

## Explaining Variation in Affiliative Relationships among Male White-Faced Capuchins (*Cebus capucinus*)

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### Key Words

Male bonding • Capuchins • *Cebus capucinus* • Affiliation • Kinship • Costa Rica

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### Abstract

Relationships among coresident male white-faced capuchins are highly variable, ranging from affiliative to aggressive. In this paper I examine the affiliative relationships of all adult and subadult males residing in four social groups in Santa Rosa National Park, Costa Rica. Relationships among males in two study groups were neutral and tolerant, while in the remaining two groups males were highly affiliative. Male-male dyadic affiliative interactions were examined to determine which variables (group size, sex ratio, age relationship, relationship duration, and rank distance) influence the quality of male relationships within the study groups. Group size explained much of the variation, with males in small groups being more affiliative. However, the duration and history of the relationship among coresident males appears to be the most important variable in understanding male-male relationships within social groups.

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### Introduction

Perceptions of the ‘typical’ male primate have changed dramatically over the past few decades. Early reports of male relationships stressed aggressive interactions and how this aggression influenced male dominance hierarchies [Hall and Devore, 1965; Kaufman, 1967; Packer, 1979]; males were described as being intolerant of one another and in constant competition for access to mates [Zuckerman, 1932]. Although male relationships in some species are best characterized as being aggressively competitive, e.g. brown capuchins [Janson, 1985]; rhesus macaques [Colvin, 1983], savanna baboons [Packer, 1979], there is a small number of species

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that is characterized by close affiliative relationships among coresident males [van Hooff and van Schaik, 1994]. As long-term studies of non-human primates increase, we are learning that relationships among males are not as easily categorized as once thought. These relationships vary both inter- and intraspecificly, and males may well display greater levels of diversity in their relationships than females [van Hooff and van Schaik 1994].

White-faced capuchins (*Cebus capucinus*) reside in multimale-multifemale social groups characterized by female philopatry and male dispersal [Fedigan, 1993]. The relationships among male white-faced capuchins (*C. capucinus*) are extremely variable both within individual long-term study groups and across study sites. For example, Perry [1998b] described male-male relationships in her study group at Lomas Barbudal, Costa Rica, as being tension-loaded and more aggressive than affiliative. Oppenheimer [1968] and Mitchell [1989] at Barro Colorado Island, Panama, and Rose [1994] at Santa Rosa, Costa Rica, all report that males in their study groups exchanged few affiliative interactions with one another. In contrast with these findings, Fedigan [1993] found that males in her Santa Rosa, Costa Rica, study groups groomed and affiliated with one another more frequently than they did with group females. Perry [pers. comm.] also reports higher levels of male affiliative interactions in her new study group at Lomas Barbudal. In this report I examine the social relationships among male white-faced capuchins residing in four social groups in Santa Rosa National Park (SRNP), Costa Rica, in an attempt to determine the factors influencing the variability in male relationships within this species.

## Causes of Variation in Male-Male Relationships

### *Male Dispersal and Kinship*

The majority of species characterized by strong affiliative bonding among resident males are male philopatric, e.g. chimpanzees [Goodall, 1986], squirrel monkeys [Boinski, 1994], hamadryas baboons [Sigg et al., 1982], red colobus monkeys [Struhsaker, 1985; Stanford, 1998] spider monkeys [Symington, 1990] and muriquis [Strier, 1994a]. This correlation between male bonding and male philopatry led to an initial assumption that kinship is a necessary precursor for bonding to occur [van Hooff, 2000; van Hooff and van Schaik, 1994]. However, there is increasing evidence for a number of species that collaborative and affiliative bonding may occur in the absence of kinship. (For reviews: van Hooff [2000], Pereira et al. [2000]; lions: Packer and Pusey [1982]; cheetahs: Caro [1994]; savannah baboons: Nöe and Sluijter [1987]; bonnet macaques: Silk [1994]; macaque sps.: Hill [1994]; chimpanzees: Mitani et al. [2000], Goldberg and Wrangham [1997]). Although groups characterized by female philopatry and male dispersal are thought to contain unrelated immigrant males, in the absence of male philopatry, kinship among group males can be maintained through parallel dispersal (kin-linked immigration; [van Hooff 2000]). Parallel dispersal can occur when male siblings emigrate together, or when males preferentially disperse into groups containing familiar, previously dispersed, males. There is evidence for kin-linked immigration in vervets and in several species of macaques where young males have been observed leaving their natal groups together [Melnick and Pearl 1987; Pusey and Packer

1987; van Hooff and van Schaik 1994]. Moore [1992] suggests that parallel dispersal can result in a level of relatedness within the new group that is comparable to that found in groups made up of philopatric individuals.

Parallel dispersal may, therefore, enable males to maintain high levels of relatedness, and it could account for observations of high rates of affiliative and cooperative interactions among some males in female philopatric species, as has been reported for bonnet macaques [Silk, 1992, 1994]. Male white-faced capuchins disperse from their natal groups at approximately 4.5 years and continue to disperse throughout their lives about every 4 years [Jack, 2001]. Parallel dispersal occurs at extremely high levels in this species (approximately 75% of all emigrations), and it does not diminish with male age, as has been reported for vervets and macaques [Jack, 2001]. Even if coresident males are not related, we have many observations of males who form long-lasting bonds that endure multiple emigrations. Familiarity and predictability of these enduring relationships will also likely be influencing male affiliative interactions within groups [Strier, 1994b].

#### *Group Size and Sex Ratio*

Hill [1994] suggests that variations in group size and composition can also act to influence the patterns of social interactions within groups. In his review of relationships among male macaques (sps.), Hill [1994] found that affiliative behavior is more frequent in smaller groups, although sex ratio also played an important role in his findings. Hill also found that in groups with highly skewed sex ratios (fewer males to females), there are more potential female and immature partners to affiliate with than in groups with similar ratios of males to females. In small groups this will also be a factor as there is a shortage of potential partners, and males may alternatively form relationships with other males.

