize the presence or absence of new individuals in a group. We could chart infant–mother relationships for all individual less than 14 years old in the main study group ("Macuco") and in two groups that broke away from the Macuco group ("Gundolf" and "Rita").

The Macuco group was provisioned daily with tangerines and bananas during the winters of 1992 and 1995 to 2006 as part of experimental studies by Janson and coworkers [Di Bitetti, 2003, 2005; Di Bitetti & Janson, 2001b; Janson, 1996, 1998; Janson & Di Bitetti, 1997].

We recorded conspicuous female pregnancies whenever possible. By following our sampling procedure, very few births could have been missed because pregnancy is usually evident 1 month before delivery.

Group/Year	91	92	93	94	95	96	97	98	99	00	01	02	03	04	05	06
Yacaratia																
Laboratorio																
Macuco																
Silver																
Rubias																
Barrio																
Gundolf																
Rita																

Fig. 1. Groups observed and intensity of the observations. ■■■■, continuous following from dawn to dusk with only a few days of interruption; ▤▤▤, censuses of between 3 hr and 7 days; ▨ ▨ ▨, sporadic censuses; ≡≡≡, continuous following from dawn to dusk from 2 days a week to 2 days a month.

We estimated conception date by counting back 5 months from the birth date. We used behavior sampling [Martin & Bateson, 1993] to record female proceptivity (sexual solicitation toward a male) and the males they followed and copulated with. We recognized proceptive periods by the display of behaviors such as eyebrow rising, chest rubbing, grimaces of the female directed to the male, and estrous calls [Carosi et al., 1999; Di Bitetti, 2001b; Fragaszy et al., 2004; Janson, 1984]. Proceptive periods could have been missed if the group was not contacted during more than 6 days, if they were very short or inconspicuous or if the female temporarily left the group with a subordinate male. In this study we do not discriminate the amount or timing of matings with different males. In order to draw proceptive periods on a timeline, we used the middle day of a period in which a female exhibited proceptive behaviors.

Focal sampling was typically used to collect data on infant behavior; however, when the infanticidal attacks took place, focal sampling was discontinued in order to observe more individuals, and we followed a continuous and opportunistic recording protocol.

To test whether the IBIs for females whose infant did not survive more than 6 months were shorter than the IBIs for females whose infants did survive, we performed a one-tailed Wilcoxon test. We used the G-test to determine whether infant mortality was independent of male replacement events and of food provisioning. We used a type I error confidence limit (α level) of 0.05.

RESULTS

During August 2004, the Macuco group went through a splitting process that lasted for at least 1 month and produced two groups: the Gundolf group, which moved to a new area, and the Macuco group, which remained in the original home range. After the split, the Macuco group was composed of five AdM, nine AdF, eight juvenile males, seven juvenile females and eight infants (Appendix A(c)). None of the AdF that gave birth during the subsequent birth season were daughters of the dominant male (GE) [Escobar-Páramo, 1999], and therefore based on results from previous studies we assume that he had high probabilities of siring their infants.

On August 22, 2004, the α (GE) and the β male (ALS) exhibited severe injures. On August 24, 2004, the α male was attacked simultaneously (and presumably killed) by the third (MAR) and fourth (HOM) ranking males. MAR and HOM were injured during the attack. MAR started behaving as the dominant male almost immediately after the decisive fight. ALS remained in the group in a peripheral position, slowly recovering from his wounds. ALS fought and defeated MAR for the dominant position in the group on December 23, 2004. The period from August 22, 2004, until the end of January 2005 was socially unstable. Three AdF at different times broke away from the main group and formed temporary subgroups with different non-dominant AdM of the Macuco group. During this period, normally past the mating season, there was a burst of sexual activity in the Macuco Group, in which seven out of nine females were seen displaying proceptive behaviors and copulating with different males (Fig. 2). Meanwhile, no female out of four in the Gundolf group exhibited such behaviors during the same time period. Infants were born between October 17, 2004, and January 6, 2005 (Fig. 2). They were sired between middle May and early August, when GE was still the α male and therefore had a high probability of being the infant's father. The fates of these infants are described below.

