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Grooming, Kinship, and Co-feeding in Captive Spider Monkeys (*Ateles geoffroyi*)

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Allo-grooming is perhaps the most powerful affiliative behavior observed in nonhuman primates. However, the functional significance of grooming in New World monkeys has not yet been fully understood, perhaps because grooming is less frequently observed in platyrrhines. To differentiate the potential role of affiliative investment and/or kinship on sharing access to food (co-feeding) in spider monkeys, behavioral data on grooming, embracing, and feeding were collected from two different groups of captive study subjects: a familiar/kin group and a nonfamiliar/non-kin group. The results of this study suggest that family-related spider monkeys that engage in grooming tend to share access to food resources more than unfamiliar conspecifics that do not groom. One explanation for this difference is that the unfamiliar study subjects had not yet invested in the affiliative social network, were not reciprocating their affiliative investments and hence, had a higher tendency toward single animal monopolizing resources. Degree of relatedness alone was not found to be a determinant for sharing the access to food, suggesting that familiarity in spider monkeys is based on the extent to which animals invest in affiliative relationships. In this study, only animals that had engaged in long-term grooming and recognized each other as familiar shared the access to food. Therefore, it might be likely that in spider monkeys, long-term grooming of high intensity has to be developed for co-feeding to occur. Zoo Biol 20:293–303, 2001.

Key words: *Ateles*; affiliative investment; co-feeding

INTRODUCTION

Familiarity is suspected to be the most important mechanism of kin recognition in vertebrates because for many species it has been demonstrated that animals treat individuals with whom they are familiar differently from those they have not en-

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countered before [Waldman, 1981; Kuester et al., 1994]. Distinguishing whether primates discriminate between *kin* and *familiar* conspecifics has been a challenging task with mixed results [Strier, 2000]. However, kin recognition appears to be a very important feature of female-bonded (FB) primate species, because FB species seek to maximize their own inclusive fitness by living in highly competitive nepotistic matrilineal societies [van Schaik, 1989]. In contrast, non–female-bonded (NFB) primate societies are egalitarian and flexible, and females mitigate intragroup competition by dispersing; therefore, kin recognition is not presumed important. The Fission–Fusion societies described by Symington [1990] fall into the NFB category described by van Schaik [1989]. This is because fission–fusion systems lack social cohesion because big groups tend to split into feeding parties to maximize foraging opportunities [Symington, 1987, 1988, 1990; Chapman et al., 1989, 1995; Kinzey and Cunningham, 1994; Wallace, 1998]. One of these fission–fusion genera is *Ateles*, which is a big-bodied platyrrhine that possesses a consistent preference for ripe fruits, which are resources of patchy distribution in tropical America [Terborgh and van Schaik, 1987; Fleagle, 1988; Ford and Davis, 1992; Pastor-Nieto and Williamson, 1998; Mittermeier et al., 1999].

Despite the fluidity of Ateline societies, a certain degree of affiliative behavior is required for maintaining group cohesion, at least temporarily. Cheney and Seyfarth [1990] and Dunbar [1992] have suggested that because of the flexible nature of fission–fusion societies, social subjects have evolved good memories to recognize familiar conspecifics. This assumption seems to be supported by studies of *Brachyteles arachnoides*, where the members of wild groups of this species have been found to recognize familiar conspecifics after temporary periods of dispersion [Strier, 1990, 1997]. However, there is a lack of information on the possible impact of social bonding for the formation of wild spider monkey subgroups or feeding parties after group fission. This maybe because of the difficulty of obtaining behavioral data of subjects that move very rapidly high up in the forest canopy.