According to our park-wide censuses, the average size of capuchin groups in SRNP is 17.2 individuals ( $n = 34$  groups; counts included adults and immatures), with group sizes ranging from 7 to 36 members [Fedigan and Jack, 2001]. Likewise, adult sex ratio (including subadult males) also varies within the SRNP capuchin population, ranging from 0.42 to 1.0, with a mean of 0.86 (M:F). It is possible that this variation in group size and adult sex ratio may produce the variation in male affiliative interactions that has been reported among male white-faced capuchins.

#### *Dominance Rank and Age*

Male dominance rank may also influence the patterning of affiliative interactions among coresident males. For example, in brown capuchins (*Cebus apella*) the alpha male spends the majority of his time interacting and affiliating with group females, while subordinate males remain together on the group's periphery [Janson, 1985]. Even among the true multimale *Cebus* species, that is *C. albifrons* and *C. capucinus*, group females are very closely bonded to alpha males and spend a great deal of their time interacting with them [Strier, 1999; Fedigan, 1993].

Age may also be an important variable influencing affiliative interactions among males. In many primate species, males pass through a transitional phase between the juvenile stage and adulthood. Known as the subadult period, these males are not physically mature but have undergone behavioral changes, and they begin to behave more like adult males than juveniles [Schapiro et al., 1995]. It is at

this time that males begin spending more time with adult females rather than similarly aged males, but this is also an important time for males to forge relationships with other males in their group. This may be particularly important for a species like white-faced capuchins, where males rely on coalitionary partners to gain entry into and maintain residency within social groups [Rose and Fedigan, 1995; Perry 1998a, 1998b]. Male white-faced capuchins do not reach full physical maturity until 10 years of age [Fedigan et al., 1996], however, subadult males still make important alliance partners, particularly when it comes to group defense [Jack, unpublished data].

In this study I examine the patterns of affiliative interactions in male white-faced capuchins, by first comparing inter- and intrasexual affiliative interactions to determine with which sex males are more closely bonded. I then examine factors influencing affiliative relationships among male-male dyads to determine why some male dyads are more closely bonded than others. I investigate the duration of the relationships among group males (proxy measure of kinship), group size, adult sex ratio, rank distance between males, and age relationship between males (i.e. adults, subadults, or adult/subadult dyad) as possible factors influencing variability in male-male relationships. Measures of affiliation include time spent in contact (all nonaggressive contact), grooming, and sustained proximity in the absence of aggression.

## Methods

Data for this study were collected in the Santa Rosa Sector of the Area de Conservacion Guanacaste, Costa Rica. Formerly known as SRNP, the area encompasses approximately 108 km<sup>2</sup> of dry deciduous forest and reclaimed pasture and is located 35 km northwest of Liberia, in the Guanacaste Province. Dr. Linda Fedigan, University of Alberta, and her students have collected observational and demographic data on the white-faced capuchins in Santa Rosa since 1983.

From February 1998 through to April 1999, all adult (n = 8) and subadult (n = 3) males residing in four groups were observed: Los Valles (LV group); Cerco de Piedra (CP group); Bosque Humedo (BH group); Cuajiniquil (CU group). A fifth study group, Cafetal (CA), was also observed during February and March 1999 after the two males from the Cuajiniquil group transferred into it. Behavioral data were only collected on these two transfer males in the Cafetal group during this period and, therefore, these data are only used descriptively in this study. Following Fedigan et al. [1996], males between 7 and 10 years were classified as subadults, and those over 10 years as adults. All members of the five study groups (males, females, and immatures) were individually recognized and identified according to their size, facial characteristics, and brow shape, and all were habituated to the presence of observers.

A total of 1198.25 h of focal data were collected on the 11 subject males. Data were collected in 15-min focal animal continuous-time samples [Altmann, 1974] during which all behaviors and interactions were recorded directly into a handheld PSION computer. A focal session was discarded if the subject was out of sight for  $\geq 120$  s during the 15-min session.

### *Dependent Variables*

*Affiliative Behaviors.* Four measures of affiliation were examined: total contact, contact rest, grooming and proximity. Total contact includes any behavior during which a subject male engaged in non-aggressive body contact with another group member. This includes resting in contact, grooming (received and directed), playing, scanning, and foraging while in contact. Contact rest and grooming rates (directed and received) are subsets of total contact. Proximity was recorded continuously throughout a focal session when a male was

**Table 1.** Independent variables for male dyads

	Age	Group size	Adult sex ratio, M:F	Rank distance <sup>1</sup>	Time known months	Dyad background
Diablo/Pirate LV	ad/ad	14	0.75	2	72	Both males joined CP in 1993, though 1 month apart, following a takeover by two other males (as a subadult, Diablo joined with them); they cooperatively overtook LV group in 1997
Diablo/Side LV	ad/ad	14	0.75	1	21	Side slowly entered LV shortly after
Side/Pirate LV	ad/ad	14	0.75	1	21	Diablo and Pirate took over the group in 1997
Leo/Regis BH	ad/sa	8	1	1	58	With the exception of Leo (who entered LV group as a subadult in 1994), all of the BH males were born in LV group.
Leo/Casey BH	ad/sa	8	1	2	58	
Leo/George BH	ad/sa	9	1.33	1	53	
George/Regis BH	sa/sa	9	1.33	1	87	All of the BH males dispersed from LV together and took over BH in 1997.
George/Casey BH	sa/sa	9	1.33	2	73	
Regis/Casey BH	sa/sa	8	1	1	80	George and Casey are believed to be maternal siblings.
Spike/Garth CU	ad/ad	6	1	1	86	Born in SE group and thought to be maternal siblings. Immigrated into LV group together in 1991, entered CU group together in 1997, and then dispersed to CA group (Garth in 08/98 and Spike in 02/99)
Nose/Trickle CP	ad/ad	9	0.5	1	25	Resided briefly together in LV group in 1997. Nose entered CP group in 01/98 and Trickle joined him in 03/98.