Fig. 2. Reproductive behavior of the Macuco group females between June 1997 and June 2005. Months in which only censuses were performed are shadowed in gray. C, infant conceived; ····, gestation period; B, infant born; B̲, infant for whom infanticide was expected under the sexual selection hypothesis; ?, infant whose birth date is not accurately known; —, infant alive; †, infant killed or disappeared; →, infant that remained alive; Em, female emigrated; ‖, male takeover. Female observed in estrous, soliciting or mating with [1], DE; [2], GE; [3], AF; [4], GD; [5], ALS; [6], MAR; [7], HOM.

Year	'97							'98												'99			
Month		Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Abr
F2	†				1	2				1			1	C[1] 2,3					B			1		→
GR			1									1	2	C[1]					B					→
GU			1		C[1]				B			3	1 2	1				2						
DO	† C				2 †B†		2		3	1 2		1						C[1]		B				→
SP							2		2			2	3	C					B†2,1					
WC		C			2	B							2	2										
TH		C[2]			2	B																		
YO																	2							
RI														3			2	3, 2						
LU									3			3					3							
α Male			DE[1]			GE[2]	DE[1]																	

Year	'99							'00											'01					
Month	May	Jun	Jul	Aug	Sep	Oct	Nov		May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug
F2	→	2,3	?		2			→	2	2		2			4		2		2					
GR	→										C				B									4
GU		1 C[1]				B	†		C			B												2
DO		3	†2						2	2	2		2		5					2,4				
SP		3							C			B										2	C	
WC		C 2,3				B		→ C			B	†							2					
TH		C[1]				B†			2	2 C			B									2	2	
YO		2	?			†			2 C			B										4	2	
RI		C				B 2		→	2	2	2				5		5,4	4,5		C				
LU		C				B	†					5								C				
MG		3,2							2 C			B												
GO				2					C			B										C 2,5		
MA									C			B												
CL									2 2 2	2														
α Male	DE[1]		GE[2]																					

Year	'01				'02							'03												
Month	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug
GR									2,4	C					B							→		
GU		4,2							2 C						B							→	2,5	4 C
DO	C				B																			
SP					B			→		5		5 5	5						5	4,5 C[2]				
WC								4	C		4		2		B						5			
TH								4,5 2	2									2 C		2				
YO		2						4	2,5	C				B					4	2	C			
RI			B							4,5	4	2,5		2	4				2,4,5	2,4,5	2 C			
LU					B	†		4		4									4,5	C				
MG								5,6	2	C					B	†			4 5	C				
GO				B				→																
CL								5 5,4	5,2,4	4,5					4,5		6,5	5,4				C		
WE								5		2				5		5	2,5,4	C						
GRE								5	4,2 C				B				5	5 2						
GV								4			4				4,5	2,4,5	4,2 C							
UR																2	6 2,4	C						
α Male									GE[2]															

Year				'04									'05											
Month	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun		
GR									C					B[6]			†				5			
GU				B				→			4,5	5 5					Em							
SP			B					→									7,5							
WC	4								C		Em													
TH		B					→		C			B[6]				†	5	7	5					
YO				B				→		2	C	6	6		B†5		5		5	5				
RI			B				→		C	6	6			B			Em							
LU		B		†			→		C		Em													
MG		B					→					6			6 5									
CL			B				→			6 2	2	6							5					
WE		B					→		Em															
GV		B					→		Em															
UR			B				→										5 5							
α Male				GE[2]								MAR[6]					ALS[5]							

