Nonconceptive Sexual Behavior in Bonobos and Capuchins

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Sexual behavior by infecundable females, and by same-sex and adult-immature dyads, occurs in wild and captive bonobos (Pan paniscus). Proposed functions of these behaviors, in social primates generally, include practice, paternity confusion, exchange, and communication as well as appeasement. We used this framework to interpret and to compare observations of sexual behavior in a captive bonobo group and a wild white-faced capuchin (Cebus capucinus) group. In both species, (a) sexual behavior was no more frequent in cycling females than in pregnant or lactating females and (b) same-sex and adult-immature dyads engaged in as much mounting or genitogenital contact as adult heterosexual dyads did. The species differed in that (a) bonobos engaged in sexual behavior 65 times as frequently as capuchins, (b) only bonobos engaged in sexual contact other than ventrodorsal mounting during focal observation, and (c) bonobo sexual contact was concentrated most heavily in socially tense situations in adult female–female dyads, whereas capuchin sexual contact was concentrated most heavily in socially tense situations in adult male–male dyads. These data and published literature indicate that (a) practice sex occurs in both species, (b) paternity confusion may be a current function of C. capucinus nonconceptive sex, (c) exchange sex remains undemonstrated in capuchins, and (d) communication sex is more

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important to members of the transferring sex—female bonobos and male capuchins—than to members of the philopatric sex.

INTRODUCTION

In many avian and mammalian species, sexual behavior occurs at higher frequencies than necessary to ensure conception or in nonconceptive forms or both (Birkhead *et al.,* 1987; Hrdy, 1988; Wrangham, 1993). these phenomena are particularly prevalent in primates and have recently attracted considerable research attention in the bonobo (*Pan paniscus*: Kuroda, 1980; Thompson-Handler *et al.,* 1984; de Waal, 1987; Furuichi, 1987, 1992; Kano, 1989, 1992). The striking convergences between *Pan* and the platyrrhine genus *Cebus,* particularly with respect to encephalization and social complexity, invite comparison between the two genera with regard to the prevalence, patterning and possible functions of nonconceptive sexual behavior. Furthermore, female–female coalitions against males, known to be effective in both *P. paniscus* (Parish, 1994, 1996) and *C. capucinus* (Perry, 1997a), are thought to be facilitated by female–female sexual interactions in bonobos; whether this link exists in capuchins is unknown. In this paper, we describe and compare the patterning of sexual interactions in a captive bonobo group and a wild white-faced capuchin (*C. capucinus*) group. Specifically, we present data on (a) temporal patterning of courtship and mating behavior by both sexes in capuchins, (b) sexual positions of bonobos, and (c) partner combinations and contexts of sexual interactions for both species. We use these data to evaluate proposed explanations for copulations by infecundable females and same-sex and adult–immature sexual interactions.

Nonconceptive Sexuality

Wrangham (1993) has identified five functional categories of sexual activities in *Pan*: conception, practice, paternity confusion (Hrdy, 1981), exchange, and communication (de Waal, 1990). Particular interactions may fall into more than one category. The first category requires no further elaboration. Practice by juveniles may be necessary for the development of effective courtship and copulatory techniques in adulthood (Tutin and McGrew, 1973). Hrdy's (1981) paternity confusion hypothesis applies to situations in which adult males pose a threat to infants unlikely to be their own offspring, as is the case in *P. troglodytes* (Nishida, 1990), *Cebus oli-*

vaceus (Valderrama *et al.*, 1990) and *C. capucinus* (Rose, 1994). In these situations, a female may therefore benefit from nonprocreative matings that induce her copulatory partners to exhibit benevolence or neutrality toward her subsequent offspring. Exchange of sexual access for nonprocreative benefits to females—food, grooming—occurs in both *Pan* species (Kuroda, 1984; Thompson-Handler *et al.*, 1984, Goodall, 1986:484; de Waal, 1990; White and Lanjouw, 1992). The paternity confusion and exchange hypotheses rest on the assumption that selection on males has produced motivations to copulate with females even when they are unlikely to conceive. Communication sex, often involving same-sex or adult–immature interaction, provides no procreative benefit to either party, yet is neither a mere substitute for heterosexual intercourse nor a manifestation of social pathology: instead, dyads use sex to communicate about their social relationship (de Waal, 1990; Smuts and Watanabe, 1990; Wrangham, 1993). Wrangham's framework does not make the potentially important distinction between communication sex and sexual behavior that functions to influence the outcome of particular social interactions, e.g., appeasement as described for bonobos by Kano (1980), Kuroda (1980), and Thompson-Handler *et al.* (1984) without affecting the dyad's overall relationship.