LV = Los Valles group; BH = Bosque Humedo group; CU = Cuajiniquil group; CP = Cerco de Piedra group; ad = adult; sa = subadult.

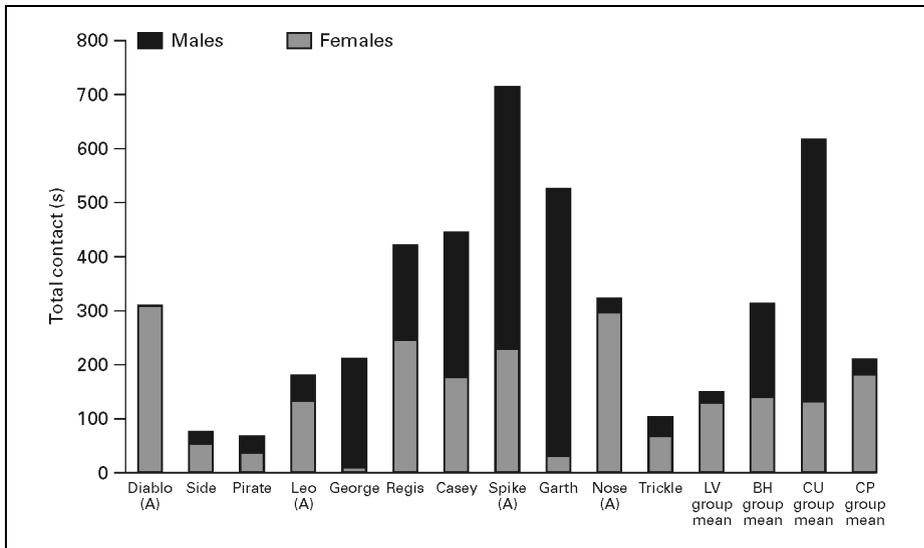
<sup>1</sup>Rank of dominant dyad partner to rank of subordinate dyad partner.

within one meter of another group member, excluding body contact. All of these behaviors were recorded as states, and the duration of each was calculated in average seconds per hour, following Perry [1998b]. Durations of male-male dyadic affiliation were calculated as the average number of seconds per hour that dyad partners affiliated.

#### *Independent Variables*

Five variables were investigated as possible factors influencing male-male relationships within groups: age relationship between males, group size, sex ratio (M:F), rank distance and duration of relationship between males. Table 1 details these variables for each of the subject male dyads. For the first variable, age-relationship, the 11 dyads were divided into the following categories: adult-adult, adult-subadult and subadult-subadult. Group size and sex ratio were also examined as variables influencing male relationships within groups. Data were collected over 15 months, during which time three of the study groups experienced changes in group composition. To keep group size and sex ratio constant it was necessary to use a subset of the focal data collected on several of the subject males. This is why sex ratios and group sizes vary for the same group in table 1.

The rank of each adult and subadult male within study groups was calculated according to the direction of submissive gestures and avoid-supplant interactions observed during focal and ad libitum data collection. Rank distance was calculated following Rose [1998], whereby the rank of the dominant individual was subtracted from that of the subordinate dyad partner. Although kinship could not be tested directly (through DNA analysis), the high rates of parallel dispersal observed in this species indicate that males within groups may indeed be closely related. As a proxy measure of kinship, I use the duration of the relation-



**Fig. 1.** Total contact time (s/h) with coresident males and females for individual males and group means. (A) = alpha male.

ship between dyad partners. Life history data were available for many of the males in the study groups [Fedigan, unpubl. data], with only two previously unknown males having entered into the study groups between 1997 and 1999. Table 1 includes a brief summary of the historical background for each dyad. The duration of the relationship between males was calculated as the minimum number of months that the males resided together in one or more groups.

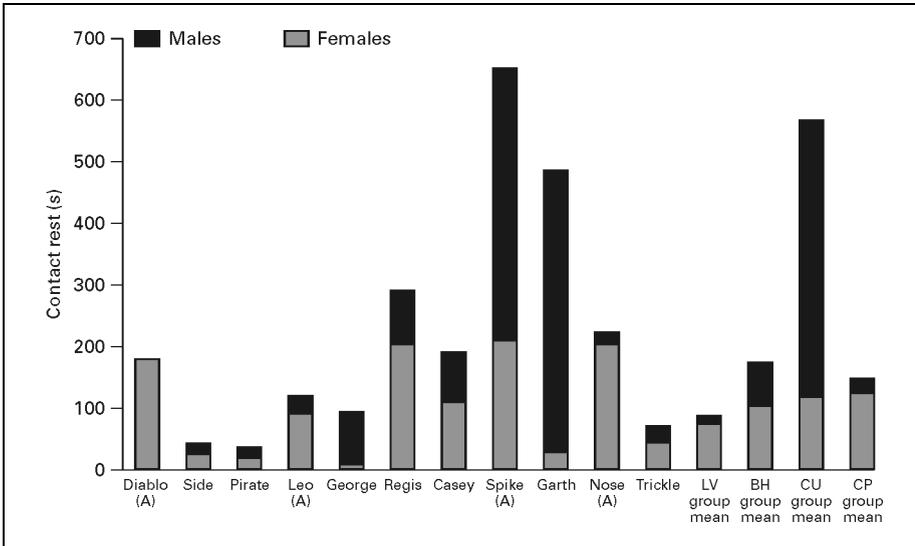
#### *Data Analysis*

Two-tailed Wilcoxon signed ranks tests were used to compare the time males spent affiliating with females versus coresident males. Multiple regression analyses were used to examine the predictive value of the five independent variables on each measure of affiliation for male-male dyads. All dependent variables were logarithmically transformed to fit a linear model [Zar, 1999], and only those variables that resulted in significant simple linear regressions were entered into the final models. Significance was set at 0.05.

