Exchange, Affiliation, and Protective Interventions in Semifree-Ranging Brown Capuchin Monkeys (*Cebus apella*)

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The ''social intelligence'' hypothesis proposes that intelligence evolved as a consequence of the need for behavioral maneuvering to deal with the complexities of social life. As a result, coalitions have received considerable attention. Here we present the patterns of coalitionary behavior observed in a semifree-ranging group of *Cebus apella* and explore the effects of kinship, spatial proximity, and rank. In contrast to descriptions of Old World monkeys and to some descriptions of capuchins, kinship did not influence the pattern of coalitionary behavior, although individuals tended to help those that remained in close proximity. Rank had the greatest influence on coalitions: those that interfered in conflicts (often the alpha) were higher ranking than both contestants and supported the most subordinate (younger) interactant. However, rank did not influence the coalitionary support when conflicts involved only adults. We found no evidence that individuals were making use of triadic knowledge, and most of the coalitions can best be described as protective interventions involving immatures. The overall low rate of coalitions may be due to a period of social stability. Am. J. Primatol. 68:765–776, 2006.   © 2006 Wiley-Liss, Inc.

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INTRODUCTION

In many social species an individual's hierarchical position is dependent not only on dyadic comparisons of intrinsic power, but also on the interference of third parties in ongoing conflicts. As a consequence, strategies of differential support based on the kinship, affiliation, or rank of the participants are observed in many primate groups [Cords, 1997; Harcourt & de Waal, 1992]. Thus, while some models predict patterns of coalition due to ecologically determined competitive regimes extrinsic to the group [e.g., Isbell & Young, 2002;

Sterck et al., 1997], coalitions are also affected by factors that are intrinsic to the social organization of each group [Chapais, 1992; Datta, 1992].

Given the possible risks of intervening in an ongoing conflict, kinship is assumed to be, and has been described as, an important variable that influences the pattern of coalitionary behavior. Both male and female primates perform low-risk (against a subordinate) and high-risk (against a dominant) interferences on behalf of relatives [Ehardt & Bernstein, 1992]; however, higher-risk interferences are performed more promptly by females on behalf of close vs. distant kin [Cheney, 1977; Silk, 1999]. This systematic differential support of kin in within-group conflicts establishes the nepotistic matrilineal social organization seen in many Old World monkey populations [Berman, 1983; Chapais, 1983, 1995; Cheney, 1977; Gouzoules & Gouzoules, 1987].

Interference on behalf of non-kin has been interpreted as an exchange of favors between individuals. Individuals are described as forming (or trying to form) affiliative relations (e.g., offering grooming to higher-ranking individuals) in order to receive support in agonistic conflicts against a third party [Seyfarth, 1977, 1983]. However, immediate benefits derived by the supporting party may be more important than exchange transactions for delayed benefits. When they interfere in non-kin contests, supporters tend to rank higher than both contestants or at least higher than the target animal, and the intervention is considered to be of low risk. The immediate benefit to the intervener seems to be the ''psychological'' victory scored over the target [Chapais, 1992, 1995; Harcourt & de Waal, 1992; Noë, 1990; Noë et al., 1991; Watts, 1997].

Most studies on coalitionary behavior in primates have been conducted on cercopithecoids and apes. Few studies have focused on platyrrhines, which exhibit social systems that are considerably more variable than those seen in cercopithecoids [Strier, 1994]. Monkeys from the genus *Cebus* are an interesting model for validating hypotheses about the evolution of sociality and intelligence. *Cebus* species have a large neocortex ratio, grooming has been described as occurring down the hierarchy [Parr et al., 1997], and the species vary in several features of their social organization, such as the number of reproductive males in the group, the occurrence of infanticide, and the degree of despotism in the dominance hierarchy [Janson, 1984, 1986; O'Brien, 1991, 1993a,b; O'Brien & Robinson, 1993; Perry, 1996b, 1997]. Observations of *C. apella* groups in noncaptive environments indicate that this species forms one-male groups (or age-graded groups, i.e., composed of an alpha male and his putative subadult male offspring), with patterns of coalitions and affiliation that markedly differ from those observed in other *Cebus* species [di Bitetti, 1997; di Bitetti & Janson, 2001; Ferreira, 2003; Izar, 2004; Izar & Sato, 1997; Izawa, 1994; Janson, 1984, 1986].