Bonobo and Capuchin Sexual Behavior

Bonobo sexuality has been described by several authors, often in explicit contrast to common chimpanzee sexuality (Kuroda, 1980; Thompson-Handler *et al.*, 1984; de Waal, 1987; Furuichi, 1987, 1992; Kano, 1989, 1992). Compared to chimpanzees, bonobo females develop their first sexual swellings earlier, resume swelling earlier following parturition, and spend a larger fraction of each cycle swollen. Bonobo copulatory positions are more varied than those of chimpanzees, and include ventroventral matings. Bonobos of both sexes frequently engage in same-sex and adult–immature sexual interactions, though Furuichi (1992) prefers to regard these interactions as pseudosexual. Chimpanzee–bonobo differences in sexuality have been linked to differences in food distribution and social structure; in particular, cofeeding and coalitions (particularly against males) among unrelated female bonobos are believed to be facilitated by sexual interaction, and these bonds, in turn, reduce the relative power of males and the overall intensity of intracommunity injury-producing aggression (Kuroda, 1980; Mori, 1984; Wrangham, 1993; Parish, 1994, 1996). Despite the availability of both qualitative reports from the wild (Furuichi, 1987; Kano, 1989; White and Lanjouw, 1992) and one quantitative data set from captivity (de Waal, 1987, 1990) indicating a strong connection between

bonobo sexual behavior and socially tense situations, a persistent common popular view (Small, 1993: 176) holds that female bonobos "are always ready for sex."

Capuchin sexuality, like chimpanzee and bonobo sexuality, appears to vary in ways related to overall social structure. Both *C. olivaceus* (Robinson, 1981) and some groups of *C. apella* (Janson, 1984) appear to have single breeding males. In *C. apella* this results from female choice for the dominant male (Janson, 1984; Welker *et al.*, 1990; Phillips *et al.*, 1994), though females seek matings with multiple males when group membership is unstable (Janson, 1994). Dominant males' abilities to control access to large, scarce fruit sources and tendencies to bias tolerance toward likely offspring at these sites, are thought to drive female mate choice (Janson, 1984). Proceptive behavior by *C. apella* females is conspicuous and generally occurs in discrete and regular intervals corresponding to a particular phase of the estrous cycle (Janson, 1984; Phillips *et al.*, 1994; Linn *et al.*, 1995; but see Welker *et al.*, 1990), but may also occur in nonfertile periods, including within a few days of parturition (Janson 1984; Visalberghi and Welker, 1986). In *C. albifrons*, mating is distributed more equitably among males than in *C. apella* (Janson, 1986). Similar, *C. capucinus* matings do not appear to be monopolized by the alpha male (Oppenheimer, 1968; Mitchell, 1989; Fedigan, 1993). Few data are available on same-sex or adult-immature sexual behavior in *Cebus*. Phillips *et al.* (1994) report that 50% of mounts of adult females were by juvenile males in two captive groups of *C. apella*. Linn *et al.* (1995) report that female–female sexual mounts were sometimes disrupted by male *C. apella* in captivity. No information has been published on the temporal patterning of female proceptive behavior, or on same-sex or adult–immature sexual interactions, in *C. capucinus*.

METHODS

Bonobos

The bonobo subjects are six adults and juveniles—one adult male, two adult females, one subadult female, and two juvenile females—of a group at the Wilhelma Zoologisch-Botanischer Garten, Stuttgart, Germany. This age–sex composition is similar to that of foraging parties in the wild population at Lomako, Zaire (White, 1992; Parish, 1994).

We collected data in two periods: 1 August–17 September 1991 and 6–27 January 1992. We conducted 15 min focal individual observations in a random, predetermined order. We sampled all individuals on each of 49

observation days and collected a total of 145 hr of focal data. We used only focal data in our analyses. Sexual interactions that occurred in the context of feeding on highly concentrated resources (Parish, 1994) are not considered here.

We computed dominance rankings from outcomes of agonistic interactions and displacements. The two adult females and the juvenile daughter of the alpha female outranked the adult male, which in turn outranked one subadult and one juvenile female (Parish, 1994). de Waal (1988) provided full descriptions of bonobo courtship and sexual behaviors to which we refer.

Capuchins

The white-faced capuchin subjects belonged to a social group of 21 monkeys living in and just outside the northern tip of Lomas Barbudal Biological Reserve, Guanacaste, Costa Rica. The area consists largely of highly seasonal tropical dry deciduous forest (Frankie *et al.,* 1988). Our data were collected between May 1991 and May 1993. We followed the social group from dawn to dusk every day for ≤25 sequential days per month. Adults and juveniles were easily identified by scars, hair color patterns, and facial contours. We assigned monkeys born before June 1990, when individuals were first identified during a preliminary study, to age classes—adult and juvenile—based on body size and, for females, signs of parity: mature nipples, nursing infant. The study group contained four adult males, six adult females, and 11 juveniles and infants.