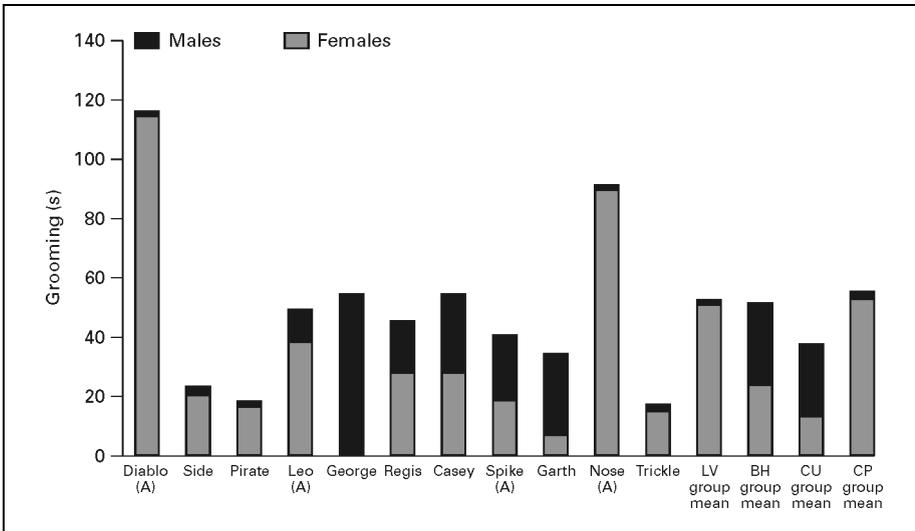
## **Results**

### *Comparison of Inter- and Intrasexual Interactions*

Males spent an average of 354 s/h (9.8% of their time) in contact with at least 1 other group member (males, females, immatures), and an additional 206 s/h (5.7% of their time) in proximity to at least 1 other group member. Figures 1–4 graphically compare the amount of time individual males spent in each of the affiliation measures with group males (adult and subadult) and adult females. No clear patterns are immediately visible from these figures, and they clearly illustrate the variation among the study males and their affiliative interactions with group members. Wilcoxon signed ranks tests were used to compare the amount of time

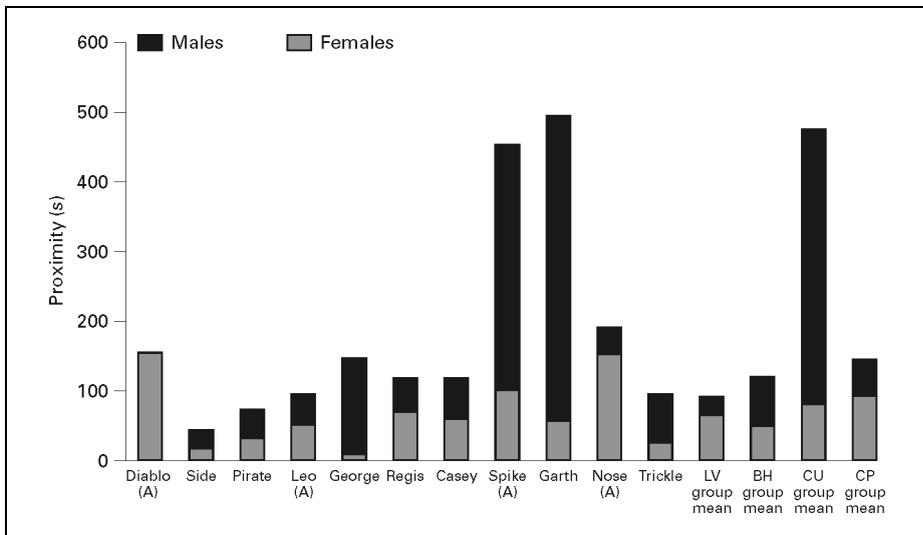


**Fig. 2.** Total time in contact rest (s/h) with coresident males and females for individual males and group means. (A) = alpha male.



**Fig. 3.** Time spent grooming (s/h) coresident males and females for individual males and group means. (A) = alpha male.

males spent affiliating with coresident males and females, and no significant differences were found for any of the four measures of affiliation. Essentially, some males spend more time interacting with group females, while others interact more with coresident males.



**Fig. 4.** Time spent in proximity (s/h) to coresident males and females for individual males and group means. (A) = alpha male.

Group means for each of the four measures of affiliation have also been calculated and these results are included in each of the figures. Males in both the LV and CP groups spent considerably more time affiliating with coresident females than males over all measures of affiliation. Conversely, the two CU males spent considerably more time affiliating with each other than group females. The BH males distributed their affiliative interactions among the males and females in their group more evenly, although with the exception of time spent in contact, they spent slightly more time affiliating with coresident males than females.

Figures 1–4 also indicate which of the males in the sample were alpha males (denoted by A), allowing for comparisons of affiliation patterns according to male status within the group. With the exception of Spike, the CU alpha male, all of the alpha males spent more time affiliating with females than they did with coresident males for each of the four affiliation measures. In fact, the LV and CP alpha males spent very little time affiliating with their coresident males.

#### *Male-Male Dyadic Interactions*

The amount of time that each of the 11 male dyads spent in total non-aggressive contact with one another is displayed in figure 5. Male dyads spent an average of 89.5 s/h (SE 42.9) in total contact with one another, but the durations of interactions were highly variable among individual dyads. For example, Diablo and Side displayed the lowest rate of interaction at 3.8 s/h, while the Spike:Garth dyad displayed the highest levels and spent over 8 min/h in contact with one another. To explain this variability, multiple regression analysis was used to examine the five independent variables (group size, sex ratio, relationship duration, rank distance, and age relationships) to determine what portion of this variation they were helpful in explaining. Of the variables investigated, group size and the duration of the rela-