It is widely recognized that the most direct mechanism in which primates invest in relationships is through social grooming [Seyfarth, 1983; Dunbar, 1991]. Although grooming evolved originally from a hygienic purpose, Dunbar [1991] suggests that it now has a primary social meaning, because it has been associated with the development of social bonding and the maintenance of group cohesiveness [Seyfarth, 1983; Dunbar, 1991]. Furthermore, other studies have found that grooming is strategically targeted toward the most valuable allies, which in turn are close kin individuals [Colvin, 1983]. It seems, then, that since birth, close familiar bonds among kin are reinforced by social grooming in primate species. The functional significance of social grooming has been extensively studied in Old World monkeys, perhaps because it is very frequently observed. De Waal [1997] provides the best evidence available on the functional significance of grooming—the exchange of food for grooming in chimpanzees. However, the function of grooming in New World primates is yet to be fully understood. Some authors agree that even if allogrooming is not a frequent behavior in platyrrhines, it serves a social purpose beyond its hygienic function [Fedigan, 1993; O'Brien, 1993]. Moreover, other affiliative behaviors yet to be understood have been observed in New World primates. For example, embracing (or pectoral sniffing) is a very conspicuous behavior observed in captive and wild *Ateles*, and has been associated with the formation of alliances and the recruitment of coalition partners [Klein and Klein, 1971; Klein, 1974; Eisenberg, 1976]

The purpose of this study is to explore the extent to which long-term affiliative investment in captive *Ateles* (through grooming and/or embracing) and/or kinship exert an effect on animals sharing the access to food (co-feeding). I do this by comparing the feeding, grooming, and embracing behaviors of a familiar (kin group) and an unfamiliar (non-kin) group of captive study subjects.

METHODS

Study Subjects

Behavioral data were collected from two groups of captive black-handed spider monkeys (*Ateles geoffroyi*) (nine animals in each group; N = 18) housed at the Centenario Zoo at Mérida Yucatán, México for a period of 15 months (July 1994–September 1995). Each group was composed of seven females, one adult male, and one juvenile male (Table 1).

The two groups studied have different histories. One group was an *unfamiliar group* (UFG) composed of nine wild-caught, unrelated animals (Table 1). The animals of the UFG were confiscated by wildlife officials, transferred to the Centenario Zoo, and then kept in individual quarantine before being incorporated into a group. Once the animals were placed in the enclosure, the UFG remained in a 4-month adaptation period before I started the collection of behavioral data.

The other group was a *familiar group* (FG), composed of nine captive-born animals currently breeding (Table 1). All members of the FG had been born in the Centenario Zoo and had remained together since 1988. However, neither the animal keepers nor the veterinarians kept records on births, deaths, and reproductive profiles.

TABLE 1. Study subjects, age, sex, focal minutes recorded, and frequency of individually monopolizing food expressed in number of events per minute

Subject	Age	Sex	Number of focal minutes	Monopolizing food (events/min)
UFG[a]				
Da	Adult	♂	1,363	0.17
Qui	Subadult	♀	1,769	0.15
Mo	Adult	♀	1,319	0.02
Ma	Juvenile	♂	1,415	0.03
Gri	Adult	♀	1,450	0.008
Go	Subadult	♀	1,798	0.043
Vi	Subadult	♀	1,406	0.006
Su	Adult	♀	1,914	0.043
Do	Adult	♀	1,464	0.013
FG[a]				
Lo	Adult	♂	1,943	0.004
Gue	Adult	♀	1,566	0.002
Fl	Adult	♀	1,914	0.006
Lu	Juvenile	♀	1,856	0.01
Fa	Adult	♀	2,088	0.004
Li	Subadult	♀	1,740	0.002
Chi	Adult	♀	1,421	0.004
Ba	Juvenile	♂	1,502	0.0002
Em	Adult	♀	1,986	0

[a] FG, familar group; UFG, unfamiliar group.

Therefore, relatedness among study subjects had to be confirmed by DNA fingerprinting tests, which were carried out at the Department of Genetics of the Chicago Zoological Society. The blood samples were analyzed as part of a project to study the phylogenetic relationships of the different species of *Ateles* [Collins and Dubach, 2000]. The results of these tests showed that only the members of the FG were related to each other. To allow the analysis of data, each dyad was assigned a coefficient of kinship (*r*) based on their position in the reconstructed genealogy [Hamilton, 1964] (Fig. 1 and Table 2). Except for the recent introduction of a subadult female (Em), the animals of the FG were housed together and almost never mixed with unfamiliar conspecifics. The fact that most members of the FG were related to each other also allowed a comparative analysis of behavior between this group and the UFG.