We collected data during 10-min focal individual follows, in which all social behaviors and the identities of the interactants were recorded. Four observers participated in the study. We collected data in teams of two observers per focal follow, to ensure accuracy in identification of individuals and behaviors. When the observers did not agree, we discarded the data. We collected 968 hr of focal data on the 10 adults in the study group during 3800 hr of contact with the group.

Females could be ranked in a linear hierarchy according to avoidance and cowering (Perry, 1996). Using these same criteria, one male was clearly dominant to all others at any given time, but dominance relationships among the subordinate males were not discernible; avoidance and cowering occurred in both directions within each subordinate male–male dyad (Perry 1997b). All males were individually dominant to all females, though female-female coalitions were highly effective in neutralizing these asymmetries (Perry, 1997a). In data tables in this paper, monkeys are listed

in dominance rank order from left to right and from top to bottom, by the first letter of their names.

Female Capuchin Reproductive States

Female *C. capucinus* show no apparent sign of ovulation or early pregnancy. There is no published information on gestation length. To establish, in retrospect, daily female reproductive state, we used the 160-day estimate of *C. apella* gestation length (Hayes *et al.,* 1972; Nagle and Denari, 1983; Phillips *et al.,* 1994). Because of probable variation in gestation length, we included the first 10 days of this 160-day period as a potentially fertile period. Reproductive states of nonpregnant females were (1) early lactation (0–2 months postpartum), (2) late lactation (2–6 months postpartum), (3) potentially cycling (6 months postpartum to 171 days before the next parturition), and (4) most likely conception period (170–151 days before parturition). These categories were delineated to minimize the likelihood of interpreting sexual behavior as nonconceptive. Interbirth intervals following the births of surviving infants can be as short as 12.5 months, but the median interbirth interval is considerably longer: 22 months in our study group (Perry, 1995) and 26.36 months in the neighboring population of *C. capucinus* at Santa Rosa National Park (Fedigan and Rose, 1995).

RESULTS

Bonobos

Sexual Positions and Techniques. Table I shows, for each bonobo dyad, rates of sexual behaviors other than ventrodorsal genitogenital contact. Although nonventrodorsal genitogenital contact was common—accounting for over half of genitogenital contacts in 9 of 12 (75%) dyads—oral sex and tongue kissing were rare and were confined to dyads that included juveniles.

Female Reproductive States and Sexual Behavior. Hormone profiles of adolescent female Kuni indicated that ovulation was unlikely during the study period (Parish and Shideler, 1997). Adult female Kombote was probably cycling, as she conceived in March 1992, <2 months after the conclusion of observations. Adult female Diatou was lactating and did not conceive until 15 months after the end of the study and was, therefore, presumably anovulatory during observations. Among these three females. Diatou engaged in the highest rate of genitogenital contact with the adult

Table I. Hourly Rates of Bonobo Sexual Behavior, Excluding Ventrodorsal Mounts, by Dyad (Designated by Age–Sex Class)

Dyad	Nonventro-dorsal[a] genitogenital contact	Genital massage	Oral sex	Mouth kissing	Tongue kissing
AF1[b]/AF2[c]	0.11 (0.57)[h]	0.14	0	0.01	0
AF1/AM[d]	0.01 (0.50)[h]	0	0	0	0
AF1/SF[e]	0.48 (0.64)[h]	0.09	0	0	0
AF1/JF1[f]	0 (—)[h]	0	0	0	0
AF1/JF2[g]	0 (—)[h]	0	0	0	0
AF2/AM	0.01 (0.10)[h]	0.01	0	0	0
AF2/SF	0.08 (0.55)[h]	0	0	0	0
AF2/JF1	0.47 (0.81)[h]	0.03	0.03	0.03	0
AF2/JF2	0.06 (1.00)[h]	0	0.08	0	0
SF/AM	0.03 (1.00)[h]	0	0	0	0
SF/JF1	0.27 (0.83)[h]	0.02	0	0.03	0.03
SF/JF2	1.42 (0.96)[h]	0	0	0	0
AM/JF1	0.11 (0.33)[h]	0	0	0	0.03
AM/JF2	0.47 (0.85)[h]	0.06	0	0	0

[a]Included ventroventral, ventroupright, and ventroopposite contacts.
[b]Kombote.
[c]Diatou.
[d]Masikini.
[e]Kuni.
[f]Kamiti.
[g]Kichele.
[h]Parentheses contain the proportion of all genitogenital contacts that were not ventrodorsal.

male, 0.14 bout/hr), compared to 0.028 bout/hr for each of the other two females.