Previous studies on the coalitionary behavior of *C. capucinus* and *C. olivaceus* suggested that relatedness increases the chances of coalitions between dyads, since most coalitionary dyads are composed of females, the philopatric sex [O'Brien & Robinson, 1993; Perry, 1996b, 1997]. However, O'Brien [1991, 1993a,b] noted that in contrast to the patterns of matrilineal support in Old World monkeys, juveniles supported adult females twice as often as adult females supported juveniles, and higher-ranking females were supported more frequently than lower-ranking females.

Studies of the exchange of grooming for support in *C. capucinus* and *C. olivaceus* found that dyads that groomed each other frequently also supported each other at higher rates compared to dyads that groomed less frequently [di Bitetti, 1997; Manson et al., 1999; O'Brien, 1993a,b; Perry, 1996, 1997]; however, only Perry [1996b] explored the direction of such behaviors. In all the

above studies, dyads that groomed frequently also remained in close proximity, leaving the hypothesis of exchange of grooming for support unassessed in most wild groups. Finally, dominance rank influences capuchins' coalitionary patterns. The alpha male and high-ranking females are the most active interveners, while subadult, subordinate males are the most common victims [di Bitetti, 1997; O'Brien, 1991, 1993a; Perry, 1996a,b, 1997, 1998]. Revolutionary coalitions are uncommon in *C. capucinus* groups [Perry, 1996a,b, 1997, 1998].

Here we analyze coalitions in a semifree-ranging, partially provisioned group of *C. apella*, and explore the influences of kinship, spatial proximity, and rank of the individuals on the expression of this behavior. Since in the study group, in contrast to wild groups, adult females are unrelated (see Materials and Methods), we hypothesized that 1) if kinship influences coalitions, support would be offered preferentially between mothers and offspring and between siblings; 2) if affiliation influences coalitions, more affiliated dyads would support each other more frequently compared to less-affiliated dyads; and 3) if rank influences the coalitionary support of these *C. apella* individuals in a way similar to that described for Old World matrilineal monkeys and *C. capucinus* and *C. olivaceus* [e.g., Perry et al., 2003], support would be offered preferentially by higher-ranking members and to the highest-ranked of the two opponents.

MATERIALS AND METHODS

Study Group and Site

The study group consisted of 20 individuals (three adult males, four adult females, two subadult males, six juvenile males, three juvenile females, and two infants). There was one clear alpha male, an alpha female, and an age/size-based hierarchy for the rest of the group [Ferreira, 2003; Izar et al., 2005]. The two subadult males were included in the analyses as adults. This group was formed after two adult males and three adult females were released into the study area. Known kinship relations among group members are shown in Table I.

The study group lived in a semifree-ranging condition in a reforested area of 18 ha within the Tietê Ecological Park (total area of 1,400 ha in eastern São Paulo County, Brazil). There are no natural predators of *Cebus* in this area, and individuals are provisioned daily with food. Although the individuals are not completely dependent on the provisioning, the distribution of food on a circular platform of 1 m diameter offers opportunities for within-group contest competition for preferred foods.

Data Collection

The group was accompanied by an observer (R.G.F.) for a total of 849 hr, and each individual was observed for a focal scan period of 10 min, five times per month. During a 10-min period of observation of a focal animal, the following data were noted at each minute: 1) focal activity and interactions, and 2) neighbors up to 1 m or 10 m distance. The data used here derive from the period after full habituation of the animals and before the death of the initial alpha female of the group (January 2000 to January 2001), totaling 196 hr of focal scan data collection (see Table I), and 344.4 hr of contact with the group.