Study Cases

Case 1, female TH

On January 27, 2005, the infant was 8 weeks old. At 13:30 we saw the new dominant male (ALS) being chased by several monkeys (at least 10), although no physical contact was made and neither TH nor her infant showed any injuries. At 13:40 while we were focal sampling TH's infant, TH initiated a second chase toward ALS while carrying her infant dorsally. Once again several monkeys joined TH in the chasing, but stopped running shortly after. We followed ALS and TH as they ran and, although the foliage blocked our vision for some seconds, we were able to pin down their positions by their movements and saw them making and breaking contact very fast. When the subjects stopped moving, we saw ALS, TH and the eldest daughter of TH (EST) close to each other and we recorded no further aggression. The infant's jaw was displaced to one side, the lips were torn apart and the infant was still alive but unable to open his eyes. Neither TH nor ALS showed any wounds. TH and EST took turns carrying the infant. At 16:50 the infant was unable to hang onto his carriers back; TH carried him on one arm. The infant was giving loud calls that resembled whistles. At 16:55 the infant fell from his mothers arm to the ground and died. We examined the dead infant and took several pictures but did not collect the body. TH attempted to make the dead infant climb onto her back by pushing it slightly with her shoulder. TH lifted the body with one arm and placed it on a horizontal branch. In an attempt to force the infant onto her back, she dropped the body to the ground. She repeatedly lifted and dropped the body until dusk, when she and EST slept 200 m away from the rest of the group. The inspection of the infant's pictures taken after the attack showed a stab wound followed by a tear near the infant's right eye, presumably made with the male's upper right canine. The jaw was displaced, apparently by the male's upper left canine (Fig. 3a). The next day, TH was still carrying the dead body with one arm. In 5.5 hr of focal observation of TH and 3 hr of focal observation of ALS, ALS did not approach TH or attempt to remove the infant's body from her. TH was not seen again until January 31, 2005, when she was no longer carrying the dead infant. On February 7, 2005 (and again during April 15–17, 2005), she was in behavioral estrus soliciting ALS. She gave birth to a new infant on October 24, 2005. On October 31, 2005 and many later occasions, ALS was seen grooming this infant during group resting bouts. On the same day ALS and TH mated while the infant was on TH's back. On November 28, 2005, ALS was also seen carrying the infant for a brief period.

Case 2, female GR

On February 2, 2005, GR's infant was 15 weeks old. When we first contacted the group at 10:00 we

Fig. 3. Wounds exhibited by the dead infants: (a) Thelma carrying its dead infant whose mandible is displaced to the left, and the side of the mouth is thorn apart; (b) detail of the gluteus and lower belly region of Grumpy's infant showing wounds, presumably caused by canine bites. Both photos by Eduardo M. Rivero.

observed a deep wound in the infant's gluteus while it was being carried by GR. The infant was unable to hold on to her mother's back and fell to the ground at 12:30. GR picked her up and climbed to a tree carrying the infant in one arm. The infant fell again and died. The body was collected and preserved. The analysis of the body revealed profound puncture wounds, presumably bites produced by canines,

reaching the peritoneum (Fig. 3b). From June 10 to 12, 2005, GR displayed proceptive behavior soliciting ALS. She gave birth to a new infant on November 11, 2005.

Case 3, female YO

YO gave birth to an infant on January 6, 2005. On January 7 the group was lost because observations were focused on ALS and MAR who separated from the group as a result of ALS chasing MAR. When the group was relocated on January 14, 2005, both ALS and MAR were in the group and the infant of YO was absent. On January 17, 2005 (and again on February 21 , on April 22 and during May 18–20, 2005) YO was in behavioral estrus and copulated with ALS. She gave birth to a new infant between October 25 and 26, 2005. On October 30, 2005, we saw ALS grooming this infant and even allowing it to hang from its face. On November 16, 2005, ALS and YO mated while the infant was dorsal to YO. On November 27, 2005, ALS was seen carrying YO's infant.