Sexual Behavior in Conceptive and Nonconceptive Dyads. We classified dyads into two categories. Conceptive dyads ($N = 3$) consisted of the adult male and any one of the three adult and subadult females. All other dyadic types were nonconceptive. By including some nonconceptive sex, i.e., with Diatou, in the conceptive category, this classification permits a conservative test of the prediction that nonconceptive sex is as prevalent as conceptive sex. We combined all genitogenital contacts by each dyad to compute a contact rate for it, expressed as contacts per hour of focal observation of the two individuals. We never observed adult females to mount adult males during focal observation, which would have raised the problem of conceptive dyads engaging in definitely nonconceptive sex. Nonconceptive dyadic contact rates were higher than conceptive dyadic mounting rates, though

this difference is not significant ($N_{conceptive}$ = 3 dyads, $X \pm$ SD contacts/hr = 0.065 $\pm$ 0.064; $N_{nonconceptive}$ = 11 dyads, $X \pm$ SD contacts/hr = = 0.403 $\pm$ 0.436; Mann–Whitney U = 7, P = 0.138).

Contexts of Genitogenital Contacts. Table II shows raw counts of genitogenital contacts during focal observation as a function of (a) context and (b) the age–sex class of the participants. Of 215 contacts, 124 (57.7%) occurred in socially tense situations, which included recent ($\leq$5 min) aggression involving one or both participants and feeding. The remainder occurred during play or in no discernible context. Genitogenital contacts in socially tense contexts were prevalent in adult female–female (92.9%), adult male–adult female (83.3%), and adult female–immature female (71.9%) dyads. Only in the adult male–immature and immature female–female dyads were most genitogenital contacts in nontense situations. Although genitogenital contacts were observed in play contexts, they were never observed in any other affiliative context: grooming or affiliative body contact.

Capuchins

Courtship and Mating Behavior. Copulations were preceded and sometimes followed by a suite of behaviors that we designate a courtship dance.

Table II. Frequency of Bonobo Genitogenital Contacts by Context and Age–Sex Classes of Participants

	Age–sex class combination				
Context	Adult female/ adult female	Adult male/ adult female	Adult female/ immature female	Adult male/ immature female	Immature female/ immature female
Conflict[a]	0	0	10	5	4
Feeding	13	10	54	8	20
Total social tension[b]	13	10	64	13	24
Play	0	0	18	10	29
Other/Unknown	1	2	7	11	13
Total nontense[c]	1	2	25	21	42

[a]Includes *postconflict type A*—mounter and mounted individual were opponents in vocal or contact aggression in past 5 min; and *postconflict type B*—one of the participating individuals was involved in vocal or contact aggression against a third individual within the past 5 min.
[b]Sum of conflict and feeding.
[c]Sum of play and other/unknown.

First, the male or the female or both made duck faces—their lips protruded such that they resembled a duck's bill, which is probably equivalent to "protruded lips" (Oppenheimer, 1973)—stared at the other monkey, and made one of two vocalizations: a grunt or a sex squeak, i.e., a very soft series of staccato notes ascending in pitch. While keeping his or her gaze fixed on the other monkey, the initiator of the dance began to spin around in a duck-face pirouette, looking at the other monkey between its legs, over the shoulder, or under an arm. Males generally piloerected while doing duck face pirouettes. In the next stage of the dance, the two monkeys chased each other back and forth, in slow motion, while maintaining their duck faces and eye contact, and producing either grunts or sex squeaks. These slow-motion chases seemed highly ritualized: movements were exaggerated, deliberate, and fairly rhythmic, and the two monkeys chased each other approximately equal distances, usually over the same branch. Sometimes one member of the pair walked backwards during these chases. Females sometimes initiated copulations by presenting their hindquarters, but usually the male gingerly grasped the female's hips to initiate a mount. Both males and females seemed highly nervous and ambivalent during dances, and often the female screamed when the male grasped her hips, thus ending the dance, at least temporarily. If the female did not scream or flee, the male mounted the female by grasping her legs with his feet and thrust several times before dismounting.

Copulation refers only to heterosexual mounts with thrusting. Ejaculation was difficult to discern because males neither displayed a conspicuous ejaculatory pause nor left a plug of coagulated ejaculate. Sometimes the male remained in mount position after thrusting ceased and rocked back and forth for several seconds. On other occasions, he remained mounted as the female began walking and lowered his feet to the branch so that the pair walked on six legs.