Data on coalitions and aggressive interactions were collected on an all-occurrences basis. Whenever signals or sounds of aggressive interactions were heard, the focal-scan sample was interrupted and only data on the aggressive/coalition event were recorded. The focal-scan collection schedule was reinitiated

TABLE I. Age, Sex, and Kinship Relations of the Individuals Observed During the Study

Name	Age[a]/Sex	Comments	Total scans Jan 2000 to Jan 2001[b]
Bisqui	Adult ♂	Alpha male	62
Suspeito	Old adult ♂	Castrated; founder	62
Medeiros	Old adult ♂	Castrated; founder	61
Eli	Subadult ♂		63
Pedro	Subadult ♂		63
Meire	Adult ♀	Alpha female; founder. Died 17 months after beginning of observations	61
Edu	Juv. III ♂	Mother: Meire. Birth 25/09/96	63
Darwin	Juv. I ♂	Mother: Meire. Birth 22/05/99	60
Ana	Adult ♀	Founder	62
Lobato	Juv. II ♂	Mother: Ana Birth ??/01/97	62
André	Infant	Mother: Ana. Birth: 30/11/99 (Died at 6 months old)	30
Janete	Adult ♀	New alpha female	61
Vasca	Juv. II ♀	Mother: Janete. Birth ??/01/97	62
Joana	Juv. I ♀	Mother: Janete. Birth: 22/10/99	61
Fis	Adult ♀	Founder	61
Frank	Juv. III ♂	Mother: Fis. Birth 15/09/96	61
Cisca	Juv. II ♀	Mother: Fis. Birth ??/07/97	60
Manoel	Juv. II ♂	Mother: Fis. Birth: 23/06/98 (first offspring born after Bisqui reached the alpha position)	62
Quimico	Juv. I ♂	Mother: Fis. Birth: 30/05/99	62
Fractal	Infant	Mother: Fis. Birth: 24/06/00	37

[a]Age at the beginning of observations.
[b]Each scan sample lasted 10 minutes.

after the end of the conflict. Approach–retreat interactions, supplants, and displays of submission (i.e., lowering of body) were categorized as ''low-intensity aggressive interactions.'' Open-mouth threats, lunges, chases, and attacks (pushes, bites, etc.) were recorded as ''high-intensity aggressive interactions.'' The distinction between these types of aggression is important because it was assumed that only during high-intensity aggressive interactions could a third party effectively (and clearly) interfere. For all episodes of aggression the following data were recorded: 1) the identities of the initiator and recipient of aggression, 2) whether escalation of aggression occurred, and 3) if a third party interfered, the identities of intervener and the recipient of support.

A coalition was defined as the directed intervention of a third party after the start of a conflict between two others, with clear support for one participant in the fight. The ''intervener'' would get close to the ''recipient'' (body contact between them was the rule), and offer support by threatening the ''victim'' of the coalition. Only the first individual to offer support to each contestant was coded as an intervener (except for polyadic interactions, when two or more individuals intervened simultaneously). Only interventions that took place while conflict was ongoing were coded as coalitionary. Aggressive interactions involving one opponent shortly after the previous conflict ended were not analyzed here, since their nature as an offer of support or as a dyadic interaction was unclear

[cf., de Waal, 1992]. Similarly, the ''cooperative attack'' of two individuals against one (i.e., at the start of the episode two individuals were already supporting each other against a third) was also not coded as a coalitionary intervention, since the initial motivation for the joint action was unknown.

Data Analyses

To test the hypothesis that kinship and affiliation influenced the dynamics of coalitions in this *C. apella* group, the intervener and recipient were categorized as 1) related, 2) unrelated/affiliated, or 3) unrelated/not affiliated. Affiliated dyads were defined based on a comparison of the Jaccard index of association for 1-m proximity between individuals ($J_{xy} = a/(a + b + c)$), where ''a'' is the number of scans in which X and Y were observed within a radius-distance of 1 m, ''b'' is the number of scans in which X was observed and Y was not, and ''c'' is the number of scans in which Y was observed and X was not). Each dyad had a unique Jaccard index. For each member of a dyad the mean and standard deviation (SD) of its Jaccard association relative to all other group members' values were calculated. Dyads with Jaccard values above the mean + 1 SD were considered affiliated partners, unless these were related individuals, in which case relatedness took priority. The 1-m distance was considered a suitable definition for affiliated dyads, based on previous analyses of spatial proximity in this group [Ferreira, 2003]. Chi-square analyses were based on the null assumption that dyads forming coalitions should occur in proportion to the number of related, unrelated/affiliated, or unrelated/not affiliated dyads in the group.