Case 4, female RI

On February 2, 2005, the day GR's infant was killed, RI left the group with a four-year-old daughter, a 15-month-old son and her 6-week-old dependent infant. On February 3, 2005, she was joined by her mother (GU) and two sisters. On February 7, 2005, one AdM (CHA) left the main group. Another AdM (HOM) left it on February 12, 2005. The only subordinate male remaining in the main group (MAR) left it on February 16, 2005. All three males were observed moving with GU and her matriline on February 21, 2005; on this day RI solicited and copulated with MAR. HOM returned to the main group on March 7, 2005. Rita's infant survived at least until August 2007.

Other Infant Disappearances

Before the directly observed infanticide attack, we had registered infant disappearances associated with male takeovers in the Macuco group (Fig. 2). Group compositions before takeovers are indicated in Appendix A. Under the sexual selection hypothesis, we predicted infanticide for five out of the 13 infants born between 1997 and 1999 (Table II). Three of these cases were followed by infant disappearances. In the two cases where expected infanticides did not take place, the infants were both 7.8 months old.

We also recorded an increase in infant disappearances associated with male takeovers in the less-studied groups. We recorded three dominant male replacements in the seven less-studied groups over a pooled total of 13 observation years (range: 1–4 years per group). Overall, we followed 104 infants during their first year in eight groups over 1–14 years. Of 80 infants born in years without male replacement,

22.5% of them disappeared or died during the first year. Of 24 infants born in years with male replacements, 62.5% of them did not survive the first year. There is as a significant positive association between infant mortality and dominant male replacements $(G = 13.871, \quad df = 1, \quad P = 0.0002)$. Subtracting the mortality in years without takeovers from the mortality during takeover years, we conservatively estimate mortality associated with takeovers to be 40% of the infants born in years with male replacements. We recorded 10 male replacements during a pooled total of 48 complete years of observation of eight groups (1–14 years each group). This yields a takeover rate of 21% per year. On the basis of this takeover rate and mortality associated with takeovers, we estimate that at least 8.4% of all infants died for reasons associated with male takeovers.

We were only able to identify the sex of five of the 15 infants that disappeared during takeover years. Three of them were females and two were males. Four out of the nine infants that survived takeover years were females and five were males.

Sixty-four infants were born in the main study group during provisioning years; 68.8% of them survived the first year. Forty infants were born during non-provisioning years; 70% of them survived. Infant mortality was independent of food provisioning $(G = 0.018, df = 1, P = 0.893)$.

Interbirth Intervals

In the Macuco group, observed IBIs when the previous infant survived at least 6 months were 20.42 ± 5.65 months (mean $\pm$ SD, $n = 34$), whereas the IBIs after the death of infants ≤ 6 months old averaged only 14.12 ± 5.32 months $(n = 17)$ (Wilcoxon, one-tailed test, χ^2 approximation $= 14.127$, df $= 1$, $P < 0.001$). All the females whose infants disappeared during the 2004–2005 birth season gave birth to a new infant in the next breeding season, giving an average IBI of 11.58 ± 1.25 months $(n = 3)$.

Proceptive Behavior

From June 1997 to June 2005 we recorded 52 births and 181 proceptive periods from 18 AdF in the Macuco and Gundolf groups (Fig. 2). All births occurred from October 1 to February 28 (96% from October 1 to January 31). Females conceived, consequently, during May–September. Proceptive behaviors were concentrated between April and September (75% of recorded proceptive periods). During years with no male takeover, proceptive behavior between October and March was typically displayed only by females that did not conceive in the previous conceptive season (17 out of 20 cases of non-conceptive estrus). Females that conceived generally showed no further proceptive behavior (88% of conceptions). However, we also recorded seven cases

TABLE II. Predicted and Observed Fates of the Infants Born in the Macuco Group in Male Takeover Years (see Fig. 2)