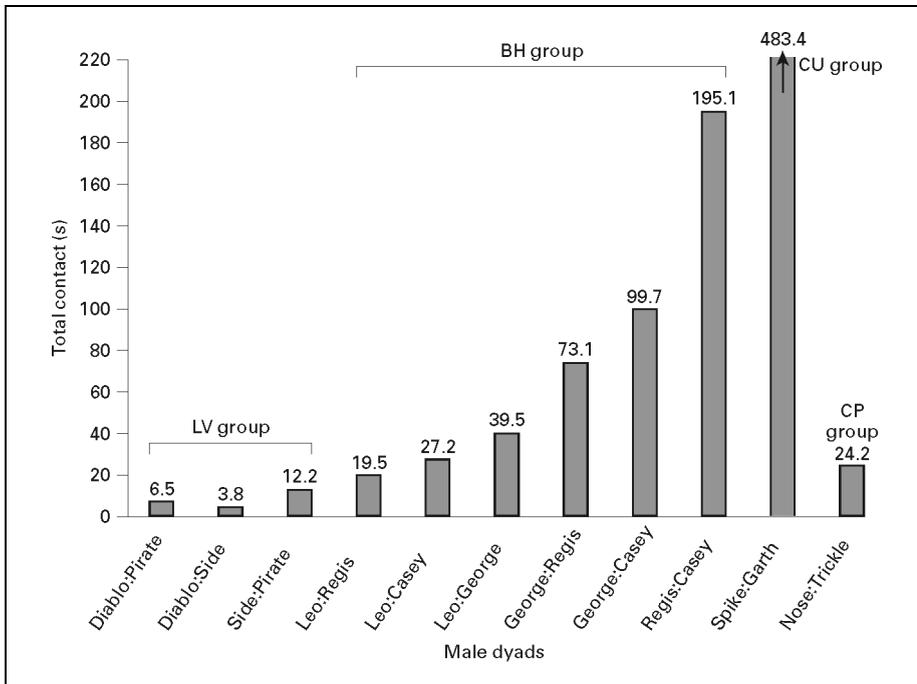


Fig. 5. Total contact time for male dyads in the four study groups.

tionship between males were the only variables that had a significant effect on the amount of time males spent in contact. Together, these variables explained 76% of the observed variation in male dyadic contact time ( $R^2 = 0.76$ ;  $F = 12.79$ ;  $p = 0.003$ ). These data indicate that males residing in smaller groups spend more time in contact with their coresident males, and the longer males have known each other (i.e. resided in groups together) the more time they spend in nonaggressive contact.

Figure 6 demonstrates that (with the exception of the CU dyad and one of the BH dyads, Regis and Casey) males spent very little time resting in contact with one another (mean = 65 s/h; SE = 39.9). Male dyads also displayed a great deal of variation for this measure of affiliation, ranging from a low of 1.5 s/h with the Diablo and Pirate dyad to over 7.5 min/hr with Spike and Garth. Of the five independent variables, only group size had a significant effect on the amount of time males spent resting in contact with one another, and group size alone explained 60% of the observed variation ( $R^2 = 0.60$ ,  $F = 13.7$ ,  $p = 0.005$ ). Again, the data indicate that males residing in smaller groups spend more time resting in contact with one another than do males in larger groups.

Overall, grooming interactions among coresident males occurred at very low levels within the four study groups (mean = 10 s/h; SE = 3.7). However, despite these overall low levels there was still considerable variation observed among the dyads. The data range from as low as 0.3 s/h (Diablo and Pirate) to 31.4 s/h (George and Casey; fig. 7). The regression model for male dyadic grooming interactions included group size, sex ratio, relationship duration, and age relationship.

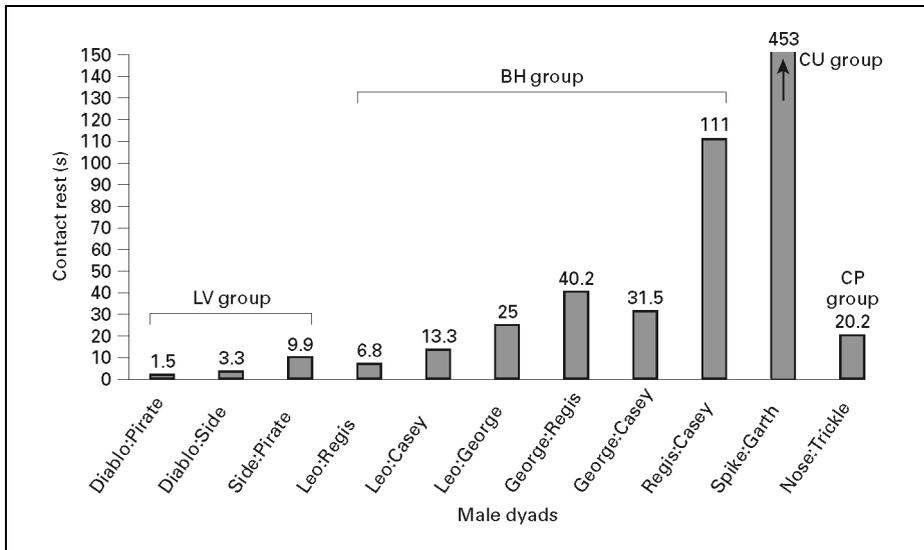


Fig. 6. Time spent in contact rest for all male dyads in the four study groups.

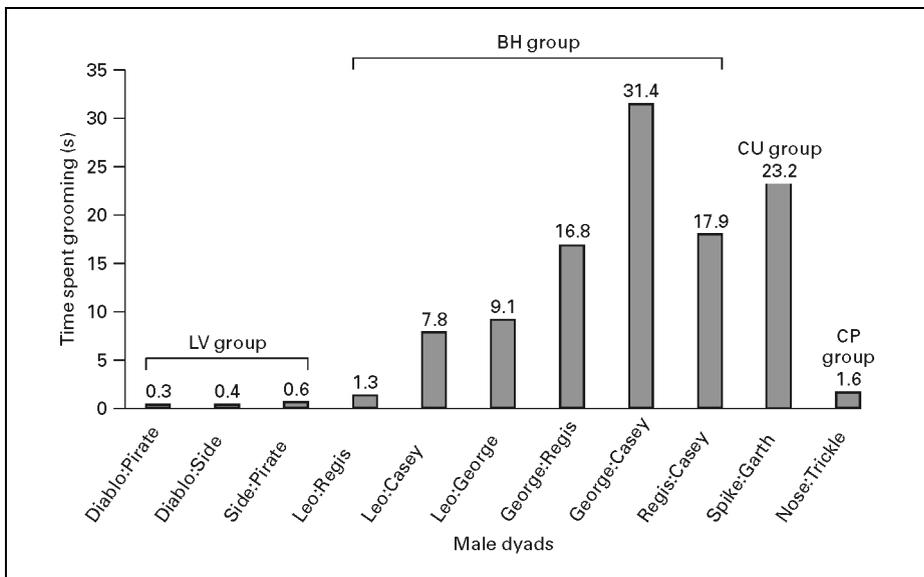


Fig. 7. Time spent grooming for all male dyads in the four study groups.