We conducted a τK_r test for matrices correlations using the program MatrixtesterPrj [Hemelrijk, 1990] to further explore the second hypothesis, comparing the Jaccard matrix (an index of proximity among all dyads) and the matrix of coalitions among dyads. The τK_r test is useful for correlating matrices of dyadic relationships because it avoids statistical dependency due to individuals recurring in several pairs. The test was set for 2,000 permutations.

For the third hypothesis, we again conducted the τK_r correlation test. Individuals were ranked by dominance such that the alpha male = 1 and the most subordinate individual = 20. Given the age/size-graded aspect of the group's hierarchy, rank and age were highly correlated (τK_r: -0.764 pl = 0.0005, with age ranked from youngest to oldest). Two sets of analyses were performed: one using age as the covariate, and one using rank as the covariate. Again τK_r tests were performed such that the number of support given, the number of support received, and the number of episodes as a victim of coalitions were correlated with the hypothetical matrix of rank of individuals. The tests were set to 2,000 permutations.

Binomial tests were also used to compare the relative rank among the three participants in each coalitionary episode as:

1. Intervener vs. recipient: value 1 = intervener ranked higher than the recipient; value 0 = recipient ranked higher than the intervener.
2. Intervener vs. victim: value 1 = intervener ranked higher than the victim; value 0 = victim ranked higher than the intervener.
3. Recipient vs. victim: value 1 = recipient ranked higher than the victim; value 0 = victim ranked higher than the recipient.

Significance was set at 0.05, and all tests were two-tailed.

RESULTS

Rate and Context of Supportive Interactions

A third party interfered in 45 aggressive episodes among members of the group during the study period, yielding a frequency of 0.13 coalitions between any age/sex class per hour. However, if we consider the frequency of high-intensity aggressive episodes (118 episodes), coalitions occurred in 38.2% of the conflicts.

Most coalitions (26 or 57.8%) occurred during contests over food. Of these, four were polyadic (i.e., two individuals simultaneously interfered in the same conflict). Polyadic coalitions involved only adult members of the group. Eight coalitions occurred during nonfood conflicts: two (4.4%) coalitions occurred when a middle-ranking individual redirected aggression toward another individual enlisting support from the higher-ranking individual toward a lower-ranking individual; two (4.4%) were opportunistic, with one subordinate individual helping the winner of a dyadic conflict; two (4.4%) interventions involved cycling females, and two (4.4%) occurred in the context of play. Finally, in 11 episodes (24.4%) the initial context of the aggressive interaction could not be determined, although all individuals were foraging when the aggression started. In all 45 cases the coalitionary dyad (or trio) succeeded in displacing the victim.

The alpha male was the single more frequent intervener (17 of 45 episodes; binomial test, $P < 0.05$). The victims were adults or subadult males (16 of 45 episodes; binomial test, $P < 0.05$), and the recipient of support was an immature in 29 of 45 episodes (binomial test, $P < 0.05$ (Table II)).

Males interfered in conflicts significantly more than females, accounting for group composition ($\chi_{21} = 12.33$, $P < 0.001$). The alpha male interfered significantly more than other males ($\chi_{21} = 39.06$, $P < 0.001$).