During this study, each group was housed in basic, temporary accommodations of identical dimensions (34.8 m^2). Each enclosure had a separate feeding area of 5 m^2. The enclosures were furnished throughout with tree trunks and ropes to enable movement in a three-dimensional environment. Food was provided twice a day, consisting of a variety of fruits and vegetables depending on the season, as well as monkey chow and freshly cut Ramon (*Brosimum alicastrum*).

Collection of Behavioral Data and Definitions of Behaviors

Focal samples were used to record general baseline behavioral patterns including grooming and embracing. Focal animal sampling consisted of observing one individual for 29 minutes, recording all grooming and embracing events each minute [Martin and Bateson, 1995] (Table 1). Grooming consisted of the groomer parting the hair of the groomee with hands and using the tongue, lips, and/or teeth to lick or nibble the fur. Embracing (also called *pectoral sniffing*) consists of animals approaching, lifting chins and arms, and placing pectoral areas close to the face of another party member [Klein and Klein, 1971; Eisenberg, 1976].

Then, total frequencies of grooming and embracing for each dyad (number of events/minute) were calculated by adding the frequency with which subject A groomed and/or embraced subject B and the frequency with which subject B groomed and/or embraced subject A [Pastor-Nieto, 1997]. In this way, total dyadic grooming and embracing frequencies were obtained [Altmann, 1974; Dunbar, 1976] (Table 2).

Because competitive behavior over food resources was very rarely observed during normal feeding times (perhaps because quantities supplied were abundant), an alternative experimental protocol was designed to promote competition between subjects for novel food items. A blue, opaque, 40 × 20-cm plastic box was adapted with a small round hole 5 cm in diameter and was attached to the mesh door of the

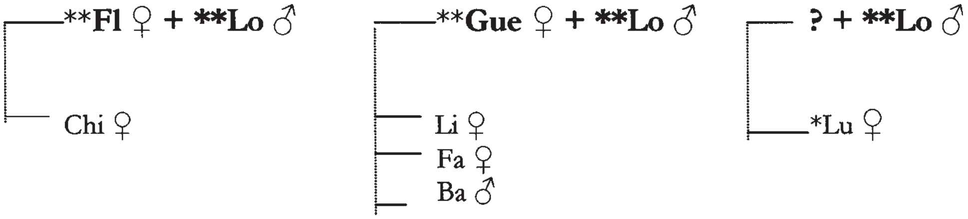

Fig. 1. Reconstructed genealogy of the familiar group. *Mother unknown; **mother and father unknown.

TABLE 2. Coefficient of kinship (r), dyadic grooming frequency, dyadic embracing frequency, access to food in the familiar group (FG) and the unfamiliar group (UFG)