For the final variable, age relationship, dyads containing two subadult males differed significantly from those with two adults, and adult and subadult combinations. Together, these four variables accounted for 90% of the variation observed in male-male grooming behavior ( $R^2 = 0.90$ ,  $F = 12.96$ ,  $p = 0.004$ ). According to these

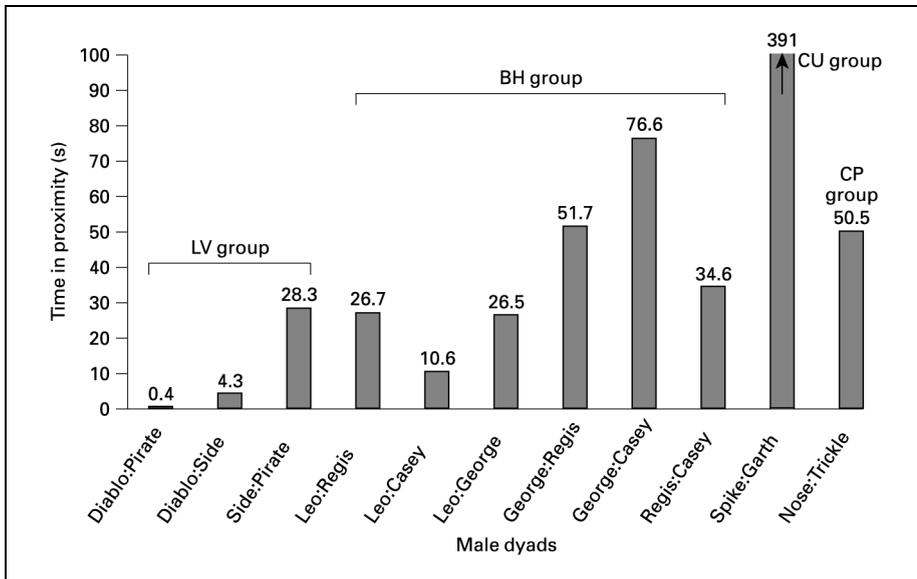


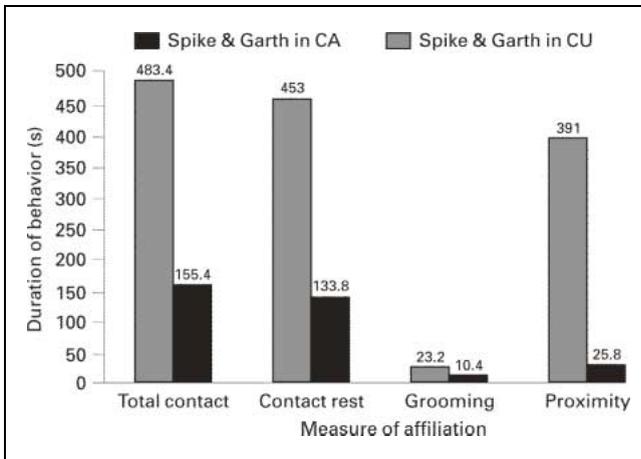
Fig. 8. Time spent in proximity for all male dyads in the four study groups.

data, it appears that coresident males residing in smaller groups groom one another more than males residing in larger groups; males in groups with a higher ratio of males to females groom one another more frequently; the longer coresident males have resided together, the more they exchange grooming interactions, and dyads of two subadult males will groom one another more than dyads containing either two adult males, or an adult and a subadult male.

Time spent in proximity by male dyads varied from 0.4 s/h to 391 s/h, with a mean of 63.7 s/h (SE = 33.4) (fig. 8). Group size was the only variable examined with a significant effect on the duration of dyadic proximity, 53% of the observed variation is explained by this model ( $R^2 = 0.53$ ,  $F = 9.928$ ,  $p = 0.012$ ). The amount of time male dyads spent in proximity to one another was negatively associated with group size. That is, males residing in larger groups generally spent less time in proximity to coresident males.

#### *Before and after Group Transfer Comparisons*

A total of 52.25 h of focal data was collected on the two CU males (Spike and Garth) following their transfer into the CA group. These two males retained their alpha (Spike) and beta (Garth) status in the CA group during the period of observation. The CA group consisted of 14 members (adults and immatures) with a M:F sex ratio of 0.80. Figure 9 compares the affiliative interactions between these two males, both before and after their group transfer. Following their transfer into the CA group, the Spike:Garth dyad displayed a dramatic decrease in the amount of time they spent affiliating with one another (over all measures). However, the levels of affiliative interactions exchanged by Spike and Garth were still very high, particularly for total contact and contact rest, where levels still greatly exceeded



**Fig. 9.** Comparisons of affiliative interactions for the Spike:Garth dyad before (CU) and after (CA) group transfer.

those displayed by most of the other dyads. The most dramatic decrease in affiliative interactions occurred in the amount of time these two males spent in proximity to one another, with levels falling from 391 s/h in the CU group to 25.8 s/h in the CA group.