Infant	Infanticide expected?	Infant disappeared?	Infant age at takeover (months)	Observations
Inf '97 GU	No	No	−2.9	Mother emigrated from the group while pregnant
Inf '97 DO	Yes	Yes	−0.9	Mother mated with the new dominant male ten days before the infant was born.
Inf '97 WC	No	No	−2.2	
Inf '97 TH	No	No	−4.2	
Inf '98 F2	Yes	No	7.8	Mother mated with the new dominant male while pregnant
Inf '98 GR	Yes	No	7.8	
Inf '98 DO	Yes	Yes	5.3	
Inf '99 GU	Yes	Yes	−3.7	
Inf '99 WC	No	No	−3.8	
Inf '99 TH	No	Yes	−3.6	While in estrus, TH was not observed soliciting the new dominant male
Inf '99 YO	No	Yes	?	
Inf '99 RI	No	No	−3.1	
Inf '99 LU	No	Yes	−3.0	While in estrus, LU was never observed soliciting the new dominant male
Inf '04 GR	Yes	No	−2.2	August 2004 takeover. Mother exhibited post-partum estrus
Inf '04 TH	Yes	No	−2.9	August 2004 takeover. Mother exhibited post-partum estrus
Inf '04 RI	Yes	No	−3.6	August 2004 takeover. Mother solicited the new dominant male 2 and 3 months before the infant was born
Inf '04 GR	Yes	Yes	3.2	December 2004 takeover. Body recovered with injures
Inf '04 TH	Yes	Yes	1.1	December 2004 takeover. Infanticide observed
Inf '04 YO	Yes	Yes	−0.5	December 2004 takeover
Inf '04 RI	Yes	No	−0.3	December 2004 takeover. Female emigrated from the group

We predicted infanticide when three criteria were met simultaneously: (a) the infants were not likely sired by a male reaching the dominant position, (b) the infant's mother could be fertilized earlier than if the infants had lived and (c) the new dominant male was likely to sire the female's next offspring. Under the third condition, we do not expect the dominant males to kill the infants of his daughters or for the subordinate males to kill infants outside the context of a takeover.

of females that exhibited proceptive behavior while pregnant. Six of them were gestating infants most likely conceived by a former dominant male before he was replaced while the females were pregnant. We also recorded post-partum estrus after six out of 32 births that took place while the group was under intensive study. Two of these estrous events were by females who had lost a newborn infant and the other four by females that gave birth to infants presumably conceived by the former dominant male, when there was a male takeover between the infant's conception and birth.

DISCUSSION

Our observations confirm the existence of the previously suspected infanticide behavior in brown capuchin monkeys [Izawa, 1994]. The infant death reported in case 1 was caused by wounds inflicted by the new dominant male, as the infant was not injured before its mother interacted with the male and no other monkeys made contact with the infant during the attack. The infant death reported in case 2

is possibly another infanticide case. The kind of wounds exhibited by the infant makes a predator attack unlikely. We suspect that the wounds were inflicted by a monkey that could have attacked the infant when it was on her mother's back.

Both these cases, plus the disappearance of YO's infant earlier, are consistent with the sexual selection hypothesis (assuming that ALS was the infanticidal male in cases 2 and 3). First, it is quite unlikely that the infanticidal male had killed his own progeny. Although the infanticidal male was present in the group when the infants were sired and could have mated with some females, his probability of siring infants is low, as the mating pattern of females hinders paternity by subordinate males. During the mating season of 2004, the previous dominant male was still undisputed and females consistently courted him during the major part of their estrous periods. Mating with subordinate males occurred only near the end of estrous periods, when females have little chance of conceiving [Carosi et al., 1999]. Regrettably, we do not have genetic data on the dead infants to know who sired them. However, what is required for infanticide

to be adaptative is that the presumed infanticidal male has a very low probability of having sired the infants he killed, and this requirement seems to be met in our study in light of what is known on the mating system of the species [Escobar-Páramo, 1999; Janson, 1984, etc.]. Second, all the females that suffered infanticide conceived a new offspring the next year. It is quite likely that the females gave birth earlier than they would have done it if their infants had survived, as their IBIs were substantially shorter than the average IBI for the cases when the infants survive. Third, the presumed infanticidal male gained sexual access to the females in the group: he was observed mating during the conception season of 2005 with the females that lost their infants and he most likely sired the females' next offspring.