Duck faces were maintained throughout all phases of the dance and copulation. Except for the substitution of the duck face for the grimace, *C. capucinus* courtship behavior is similar to that reported for *C. apella* by Janson (1984) and Linn *et al.* (1995). All mounts were ventrodorsal.

Many of the behavioral elements characteristic of courtship and copulation also occurred in wheeze dances. The primary differences between courtship dances and wheeze dances were that in the latter (a) the wheeze—a vocalization similar to the twitter (Oppenheimer, 1973), but higher-pitched, louder, and smooth rather than staccato—was used and (b) monkeys did not produce duck faces, presumably because this facial configuration makes it impossible to wheeze. Wheeze dances ended either in the mutual departure of the participants from the area or in a sexual interaction. In the latter case, the two monkeys involved, usually males, took

turns mounting and thrusting on one another in the same positions used by heterosexual mating pairs. Both participants usually ceased wheezing and made duck faces during mounts.

Temporal Patterning of Mating and Courtship Behavior. Nine of the 15 copulations between adult females and adult males during focal observation occurred while the female participant was pregnant, including four matings <50 days before parturition, and two matings occurred during early lactation. We observed no copulation with an adult male ≤10 days of an estimated conception date. Because copulations occurred during all female reproductive states, we estimated copulation rate by dividing the number of copulations by the total number of focal observation hours for each female; this yielded a median rate of 0.05 copulation/hr (range, 0-0.06).

Table III shows the proportion of 10-min focal samples of females in which female courtship behaviors—duck faces or dance initiations toward males—occurred, according to female reproductive state. Females exhibited courtship behaviors in all reproductive states, but there was considerable variation among individuals as to which state was accompanied by the highest rates of courtship behavior. Only primiparous Nanny and nulliparous Diablita exhibited courtship behavior during the 20-day periods in which

Table III. Proportion of 10-Min Samples in Which Capuchin Females Exhibited Courtship Behavior, in Relation to Female Reproductive State and Parity

Female (parity)	Pregnant[d]	0–2 mo postpartum	2–6 mo postpartum	Potentially cycling[e]	Within 10 days of estimated conception[f]
A (M)[a]	0.047	0	0	0.007	0
S (M)[a]	—[g]	0.028	0	0.004	—[g]
N (P)[b]	0.009	0	0	0.033	0.148
D (N)[c]	0	—[g]	—[g]	0.083	0.040
W (M)[a]	0.016	0	0.012	0.038	0
T (M)[a]	0.034	0	0.009	0	0
Mean multiparous females	0.032	0.007	0.005	0.012	0
N + D	0.005	0	0	0.058	0.094
Overall	0.0212	0.0056	0.0042	0.0275	0.0376

[a]Multiparous.
[b]Primiparous.
[c]Nulliparous.
[d]Parturition minus 150 days to parturition.
[e]Six months postpartum to parturition minus 171 days.
[f]Parturition minus 170 days to parturition minus 151 days.
[g]No observation of the female in that reproductive state.

they presumably conceived. These two young females courted males conspicuously and were particularly assertive in their courtship during the time in which they conceived. On one occasion, Nanny took alpha male Paul's tail in her teeth and dropped him out of a tree after he persistently failed to respond to her duck faces and dance initiations. Expanding the data set to include ad libitum observations of proceptive behavior produced qualitatively similar results. The four females observed in late pregnancy, i.e., ≤50 days of parturition, exhibited courtship behavior on 0.13–0.33 of the observation days during that period (median among four females, 0.19).

Among multiparous females, male courtship behavior toward females was somewhat more concordant with female reproductive state than female courtship behavior was. Table IV shows the proportion of 10-min focal samples in which males directed duck faces or dance initiations toward females, as a function of female reproductive state. However two of three multiparous females were not courted at all during focal observation ≤10 days of estimated conception dates. Males may have been motivated to court females more on the basis of olfactory cues than on the basis of female behavior. Males were extremely interested in female urine and frequently stopped to sniff locations in which females had been sitting.