## Discussion

The results obtained in this study further confirm that the relationships among coresident male white-faced capuchins are highly variable within and among groups. In some groups, males preferentially affiliate with adult females while others spend the majority of their time in the company of coresident males. The relationships among the males in the four study groups ran the gamut; the LV and CP males displayed neutral relationships while the BH and CU males were highly affiliative. Aggressive interactions were rarely observed among any of the males in the four study groups [Jack, unpubl. data], indicating that, even in the LV and CP groups (where males did not frequently affiliate), male relationships are best characterized as being tolerant rather than despotic, as has been reported in *Cebus apella* [Fragaszy et al., in press].

Of the independent variables investigated, group size was a significant factor in explaining the variation among male dyads for all four measures of affiliation. In all cases, males residing in the smaller groups were more affiliative towards one another than those residing in the larger groups. Hill [1994] suggested that affiliative behavior among coresident males is more frequent in smaller groups, simply as a result of there being fewer partners available from which to choose. This argument does not, however, explain the findings described in this study. For example, the CU group was comprised of only 6 members, 2 of which were adult males (Spike and Garth). These males spent the vast majority of their time affiliating with

one another rather than with the other four group members. This finding cannot be explained solely by a lack of available partners; these males could just as easily have interacted with the 2 adult females in their group.

Additional data collected on these two males may give further insight into Hill's proposition. Spike and Garth emigrated from the CU group, which had a 1:1 sex ratio, and joined the neighboring CA group, which consisted of 14 members and had a sex ratio of 0.80. In the CA group, Spike and Garth remained one another's preferred affiliation partners, although their rates of affiliative interactions dropped to almost half of that observed when they had been in the CU group. Their affiliation levels in the CA group were more on par with those of the BH group males, but still much higher than the males of the LV group, which had the same number of members and a slightly lower sex ratio (0.75). Fedigan [1993] also reported high levels of male-male affiliation in her two study groups of white-faced capuchins in SRNP, with males spending significantly more time affiliating with coresident males than females. Although one of her study groups was small, containing only 12 animals, the other was much larger at 23 members, making the unavailability of partners an unlikely explanation. Combined with the information presented on the CA group, these data indicate that the number of available partners within a group may not easily define the relationships among males.

Although the most affiliative male dyads did reside in the two smallest group, it is important to note that these same dyads are also comprised of males who were born into the same natal groups. Perhaps, then, the more telling of the independent variables is the duration of the relationship between males. I found a significant positive correlation between the number of months male dyad partners have resided together (often in more than one group) and the amount of time they spent in nonaggressive contact and in grooming interactions. Kinship and familiarity have long been assumed to facilitate the formation of affiliative bonds between males and there is increasing evidence of a tendency towards above-average relatedness between males in those species characterized by male tolerance or male bonding [van Hooff, 2000]. This may well be the case even for a female philopatric species, such as white-faced capuchins, where male relatedness may be retained through parallel dispersal. As previously mentioned, parallel dispersal is very common among the SRNP capuchins. We have observed young natal males changing groups together, coresident adult and subadult males collectively emigrating and taking over neighboring groups, and males immigrating into new groups containing males who disappeared from our study groups as many as 5 years previously [Jack, 2001].

If we examine male dyadic interactions and the duration of bonds among coresident males more closely, we do see a pattern emerge. Five of the 11 dyads in the samples have long histories together ( $\geq 6$  years; table 1) and all of these dyads have resided in at least 2 groups with one another. With the exception of the Diablo and Pirate dyad, the remaining 4 dyads had the highest scores for total contact, contact rest and grooming, and each of these dyads were comprised of males from the same natal cohort. This may be the key to explaining their levels of affiliation, but how can we explain the low levels of affiliation exchanged between Diablo and Pirate? These two males resided together for a minimum of 6 years, but they displayed the lowest dyadic rates of contact rest, groom, and proximity in the study. Although these two males did share a long history, the relationship between them was never affiliative [K. MacKinnon, pers. comm.]. In 1993, these two males independently

immigrated into the CP group, Pirate as an adult male and Diablo as a subadult [Fedigan, unpubl. data]. Although we are uncertain if these males emigrated from the same group (i.e. parallel dispersal), our preliminary analyses of genetic relationships among group males indicate that it is very unlikely that these males are closely related, e.g. half siblings [Jack and Fedigan, unpubl. data].

These findings demonstrate that although the length of time males have resided together may be an important factor influencing the quality of their relationship, the history of these relationships may be equally telling. All of the subadult BH males and the two CU males were from the same natal group, grew up with one another, were close in age, and may even be related. Diablo and Pirate, on the other hand, were a minimum of 4 years apart in age, may not have come from the same natal group (are unlikely to be related) and, although their relationship was cooperative, it was never highly affiliative.

The data presented in this study further illustrate the variability in the social relations of male white-faced capuchins and demonstrate that some males do form close, enduring affiliative bonds. As our long-term research on white-faced capuchins continues in SRNP, Lomas Barbudal and several other sites throughout Costa Rica, so too will our understanding of the conditions that lead to the close affiliative relationships observed between males like Spike and Garth. Although it is inherently difficult to monitor the movement of males through multiple migrations, this is a very important issue in the behavioral ecology of species characterized by male dispersal, and this information is absent for most primate species. This missing piece of the puzzle is necessary before any definitive conclusions regarding the quality of male relationships can be made.

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### References

- Altmann J (1974). Observational study of behavior: Sampling methods. *Behaviour* 49: 227–266.
- Boinski S (1994). Affiliation patterns among male Costa Rican squirrel monkeys. *Behaviour* 130: 191–209.
- Caro TM (1994). *Cheetahs of the Serengeti Plains*. Chicago, University of Chicago Press.
- Colvin JD (1983). Influences of the social situation on male emigration. In *Primate Social Relationships: An Integrated Approach* (Hinde RA, ed.), pp 160–171. London, Blackwell Scientific Publications.