Alternatives to the sexual selection hypothesis (Table I) cannot fully explain our observations. Only the infant was wounded in the attack we witnessed, and all aggression ceased after the male reached the infant. The male did not continue attacking the mother nor did the mother or other relatives show further aggression against the infanticidal male. These observations contradict the predictions of the hypotheses of infanticide as social pathology or as a by-product of male aggression. Further evidence against the social pathology hypothesis is the fact that the infanticidal male provided care to the infants born in the next breeding season, even when all the possible anthropogenic habitat disturbances remained constant or even increased. (The National Park received more visitors than the previous year, construction was carried out on a hotel within the monkeys' home range, and small planes began to fly over the study site.) Another alternative hypothesis is cannibalism. In this study, one mother carried the dead body of her infant for 2 days, arguing strongly against the idea that the male consumed, or intended to consume, the infant. The resource competition hypothesis is not supported because no juvenile disappeared from the group during the period when these events occurred. Under the adoption avoidance hypothesis it could be expected that the infanticidal male would kill not only the unweaned infants but also 1- and 2-year-old immatures, which are normally tolerated by the dominant male at feeding patches and protected when receiving aggression from subordinate AdM [cf. Janson, 1984]. Only unweaned infants disappeared during male takeovers in this study. Finally, the elimination of future rivals hypothesis is not supported because in this study a female infant was also killed. The long-term data for our population suggest that almost the same number of males and females disappeared during takeover years and that there is no bias toward females in infants that survived takeovers. Furthermore, male infants cannot be future reproductive rivals to a dominant male in this population because all males emigrate when they reach sexual maturity.

We witnessed unusual cases of sexual receptivity by several females in the Macuco group following the male replacements of 2004. These estrous periods were well outside the documented mating season for this population [Di Bitetti & Janson, 2001a], and several copulations were observed. AdF in another study group did not show estrous periods at the same time, suggesting that this sexual activity was related to the male replacements. Two females were nursing infants less than 10-weeks old when they came into estrus. Recabarren et al. [2000] demonstrate that among captive brown capuchin monkeys, nursing females do not recover menstrual cycles until 150–190 days post-partum, and lactation extends the residual infertility period (mating but not conceiving) for another 9–11 months. If the females were unable to conceive from October through January (no offspring were born from these matings), then the question remains why they copulated with the new dominant males. This sexual activity, which is not likely aimed at reproduction, could be explained as female anti-infanticide behaviors. An alternate hypothesis is that females mate with the male to enlist his support to increase their dominance rank after the replacement.

Two of the four females that gave birth in the Macuco group during the 2004 breeding season were pregnant when they mated with the new dominant male (MAR), and their newborns were not killed by him. Mating during pregnancy in the Macuco group was also registered in three out of the four females that were gestating infants during the takeover attempt of September–October 1997. It is likely that mating during pregnancy represents an anti-infanticide female strategy. In *C. capucinus* there are reports of wild pregnant females copulating with a newly immigrant male [Manson et al., 1997], and there is evidence suggesting that pregnant females usually mate with subordinate males [Carnegie et al., 2006]. By contrast, mating during pregnancy is not the rule for *C. apella*, but is strongly restricted to takeover events.

Post-partum estrus may be another anti-infanticide strategy, as it was observed in two females that delivered infants probably sired by a former dominant male. However, we need more data before reaching any reliable conclusions about the role of post-partum estrus.

The emigration of an AdF (RI) with a dependent infant on the very day of the last infanticide in her group can be interpreted as an extreme case of infanticide avoidance by this female, given that females are normally philopatric in this population. Her infant was the only survivor from this cohort.

Six of the 12 cases in which infanticide could be expected were followed by infant disappearances or infanticide. Of the six cases in which vulnerable infants survived a male takeover, four can be explained by means of the anti-infanticide behaviors

proposed above (mating during pregnancy, post-partum estrous and emigration). In the two remaining cases, the infants were both 7.8-months old during the takeover, and we suggest that they were beyond the vulnerable age for infanticide.