Table IV. Proportion of 10-Min Samples in Which Capuchin Females Received Male Courtship Behavior, in Relation to Female Reproductive State and Parity

Female (parity)	Pregnant[d]	0–2 mo postpartum	2–6 mo postpartum	Potentially cycling[e]	Within 10 days of estimated conception[f]
A (M)[a]	0.047	0	0	0.007	0.080
S (M)[a]	—[g]	0	0	0.035	—[g]
N (P)[b]	0.028	0.018	0	0.020	0.037
D (N)[c]	0	—[g]	—[g]	0.007	0.040
W (M)[a]	0.011	0	0.025	0.032	0
T (M)[a]	0.026	0.028	0	0.021	0
Mean multiparous females	0.028	0.007	0.006	0.024	0.030
N + D	0.014	0.018	0	0.014	0.039
Overall	0.018	0.009	0.005	0.020	0.031

[a]Multiparous.
[b]Primiparous.
[c]Nulliparous.
[d]Parturition minus 150 days to parturition.
[e]Six months postpartum to parturition minus 171 days.
[f]Parturition minus 170 days to parturition minus 151 days.
[g]No observation of the female in that reproductive state.

Female Behavior Toward an Immigrant Male. Adult male Ichabod joined the study group in November 1992, when all six adult females were potentially cycling. Examination of both focal and ad libitum data revealed that four adult females solicited Ichabod sexually—directed duck faces or dance initiations toward him—within 44 days of his immigration, including three that did so within 16 days of his immigration. Adult female Abby's estimated conception date was the same day as Ichabod's immigration; she was first observed to solicit him 45 days after his immigration. Adult females Nanny, Abby, Diablita, and Wiggy copulated with Ichabod, respectively, 43 days before, 122 days after, 101 days after and 97 days after their estimated conception dates. However, Ichabod also received relatively high rates of aggression, including facial threats as well as chases and contact aggression, from resident females [median among six females, 0.015 aggressive bout/hr; median rank order among four males in aggression received, second; median rank order in severe aggression (chasing and contact aggression) received, first].

Sexual Behavior in Conceptive and Nonconceptive Dyads. As in our analysis of the bonobo data, we classified dyads into conceptive and nonconceptive categories. Conceptive dyads consist of an adult male and an adult female, regardless of the female's reproductive state. We combined all mounts by each dyad regardless of the identity of the mounter to compute a mounting rate for it, expressed as mounts per hour of focal observation of the two individuals. As in the bonobo data set, adult females never mounted adult males. Nonconceptive dyadic mounting rates were higher than conceptive dyadic mounting rates, though this difference is not significant ($N_{conceptive}$ = 24 dyads, $X \pm$ SD mounts/hr = 0.0035 $\pm$ 0.0052; $N_{nonconceptive}$ = 121 dyads, $X \pm$ SD mounts/hr = 0.0059 $\pm$ 0.0151; Mann–Whitney U = 1270.5, P = 0.19).

Contexts of Mounts. Table V shows raw counts of mounts during focal observation as a function of (a) context and (b) the age–sex classes of the participants. Of 85 mounts, 36 (42.3%) occurred in socially tense situations, which included aggressive coalitions between the participants and a third party (Perry, 1997a), recent (≤ 5 min) vocal or contact aggression involving one or both participants, feeding, social fur-rubbing (Baker, 1996), reunion following a participant's absence from the group, and participant vocalizations usually indicating social excitement. The remaining 49 mounts occurred during play (20 cases = 23.5% of the total) or in no discernible context, except one case in which an adult male mounted a juvenile male while both displayed at a boa constrictor. Mounts in socially tense contexts were particularly prevalent when adult males mounted other adult males, accounting for seven of nine (77.8%) adult male–male mounts. In contrast, one of five (20%) adult female–female mounts occurred in socially tense

Table V. Frequency of Capuchin Mounts by Context and Age–Sex Classes of Participants

Age-sex class of mounter	Age-sex class of mounted individual		
	Adult female	Adult male	Immature
Adult male			
Conflict[a]	5	6	2
Feeding[b]	1	0	3
Other tension[c]	0	1	1
Total social tension[d]	6	7	6
Play	2	0	9
Other/unknown[e]	5	2	4
Total nontense[f]	7	2	13
Adult female			
Conflict[a]	1	0	3
Feeding[b]	0	0	3
Other tension[c]	0	0	0
Total social tension[d]	1	0	6
Play	2	0	1
Other/unknown[e]	2	0	7
Total nontense[f]	4	0	8
Immature			
Conflict[a]	2	3	—
Feeding[b]	3	1	—
Other tension[c]	0	1	—
Total social tension[d]	5	5	—
Play	3	3	—
Other/unknown[e]	9	0	—
Total nontense[f]	12	3	—