	FG				UFG				
Dyad	**r[a]**	**Grooming[b]**	**Embrace[b]**	**Co-feed[b]**	**Dyad**	**r[a]**	**Grooming[b]**	**Embrace[b]**	**Co-feed[b]**
Lo-Gue	0.00	0.0062	0.0520	0.0030	Da-Qui	0.00	0.0090	0.0390	0.0014
Lo-Fl	0.00	0.0100	0.0750	0.0110	Da-Mo	0.00	0.0094	0.0270	0.0007
Lo-Lu	0.50	0.0151	0.0590	0.0020	Da-Gor	0.00	0.0180	0.0880	0.0010
Lo-Fa	0.50	0.0850	0.0450	0.0000	Da-Gri	0.00	0.0000	0.0099	0.0000
Lo-Li	0.50	0.0016	0.0260	0.0000	Da-Vi	0.00	0.0000	0.0100	0.0000
Lo-Chi	0.00	0.0060	0.0540	0.0015	Da-Su	0.00	0.0000	0.0120	0.0000
Lo-Ba	0.50	0.0040	0.0820	0.0250	Da-Do	0.00	0.0000	0.0066	0.0000
Lo-Em	0.00	0.0000	0.0080	0.0005	Da-Ma	0.00	0.0000	0.420	0.0000
Gue-Fl	0.00	0.0800	0.0490	0.0015	Qui Mo	0.00	0.0040	0.0057	0.0000
Gue-Lu	0.00	0.0135	0.0580	0.0009	Qui-Gor	0.00	0.0000	0.0190	0.0000
Gue-Fa	0.50	0.0157	0.0340	0.0005	Qui Gri	0.00	0.0068	0.0110	0.0000
Gue-Li	0.50	0.0111	0.0220	0.0002	Qui-Vi	0.00	0.0000	0.0170	0.0000
Gue-Chi	0.00	0.0170	0.0380	0.0080	Qui-Su	0.00	0.0168	0.0300	0.0000
Gue-Ba	0.50	0.0500	0.2800	0.0007	Qui-Do	0.00	0.0000	0.0130	0.0000
Gue-Em	0.00	0.0000	0.0027	0.0000	Qui-Ma	0.00	0.0050	0.0100	0.0050
Fl-Lu	0.00	0.0063	0.0380	0.0005	Mo-Gor	0.00	0.0046	0.0290	0.0000
Fl-Fa	0.00	0.0009	0.0530	0.0002	Mo-Gri	0.00	0.0000	0.0110	0.0000
Fl-Li	0.00	0.0066	0.0650	0.0001	Mo-Vi	0.00	0.0000	0.0150	0.0000
Fl-Chi	0.50	0.1000	0.0800	0.0008	Mo-Su	0.00	0.0062	0.0300	0.0000
Fl-Ba	0.00	0.0030	0.0050	0.0020	Mo-Do	0.00	0.0000	0.0350	0.0000
Fl-Em	0.00	0.0060	0.0020	0.0000	Mo-Ma	0.00	0.0008	0.0050	0.0000
Lu-Fa	0.25	0.0021	0.0670	0.0010	Gri-Vi	0.00	0.0000	0.0100	0.0000
Lu-Li	0.25	0.0043	0.0250	0.0000	Gri-Su	0.00	0.0000	0.0070	0.0000
Lu-Chi	0.25	0.0083	0.0580	0.0000	Gri-Do	0.00	0.0000	0.0040	0.0000
Lu-Ba	0.25	0.0003	0.0620	0.0090	Gri-Gor	0.00	0.0016	0.0090	0.0000
Lu-Em	0.00	0.0010	0.0030	0.0000	Gri-Ma	0.00	0.0001	0.0110	0.0000
Fa-Li	0.50	0.0197	0.0038	0.0004	Gor-Vi	0.00	0.0000	0.0140	0.0000
Fa-Chi	0.25	0.0075	0.0660	0.0004	Gor-Su	0.00	0.0116	0.0440	0.0000
Fa-Ba	0.50	0.1120	0.0002	0.0002	Gor-Do	0.00	0.0000	0.0250	0.0000
Fa-Em	0.00	0.0000	0.0001	0.0000	Gor-Ma	0.00	0.0020	0.0610	0.0080
Li-Chi	0.25	0.0054	0.0047	0.0057	Vi-Su	0.00	0.0015	0.0050	0.0000
Li-Ba	0.50	0.1110	0.0060	0.0000	Vi-Do	0.00	0.0000	0.0320	0.0000
Li-Em	0.00	0.0000	0.0003	0.0000	Vi-Ma	0.00	0.0000	0.0070	0.0000
Chi-Ba	0.25	0.0040	0.0080	0.0008	Su-Do	0.00	0.0095	0.0020	0.0000
Chi-Em	0.00	0.0140	0.0056	0.0000	Su-Ma	0.00	0.0020	0.0009	0.0000
Ba-Em	0.00	0.0020	0.0002	0.0000	Do-Ma	0.00	0.0010	0.0008	0.0000

[a] r calculated according to Hamilton (1964), which correspond to the proportion of genes shared through the common descent: 0.50—parent < > sibling, full siblings; 0.25—half siblings, grandparent < > grandchild.