We found evidence that mortality associated with male replacements is more important than the mortality related to periods of food shortage, given that infant disappearances occurred at the same rate in provisioned and unprovisioned groups. Our data suggest that mortality associated with male takeovers is the main cause of death for black capuchin infants below 1 year of age.

The new evidence showing the existence of infanticide in *C. apella* opens questions about its importance for the behavior and the demography of this species. Infanticide may have selected for female anti-infanticide behaviors such as mating with subordinate males on the last day of the estrous period [Janson, 1984] and mating while pregnant and at other periods when they cannot conceive (this study). With regard to demography, our very conservative estimates indicate that at least 8% of the infants die for reasons associated with male takeovers. Thus, infanticidal behavior should be reconsidered as a factor affecting social and mating behavior in members of the *C. apella* superspecies.

APPENDIX A

Macuco group composition before the takeovers of September 1997 (a), June 1999 (b), August 2004 (c) and Gundolf group composition in August 2004 (d). The Gundolf group began splitting from the Macuco group before the takeover of August 2004. Estimated age in years and dominance rank are indicated in parentheses. Inf_c, adult female that conceived an infant before a takeover; Inf_b, adult female that gave birth to an infant before a takeover.

(a)

Adult males	Adult females	Juvenile males	Juvenile females	Infants
DE (>21; α)	F2 (>21; α)	JD (9)	LU (5)	SA (1)
GE (>13; β)	GR (>21)	DF (8)	YO (4)	GRE (1)
TU (>13; γ)	GU (>16)Inf_c	IDO (7)	RI (4)	
AF? (>7; δ)	DO (>12)Inf_c	IGU (6)	MF (3)	
	SP (~10)	GY (5)	MG (3)	
	WC (~9) Inf_c	GI (2)	GO (3)	
	TH (5) Inf_c		CL (3)	
			WE (2)	

(b)

Adult males	Adult females	Juvenile males	Juvenile females	Infants
DE (>23; α)	F2 (>23; α) Inf_b	DF (9.5)	MF (4.5)	GV (1.5)
GE (>15; β)	GR (>23) Inf_b	GY (6.5)	MG (4.5)	JU (1.5)
AF (>9; γ)	GU (>18) Inf_c	GI (3.5)	GO (4.5)	MI (1.5)
	DO (>14) Inf_b	SA (2.5)	CL (4.5)	UR (0.7)
	SP (~12)		WE (3.5)	DI (0.7)
	WC (11) Inf_c		GRE (2.5)	ME (0.4)
	TH (7) Inf_c			
	LU (7) Inf_c			
	RI (6) Inf_c			
	YO (6)			

(c)

Adult males	Adult females	Juvenile males	Juvenile females	Infants
GE (>20; α)	YO (11; α) Inf$_c$	JU (7)	DUL (4)	SB (1)
ALS ($\sim$12; β)	TH (12; β) Inf$_c$	DI (6)	EST (4)	EVA (1)
MAR ($\sim$9; γ)	RI (11) Inf$_b$	IB (5)	ELL (4)	MAY (1)
HOM ($\sim$8; δ)	GR (>28) Inf$_b$	FE (5)	OL (4)	BEN (1)
CHA ($\sim$7; ε)	GU (>23)	MT (4)	CHI (3)	BIA (1)
	SP (17)	AN (4)	JOS (3)	SN (1)
	MG (10)	GUI (4)	CAR (3)	TOB (1)
	CL (8)	PAB (2)		YAM (1)
	UR (6)			

(d)

Adult males	Adult females	Juvenile males	Juvenile females	Infants
GD ($\sim$13)	WC (16) Inf$_c$		SUS (2)	KIN (1)
	LU (12) Inf$_c$			CON (1)
	WE (9)			
	GV (8)			

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