[a]Includes *coalition*—mounter and mounted individual jointly threaten a third individual; *postconflict type A*—mounter and mounted individual were opponents in vocal or contact aggression in past 5 min; and *postconflict type B*—one of the participating individuals was involved in vocal or contact aggression against a third individual within the past 5 min.
[b]Includes, besides feeding, three of *social fur-rubbing* (Baker, 1996).
[c]Includes one reunion (one monkey rejoined the group after an absence of several hours) and two cases in which an adult male participant had emitted *burst-twitter-bray* vocalizations (sometimes indicates social excitement) within the past 5 min.
[d]Sum of conflict, feeding, and other tension.
[e]Includes one case in which mounter and mounted individuals were jointly displaying at a boa constrictor.
[f]Sum of play and other/unknown.

situations (Fisher's exact $P = 0.063$). Six of the seven male–male mounts in socially tense situations were between two subordinate males—Curmudgeon and Guapo—and all six occurred during a 5-month period immediately after Curmudgeon was deposed as alpha male by Paul in November 1992 (Perry, 1995, 1997c).

During the 6-month period between this rank reversal and the end of observations, we observed (a) a fourfold increase in rates of severe aggression among adult males, (b) virtually all wounds, and (c) the occurrence of 149 of 152 (98%) of all observed wheeze dances, compared to 3 (2%) in the preceding 18 months.

Wheeze dances and mounts between Curmudgeon and Guapo, including several during ad libitum observation, were always disrupted by the new alpha male Paul when he witnessed them, and usually culminated in one of the two subordinates breaking off the interaction and joining Paul in threatening the other (Perry, 1995, 1997b). Only one of nine (11%) male–male mounts involved the alpha male; in that case, the alpha male mounted the subordinate.

DISCUSSION

From the data presented here and from published literature, several similarities and differences between bonobo and white-faced capuchin sexuality emerge. A large fraction of sexual behavior is nonconceptive in both species. This pattern results from both (a) the decoupling of female proceptivity from fertility and (b) a high relative frequency of same-sex and adult–immature sexual interactions, compared to adult heterosexual interactions. The frequent participation of immatures in sexual interactions in both species is consistent with the view that practice is one function of this behavior.

Data from our small sample of *C. capucinus* suggest that multiparous females are less likely than younger females to court males while fertile. In some catarrhines, e.g., rhesus macaques (Perry and Manson, 1995), adolescent females court males more vigorously than adult females. Because adolescents may be less likely than adults to successfully bear and rear offspring, selection on males may have reduced the sexual attractiveness of adolescents (Anderson, 1986). Vigorous courtship may represent a means to compensate for low attraction.

Wrangham (1993) argued that the prevalence of paternity-confusion sex was the starting point for the evolution of exchange sex in *Pan* and of communication sex in *P. paniscus*. There is currently no evidence that suggests a threat of infanticide in extant bonobos. Some elements of capuchin

sexuality are consistent with Hrdy's (1981) paternity confusion hypothesis, which predicts that nonconceptive sexuality will be associated with multi-male groups. Female proceptivity appears to be more tightly linked to fertility in functionally one-male grouping *C. apella* than in multimale *C. capucinus* (Janson, 1984; Phillips *et al.*, 1994; Linn *et al.*, 1995; but see Welker *et al.*, 1990). Rose (1994, personal communication) reports a case of infanticide in wild *C. capucinus* under conditions roughly consistent with the sexually selected infanticide hypothesis (Hrdy, 1974), except that the killer was not observed subsequently to mate with the victim's mother. In our subjects, most females sexually solicited a recent immigrant male, even if pregnant, though they also were aggressive toward him more frequently than toward other adult males, and sometimes appeared determined to drive him from the group (Perry, 1995, 1997a). Furthermore, most females that copulated with adult males during focal observation had >1 copulatory partner (Perry, 1997a). Since multiparous females conceived yet were not observed to exhibit courtship behavior while fertile, we infer that conceptive copulations occurred cryptically—e.g., at night—which could provide a means by which fertile females could copulate with multiple males including subordinates, thereby confusing paternity. On the other hand, the paternity confusion hypothesis is weakened by the difficulty of imagining how copulations during late pregnancy or early lactation could, over evolutionary time, continue to deceive males into altering their behavior toward subsequent infants.

Bonobos engage in sexual interaction at a considerably higher rate than that of white-faced capuchins. In our data sets, this is an approximately 65-fold difference. Caution is required in interpreting this result because our bonobo data are from captivity, whereas our white-faced capuchin data are from wild subjects. However, one form of sexual behavior, adult heterosexual copulation, occurred about three times more frequently in a wild bonobo community (Furuichi, 1992) than in our white-faced capuchin subjects. Furthermore, we have not observed in white-faced capuchins, the variety of sexual position and techniques reported for bonobos. There was no ventroventral mounting. However, face-to-face copulation has been reported for captive *C. apella* (Visalberghi and Welker, 1986). In our capuchin study group, oral sex and genital massage were extremely rare and never occurred during focal observation of adults.