Kinship, Affiliation, and Support

The first analyses of kinship and affiliation effects on coalitions included only confirmed mother–immature dyads. In this case, of the 190 possible dyads within the group, 25 (13.2%) were related, 20 (10.5%) were unrelated/affiliated, and 145 (76.3%) dyads were neither related nor affiliated (see Table I). Thirty-two

TABLE II. Role of Age-Sex Classes During Three Types of Conflicts: Involving Only Adults, Adults vs. Immatures, and Immatures vs. Immatures

Type of conflict	Role	α♂	α♀	♂	♀	Juv♂	Juv♀	Inf	Total
Adult vs. adult	Intervener	6	2	3	2				13
	Recipient	1	1	4	7				
	Victim		1	8	4				
Adult vs. immature	Intervener	6	1	6	3		1		17
	Recipient			1	2	11	3		
	Victim			8	6	2	1		
Immature vs. immature	Intervener	5		5	1	3	1		15
	Recipient					7	4	4	
	Victim					9	6		
Total	Intervener	17	3	14	6	3	2		45
	Recipient	1	1	5	9	18	7	4	
	Victim		1	16	10	11	7		

TABLE III. Rank of the Participants in Coalitionary Episodes

	Higher ranking individual			Dyads with equal rank
	Intervener	Recipient	Victim	
Intervener × victim	42		3	
Immature × immature	15		0	
Immature × adults	14		3	
Adults × adults	13		0	
Intervener × recipient	39	6		
Immature × immature	14	1		
Immature × adults	15	2		
Adults × adults	10	3		
Recipient × victim		14	31	
Immature × immature		3	11	1
Immature × adults		2	15	
Adults × adults		8	5	

different intervener–recipient dyads performed the 45 coalitionary episodes observed. Two (6.2%) intervener–recipient dyads were related, eight (25%) dyads were unrelated/affiliated, and 22 (68.8%) dyads were neither related nor affiliated. Related and affiliated dyads supported each other in ways that were not predicted by chance ($\chi_{22} = 23.17$, $P < 0.001$). Related dyads supported each other less than expected ($\chi_{21} = 4.48$, $P < 0.05$), while affiliated dyads supported each other more than expected ($\chi_{21} = 22.17$, $P < 0.001$).

When we separated coalitionary episodes that involved adults from those that involved only immatures or adults with immatures, we found that adults supported affiliated adults and affiliated immatures more than expected ($\chi_{21} = 14.78$, $P < 0.001$, $\chi_{21} = 30.7$, $P < 0.001$, respectively). Matrilineal relatedness did not influence adult support of immatures, since female adults supported kin immatures as expected from their proportions in the group ($\chi_{21} = 3.51$, $P = 0.061$). However, the alpha male (as the putative father) supported "his" offspring more than expected ($\chi_{21} = 18.14$, $P < 0.001$).

The supportive behavior was positively correlated to the index of Jaccard between dyads (τ $K_r = 0.111$; $p_r = 0.03$), i.e., dyads that maintained close proximity supported each other more than dyads that were less frequently in close proximity. The Jaccard proximity index of the intervener/recipient (mean = 0.0263) was significantly higher than that of the intervener/victim (mean = 0.016; Mann-Whitney z = −2.011, df = 41, $P < 0.05$).

Rank and Support

Receiving support was negatively correlated with rank (controlling for age: τ $K_{r} = -0.192$, $p_l = 0.025$); the intervener of support ranked higher than the recipient. The rank of the intervener and the victims correlated negatively (τ $K_r = -0.181$, $p_l = 0.049$); again, the intervener ranked higher than the victim (see Table III).

However, when the coalitionary episodes were separated by age/sex classes (see Table III), interveners ranked higher than both recipients and victims in conflicts involving only immatures ($P < 0.001$), and in conflicts involving adults and immatures ($P < 0.001$). Interveners did not rank higher than recipients of

support in conflicts between adults (binomial test: NS), although they again ranked higher then the victims (binomial test: $P < 0.001$).

Recipients of support ranked lower than the victim in most coalitionary episodes (binomial test: $P < 0.05$; Table IV). Again, this pattern of supporting the most subordinate was found in conflicts involving only immatures (binomial test: $P = 0.057$, excluding one equal-rank dyad) and for conflicts between adults and immatures (binomial test: $P < 0.05$). No influence of rank was found in conflicts that involved only adults (binomial test: NS).