[b] Number of events per minute.

feeding area of both enclosures. The box was baited with different food items, such as biscuits, raisins, or sweetened cereals. Continuous samples of 20-minute duration [Martin and Bateson, 1995] were performed for each group to record the identity of subjects that accessed the snackbox each of those 20 minutes. These samples were called "snackbox sessions." Two initial snackbox trials were performed in each group, to verify that the experimental protocol designed did not increase levels of aggression, and therefore compromise the well-being of the animals. Once I established that it was a safe procedure, one snackbox session per day was performed in each group. Twenty-three snackbox sessions were recorded in the UFG and 24 in the FG. A total of 460 continuous minutes in the snackbox were recorded in UFG and a total of 480 in the FG. The behavioral data collected consisted of recording the identity of the animals that accessed the baited box alone (monopolizing), or in close proximity to each other (co-feeding), each minute. Therefore, I considered co-feeding when two or more subjects fed from the snackbox in close proximity (within an arm's reach) [Feistner and McGrew, 1989]. As a result, frequencies (number of events/minute) of animals co-feeding or individually monopolizing the food from the box were calculated [Dunbar, 1976]. Spearman rank correlation coefficients were calculated to explore the possible associations between co-feeding, grooming, embracing, and kinship (r) [Martin and Bateson, 1995; Sokal and Rohlf, 1995]. To perform cross-comparisons on grooming, embracing, and feeding behavior between groups, Mann-Whitney U-tests were used [Sokal and Rohlf, 1995]. Significant results were considered at $P < 0.05$. I was unable to carry out behavioral comparisons between sexes because of the small male sample size (N = 4).

RESULTS

Familiar Group

The correlation coefficients calculated for the FG suggest a significant association between frequency of dyadic grooming and frequency of co-feeding ($r_s = 0.55$, two-tailed $P < 0.001$, N = 36), and a significant association between dyadic frequencies of embracing and co-feeding ($r_s = 0.47$, two-tailed $P < 0.01$, N = 36). However, a non-significant association between kinship (r) and frequency of co-feeding was obtained ($r_s = 0.22$, two-tailed $P > 0.1$, N = 36), suggesting that the sharing access to resources in the FG might be a function of affiliative investment among co-members, more than an effect of genetic relatedness or kinship.

To evaluate which of the affiliative investments (grooming or embracing) was the most effective strategy to gain shared access to food in the FG, a stepwise regression was calculated. The results obtained showed that embracing was the excluded variable from the model (ANOVA, $F = 0.01$, $P > 0.5$) and that grooming was the variable that better explained the co-feeding frequencies observed in the FG ($y = 0.5973x + 0.010$, $R^2 = 0.1977$, ANOVA, $F = 8.32$, $P < 0.01$). This model assumes that almost 20% of the dyads of the FG that shared the access to the baited box engaged in high frequencies of grooming (Fig. 2).

Unfamiliar Group

The lack of sharing access to food among co-members of this group was expected, because the subjects were consistently observed monopolizing the baited box individually. However, a significant correlation was obtained between grooming and embracing frequencies ($r_s = 0.46$, one-tailed $P > 0.05$, N = 36) in the UFG. This result suggests that despite being unsuccessful in reciprocating by sharing access to food, the subjects of the UFG might be initially investing in the affiliative social network.

Differences Between Groups

When comparing both groups in terms of co-feeding and monopolizing the access to food, the results obtained showed striking differences. On the one hand, the