Unlike bonobos and chimpanzees (Kuroda, 1984; Goodall, 1986, p. 484; de Waal, 1990; Parish, 1994), capuchins have not been observed to directly exchange sexual access for food or other social favors. This difference is particularly striking in light of findings of social exchange, grooming for coalitionary support (Perry, 1997a) and food-sharing (de Waal *et al.*, 1993; Perry and Rose, 1994) in capuchins, phenomena reminiscent of be-

havior in *Pan* (de Waal, 1996, pp. 144-154). It is not clear why sexual access has become decoupled from fertility, yet has apparently failed to become a currency of social exchange, in *Cebus*.

Our data agree with previous findings (Kano, 1980, 1989, 1992; Kuroda, 1980; Thompson-Handler *et al.*, 1984; de Waal, 1987, 1990; Parish, 1994, 1996) that bonobos use nonconceptive sexual interactions (a) to ameliorate tension caused by feeding competition and other interindividual conflicts and (b) to forge cooperative social relationships. Sexual interactions were concentrated in socially tense situations, particularly feeding, in all age-sex class combinations that included adult females. Thus, female bonobo sexual receptivity and proceptivity should be regarded as goal-directed and situation-specific, rather than continuous. Wild female bonobos form close, relaxed social relationships with other females (particularly one senior female) after transferring from their natal community, a process apparently facilitated by genitogenital rubbing (Idani, 1991; Kano, 1992). Consistent with these observations, the only subadult female in our bonobo study group directed 18 of 19 (94.7%) of her sexual presents toward the dominant female. Male-male sexual interactions—mounting, penis fencing, rump-rubbing—may serve to appease subordinates during feeding competition (Kano, 1992), but they have not been shown to promote long-term dyadic bonding. We cannot address this issue with our data set, as our study group contained only one adult male.

In contrast, to the extent that white-faced capuchin nonconceptive sex serves a communicative function, it does so for males more than for females. Of all age-sex class combinations, adult female-female dyads performed the smallest whereas adult male-male dyads performed the largest, proportion of their mounts in socially tense situations, mostly during coalition formation attempts and immediately after fights. Male-male mounting was also associated with social tension on a long time scale: it occurred most frequently during a period of unsettled social relationships following a dominance rank reversal. Two subordinate males, which engaged in more mounts than any other male-male dyad, may have been trying to form an enduring alliance against the alpha male, though they never succeeded in doing so (Perry, 1995, 1997b). Since, in capuchins, males are the transferring sex (Robinson and Janson, 1987; Fedigan *et al.*, 1997), it may be hypothesized that members of the transferring sex, relative to members of the philopatric sex, require more exaggerated communicative gestures if they are to form cooperative relationships. Immigrants are not only unrelated and strangers to each other. Because of the likelihood of future immigration, they lack the potentially long period of future social interaction that drives the formation of reciprocal relationships (Axelrod and Hamilton, 1981; but see Boyd, 1987).

Smuts and Watanabe (1990) have argued that sex-derived greeting behaviors—mounting and genital manipulation—between male olive baboons function to communicate commitment to form aggressive coalitions. They suggest that the vulnerability to surprise attack entailed by intimate contact makes sexual interaction particularly suitable as a means of building trust and communicating honestly about social bonds. However, Silk (1994) showed that similar greeting behavior among male bonnet macaques is most reasonably interpreted as an assessment of competitive ability between closely matched rivals.

Alternatively, sexual interactions may serve to conspicuously display social bonds to third parties (Wrangham, 1993). Finally, sexual interactions may function to appease potential aggressors, although this hypothesis seems unlikely for male *Cebus capucinus* since only two of nine male–male mounts occurred in contexts suggesting appeasement: one between the alpha male and a subordinate male, the other between two subordinate males immediately following aggression between them. Because our capuchin data set is too small to permit compelling tests among these alternative functional hypotheses, resolution of this question must await further research.

Another issue for future investigation in both bonobos and capuchins is the timing of female sexual behavior on short time scales. Although proceptivity appears to be decoupled from fertility on long time scales, i.e., pregnant and lactating females solicit males, it is not known whether, within individual ovarian cycles, females solicit males more while periovulatory than at other times. Such behavioral cyclicity is seen in *C. apella* (Janson, 1984; Phillips *et al.*, 1994; Linn *et al.*, 1995; but see Welker *et al.*, 1990), but no information is available on the relationship between ovarian steroid hormone profiles and behavior in any wild capuchin population. The relationship between these variables is currently under investigation in captive bonobos (Parish and Shideler, 1997).

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