DISCUSSION

The low rate of third-party interference observed in this study compared to the rate observed by Perry [1996b, 1997, 1998, 2003] in *C. capucinus* may be related to the stability of the dominance hierarchy and low occurrence of high-intensity agonistic episodes in the study group. Indeed, Perry's studies involved a period of social instability due to reversals in the male hierarchy. During the period of data collection in the present study, only 34 high-intensity agonistic events occurred for every 100 hr of observation. Nevertheless, third-party interference influenced the outcome of almost 40% of all high-intensity aggressive interactions involving two members of the group, which suggests that support is an important factor in the social dynamics of this group. During a later period of social instability in this group [Falótico et al., 2003], much higher aggressive rates and a different pattern of coalitionary behavior were observed.

Notwithstanding this low rate, some trends in the dynamics of coalitionary behavior could be discerned.

Sexual Competition and Protective Interference

Females infrequently interfered in contests (9 of 45 episodes) and did not form coalitions with each other to defend feeding sites. This contrasts to descriptions of other *Cebus* groups (especially *C. capucinus* [Perry, 1996b]) in which females were the most active participants in coalitionary interactions. Furthermore, even though all of the females had infants and juvenile offspring, the females did not interfere disproportionately on behalf of their offspring. Although these results contrast with previous descriptions of wild *Cebus* groups, they are in accordance with predictions that when groups of unrelated females inhabit areas where food is not a limiting factor, females are not expected to form coalitions with each other, and no differential support of kin is necessary to guarantee reproductive success [Isbell & Young, 2002; Sterck et al., 1997]. Furthermore, in a recent paper Izar [2004] described the same lack of matrilineal support during conflicts in a wild *C. apella* group in the Atlantic Forest. The pattern observed in the present study is unlikely to be an atypical consequence of the provisioning of these animals.

In two of the few papers that have described the social dynamics of wild *C. apella*, Janson [1984, 1986] argued that the organization of *C. apella* groups is profoundly influenced by the preference of adult females to mate with the alpha male. He related this female preference to the alpha males' ability to monopolize and exclude the immatures of other adult males from feeding sites. The preponderant role of the alpha male in supporting immatures against adult males observed in this group suggests that by intervening in competitive interactions during foraging activities, the alpha male may decrease the level of resource competition experienced by immatures that are probably his offspring. In this case, the pattern of intervention by the alpha male could be considered as

direct parental investment. Second, by protecting his probable offspring, the alpha male may simultaneously be displaying to females his abilities not only in terms of food defense but also as a protector of immatures against potential harassment, as has been observed in gorillas. If this is the case, Janson's suggestion can be expanded, in that behaviors other than tolerance in feeding sites may contribute to females' preferences for mating with the alpha male.

In addition to supporting immatures against adults, the alpha male consistently intervened in favor of the most subordinate of two immature contestants. The overall pattern suggests a social role as protector, with the alpha male minimizing possible social disruptions resulting from conflict among group members [Ehardt & Bernstein, 1992]. Descriptions from studies of wild *C. apella* in which the alpha male was also responsible for group defense against predators and other groups support this suggestion [Izar, 2004; Janson, 1986]. Similarly, Perry [1998] described ''separating interventions,'' in which *C. capucinus* alpha males disrupted affiliative interactions between subordinate males. Thus, the protective role played by *C. apella* alpha males may be similar to that observed in lemurs [Roeder et al., 2002] and one-male groups of gorillas [Watts, 1997].

Affiliation and Coalitions

Our results indicate that affiliated individuals tended to support each other more than non-affiliated individuals. This pattern is not simply due to the proximity of affiliated individuals to conflicts, since support was offered to the opponent with the higher index of proximity with the intervener. This influence of affiliation on supportive behavior was independent of relatedness.