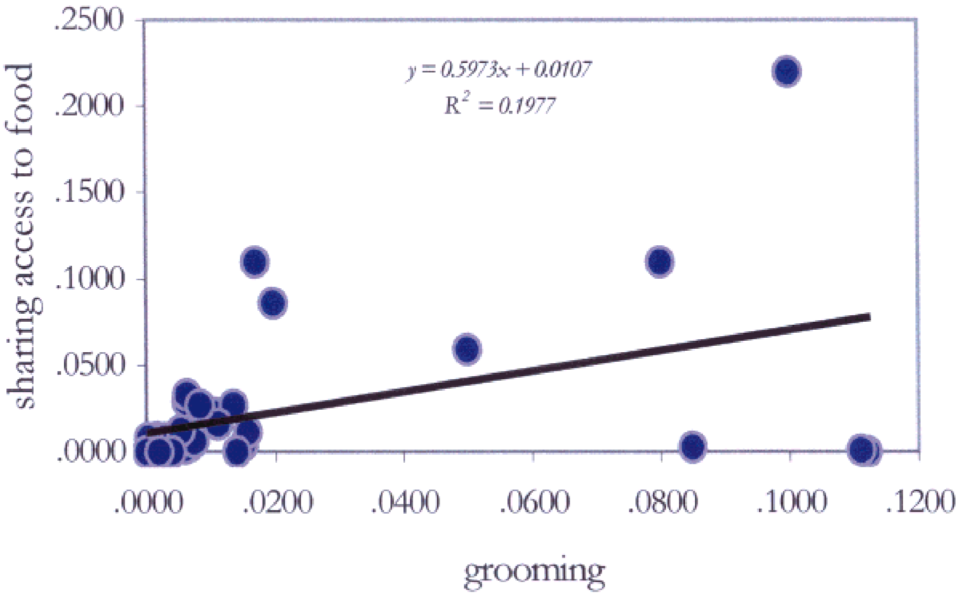

Fig. 2. Dyads that co-feed engage in high levels of grooming in the familiar group. Frequencies of behavior are expressed as number of events per minute.

subjects of the FG tended to share the access to the box at high frequencies, whereas the members of the UFG were never observed sharing. On the other hand, the members of the UFG tended to individually monopolize the access to the box at significantly higher frequencies than the members of the FG (Mann-Whitney *U*-test, $Z = -3.14$, two-tailed $P < 0.001$) (Fig. 3). These results might indicate a tendency for subjects living in a familiar environment to share access to food, in contrast to unfamiliar subjects who seemed to be less willing to share and are more likely to monopolize resources. Also, the two groups differed greatly in relation to frequency of social grooming (Mann-Whitney *U* test, $Z = -3.89$, two-tailed $P < 0.001$) and embracing (Mann-Whitney *U*-test, $Z = -4.12$, two-tailed $P < 0.001$), which suggests a profound difference in terms of social bonding between members of both groups (Fig. 3).

In the FG, the study subjects tended to feed in groups of two to three individuals, whereas the rest of the group was observed waiting in close proximity to one another before being permitted to feed. Interestingly, the male of the FG allowed females to feed first in 80% of the feeding sessions, even though he was the highest ranking subject of this group [Pastor-Nieto, 1997]. Notably, Em (the only unrelated subject of the FG) was never observed sharing access to food with other group members. This female ate the leftovers from the ground once the rest of the group had finished eating.

In contrast, the frequencies of one single subject monopolizing the food in the box were higher in the UFG. The male of this group accessed the box first in 100% of all feeding sessions and fed alone until satisfied. The high frequency with which Da (the male of the UFG) monopolized the snackbox was consistent with the fact that he possessed the highest rank within the hierarchy of the UFG [Pastor-Nieto, 1997]. In the UFG, access to the box worked as a succession of subjects reaching the box one by one.

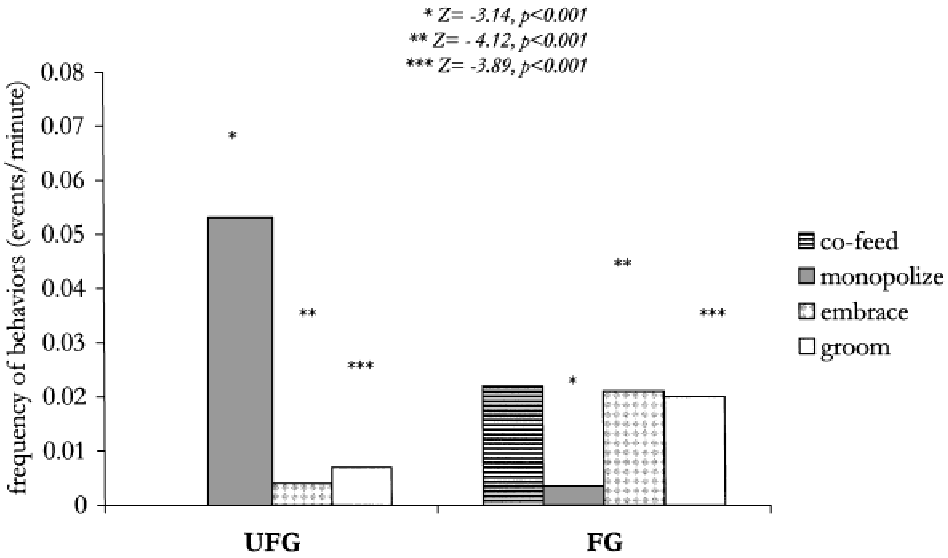

Fig. 3. Differences between the unfamiliar group and familiar group in mean dyadic frequency of co-feeding, individually monopolizing food, and dyadic embracing and grooming. Frequencies of behavior are expressed as number of events per minute.