Affiliative relationships are also related to the amount of grooming exchanged between a dyad (grooming and high social proximity were correlated in this group) [Ferreira, 2003]. Interchange of grooming for support in *Cebus* species has not yet been conclusively reported, but affiliated individuals (inferred from high rates of resting in contact and nearest-neighbor preferences) support each other more than do non-affiliated individuals. In *C. apella*, di Bitetti [1997] found that the dyads that were most often observed grooming were also those that formed the most coalitions against other individuals. Izar [1994] observed preferential partnerships between *C. apella* male–female dyads, characterized by grooming exchange, increased proximity, and support in conflicts. Perry [1996b] also found that *C. capucinus* females that exchanged higher rates of grooming and maintained close proximity also supported each other more compared to other female–female dyads.

Coalitions Among Adults

Protective interventions of adults supporting immatures accounted for the bulk of coalitions we observed. When conflicts involved two adults, the intervener ranked higher than the victim but did not always rank higher than the recipient of his or her support. Support in conflict among adults was not as clearly protective, with some higher-ranking adults being supported against lower-ranking ones.

Coalitions among adults usually involved more than three participants (i.e., two individuals interfered simultaneously; see Materials and Methods) and more intense aggression than the conflicts involving immatures. In three conflicts among adults, two individuals interfered simultaneously in helping the same recipient, while in a fourth conflict each contestant received support from a different individual. This type of coalition has the following characteristics:

1) unpredictability, with the individuals reversing their roles or refraining from interfering in the conflict as a function of the identity of the antagonists; 2) the episodes involved only adult (or subadult) members of the group, suggesting that some learning may be necessary for effective social action; and 3) the episodes normally involved more than three individuals, suggesting that considerable simultaneous information has be integrated and acted upon. Notwithstanding the low number of adult–adult coalitions, we suggest that such episodes may represent the type of coalitions searched for in the studies of social intelligence, in which the individuals are calculating whom to support against whom, on the spur of the moment, reflecting relatively high levels of social intelligence.

Two recent studies focused on whether the pattern of soliciting support in triadic conflicts provided evidence of social knowledge in monkeys. Silk [1999] showed that male bonnet macaques based their decisions on individuals' rank, and solicited support from individuals that outranked their opponent. Similarly, Perry et al. [2003] found that *C. capucinus* based their coalition decisions on both the quality of the social relationship and rank: support was solicited from individuals that either have more affiliative relations to ego than to their opponent, or to those that outrank the opponent, or where both factors combine.

In this study we found that individual coalitionary decisions were made to support the most subordinate of two opponents. However, supporting the victim or losing party in a fight per se is not evidence of an understanding of rank relations between two others. A less complex, cognitively based explanation using simple rules of thumb cannot be excluded, for example, to support those displaying more signals of need during the conflict who are typically the more subordinate.

CONCLUSIONS

Social factors influenced the pattern of coalitionary behavior observed in this semifree-ranging group of *Cebus apella*. Relative rank underlies decisions about whether an individual will join an ongoing fight, and which individual will be supported. Increased spatial proximity (or tolerance of proximity) between dyads was correlated with an increased chance of receiving support from close associates.

The main pattern of coalitionary behavior observed in these *C. apella* was a protective intervention by the alpha male on behalf of immatures and the most subordinate contestant. This pattern of protective intervention mirrors suggestions made by Janson [1984, 1986] regarding the role of the alpha male in *C. apella* groups. Strategic decisions about forming coalitions could not be quantified, but interference in conflicts that involve only adults appear to follow more contextual rules than predicted by simple rules of thumb.

Finally, although this study was based on only one social group and a few coalitionary interactions, the pattern observed here could occur in wild *C. apella* groups, especially during periods of social stability. In large-brained species with wide dietary variability, such as *C. apella*, intraspecific variation in social organization may be great, reflecting a broad continuum rather than discrete categories. Furthermore, it emphasizes the importance of females' preferences for males as a determinant of social structure. The universal characterization of this species as ''female-bonded'' or ''resident-nepotistic'' may be unwarranted, and the light shed on internal group dynamics by studies of coalitions and proximity may help illuminate this variation.

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