DISCUSSION

In the FG, the subjects were observed to accept each other's presence when accessing the food in the box, which they tended to share. Interestingly, the adult male of this group (Lo) seemed to provide females with preferential access to food, despite being the highest ranking subject in the group [Pastor-Nieto, 1997]. In contrast, the subjects of the UFG did not share food resources, but rather monopolized them. Because the UFG was a recently convened group, its members had not yet been reciprocating each other's affiliative investments [Pastor-Nieto, 1997]. The adult male of the UFG (Da) monopolized the snackbox consistently, and the females in this group were never observed co-feeding.

The results of this study suggest that most members of the FG had developed close bonds between each other, probably through grooming. The statistical results also suggest that it is likely that grooming might be the main affiliative strategy used to reciprocate feeding tolerance. The fact that the members of the UFG tended to monopolize the access to food perhaps suggests that unfamiliar subjects are unable to reciprocate because they might require investing in grooming for a longer time and in higher frequencies. In addition, the results presented here suggest that grooming, as a means of creating stable social bonds and familiar relationships in the long term, might be having an important effect in the formation of feeding parties in *Ateles*. Kinship itself was not found to be significantly associated with co-feeding. This finding seems to concur with Boyd [1992] in the sense that reciprocity among the co-members of the FG has evolved as a consequence of subjects interacting with each other during a lengthy period. As suggested by other authors, evidence of altruistic behavior toward kin is strongest among primates who live with their kin because subjects that interact with their kin develop familiar relationships. The best example of kin selection takes place among female Cercopithecine primates, such as baboons, macaques, and vervet monkeys, because females generally remain in their natal groups among their matrilineal relatives for life [Kawai, 1958; Sade et al., 1976; Bernstein, 1999; Strier, 2000]. The fact that the members of the FG were closely bonded and reciprocated each other's investments may indicate that spider monkeys living under captive or provisioned environments are able to develop a high degree of socialization [Strier, 2000]. Moreover, the differences in social behavior between the FG and the UFG concurs with Kinzey and Cunningham [1994] in relation to the plasticity of platyrrhine sociality, because two extremely different social systems were observed in this study: the UFG showed a non-reciprocal sociality and the FG a reciprocal one. The results of this study also provide further evidence on the social adaptability of fission–fusion species [de Waal, 1994] and contradicts the findings of other authors on an *Ateles* "species-typical" behavior in captivity [Anaya-Huertas and Mondragon-Ceballos, 1998].

The results presented here provide evidence on the role of familiarity for the development of feeding tolerance in *Ateles*. The results of this study suggest that *Ateles*, despite having evolved a very flexible sociality is, as any other anthropoid primate, capable of developing reciprocal relationships through social grooming. Finally, the results presented here also suggest that even if grooming is not a common behavior observed in New World primates, it is a very powerful bonding mechanism in the long term when it occurs. In this study, sharing access to food seems to depend on whether animals have been able establish grooming relationships of high intensity during long socialization periods.

There is a large knowledge gap on how the social networks of wild spider monkeys are formed and maintained. The results of this study suggest that social grooming might be involved in the formation of feeding subgroups in wild *Ateles*.

CONCLUSIONS

1. Captive spider monkeys living in familiar environments tend to engage in social grooming and embracing in higher frequencies than unfamiliar conspecifics. Familiar spider monkeys seem to reciprocate food sharing with social grooming. Therefore, affiliative investment through grooming might be an important factor associated with feeding tolerance among familiar conspecifics.
2. In this study, unfamiliar spider monkeys had not yet invested in the social network and were consequently incapable of reciprocating each other's investments by sharing access to food. Therefore, unfamiliar subjects were found to possess a stronger tendency to individually monopolize resources. One explanation for this is that, in this study, unfamiliar spider monkeys might not have yet developed long-term affiliative relationships for co-feeding to occur.
3. This study provides evidence on the role of grooming in the formation of feeding parties in captive spider monkeys, and how subjects of this species might be investing and reciprocating differentially with familiar conspecifics.

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