- Fedigan LM (1993). Sex differences and intersexual relations in adult white-faced capuchins (*Cebus capucinus*). *International Journal of Primatology* 14: 853–877.
- Fedigan LM, Jack KM (2001). Neotropical primates in a regenerating Costa Rican dry forest: A comparison of howler and capuchin population patterns. *International Journal of Primatology* 22: 689–713.
- Fedigan LM, Rose LM, Avila RM (1996). See how they grow: Tracking capuchin monkey populations in a regenerating Costa Rican dry forest. In *Adaptive Radiations of Neotropical Primates* (Norconk M, Rosenberger A, Garber P, eds.), pp. 289–308. New York, Plenum Press.
- Fragaszy DM, Visalberghi E, Robinson JG (1990). Variability and adaptability in the genus *Cebus*. *Folia Primatologica* 54: 114–118.
- Fragaszy DM, Fedigan LM, Visalberghi E. (in press). Social behavior: Interaction, relationships and social structure. In *The Complete Capuchin Monkey* (Fragaszy DM, Fedigan LM, Visalberghi E, eds.). Cambridge, Cambridge University Press.
- Goldberg TA, Wrangham RW (1997). Genetic correlates of social behavior in wild chimpanzees: Evidence from mitochondrial DNA. *Animal Behaviour* 54: 559–570.
- Goodall J. (1986). *The Chimpanzees of Gombe*. Cambridge, Harvard University Press.
- Hall KRL, Devore I (1965). Baboon social behavior. In *Primate Behavior* (Devore I, ed.), pp. 53–110. New York, Holt, Rinehardt, and Winston.
- Hill DA (1994) Affiliative behaviour between adult males of the genus *Macaca*. *Behaviour* 130: 293–308.
- van Hooff JARAM (2000). Relationships among non-human primate males: A deductive framework. In *Primate Males: Causes and Consequences of Variation in Group Composition* (Kappeler PM, ed.), pp. 183–191. Cambridge, Cambridge University Press.
- van Hooff JARAM, van Schaik CP (1994). Male bonds: Affiliative Relationships among Nonhuman Primate Males. *Behaviour* 130: 309–337.
- Jack KM (2001). *Life history patterns of male white-faced capuchins (Cebus capucinus): Male-bonding and the evolution of multimale groups*. PhD diss, University of Alberta, University Microfilms International.
- Janson CH (1985). Aggressive competition and individual food consumption in wild brown capuchin monkeys (*Cebus apella*). *Behavioural Ecology and Sociobiology* 18: 125–138.
- Kaufmann JH (1967). Social relations of adult males in a free-ranging band of rhesus macaques. In *Social Communication among Primates* (Altmann SA, ed.), pp. 73–98. Chicago, University of Chicago Press.
- Melnick DJ, Pearl MC (1987). Cercopithecines in multimale groups: Genetic diversity and population structure. In *Primate Societies* (Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, eds.), pp. 121–134. Chicago, University of Chicago Press.
- Mitchell BJ (1990). Resources, group behavior, and infant development in white-faced capuchin monkeys, *Cebus capucinus*. *Dissertation Abstracts International* B51(5): 2172.
- Moore J (1992). Dispersal, nepotism, and primate social behavior. *International Journal of Primatology* 131: 361–378.
- Nöe R, Sluijter AA (1968). Which adult male savanna baboons form coalitions? *International Journal of Primatology* 16: 77–105.
- Oppenheimer JR (1968). *Behavior and ecology of the white-faced monkey, Cebus capucinus on Barro Colorado Island, Canal Zone*. PhD diss, University of Illinois-Urbana, University Microfilms International.
- Packer C (1979). Intertroop transfer and inbreeding avoidance in *Papio anubis*. *Animal Behaviour* 27: 1–36.
- Packer C, Pusey AE (1982). Cooperation and competition within coalitions of male lions: Kin selection or game theory? *Nature* 296: 740–742.
- Pereira ME, Clutton-Brock TH, Kappeler PM (2000). Understanding male primates. In *Primate Males: Causes and Consequences of Variation in Group Composition* (Kappeler PM, ed.), pp. 271–277. Cambridge, Cambridge University Press.
- Perry SE (1998a). A case report of a male rank reversal in a group of wild white-faced capuchins, *Cebus capucinus*. *Primates* 39: 51–70.
- Perry, SE (1998b). Male-male social relationships in wild white-faced capuchins, *Cebus capucinus*. *Behaviour* 135: 139–172.
- Pusey, AE, Packer C (1987). Dispersal and philopatry. In *Primate Societies* (Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, eds.), pp. 250–266. Chicago, University of Chicago Press.
- Rose LM (1994). Benefits and costs of resident males to females in white-faced capuchins (*Cebus capucinus*). *American Journal of Primatology* 32: 235–248.
- Rose LM (1998). *Behavioral ecology of white-faced capuchins (Cebus capucinus) in Costa Rica*. PhD diss, Washington University-St. Louis MI, University Microfilms International.
- Rose LM, Fedigan LM (1995). Vigilance in white-faced capuchins, *Cebus capucinus*, in Costa Rica. *Animal Behaviour* 49: 63–70.

- Schapiro SJ, Porter LM, Suarez SA, Bloomsmith MA (1995). Age and social experience affect the breeding performance of subadult male rhesus monkeys. *Contemporary Topics in Laboratory Animal Science* 34: 93–95.
- Sigg H, Stolba A, Albeggen JJ, Dasser V (1982). Life history of hamadryas baboons: Physical development, infant mortality, reproductive parameters, and family relationships. *Primates* 23: 473–487.
- Silk JB (1992). Patterns of intervention and agonistic contests among male bonnet macaques. In *Coalitions and Alliances in Humans and Other Animals* (Harcourt AH, de Waal F, eds.), pp. 215–232. Oxford, Oxford University Press.
- Silk JB (1994). Social relationships of male bonnet macaques: Male bonding in a matrilineal society. *Behaviour* 130: 271–291.
- Stanford CB (1998). Predation and male bonds in primate societies. *Behaviour* 135: 513–533.
- Strier KB (1994a). Brotherhoods among atelins: Kinship, affiliation and competition. *Behaviour* 130: 151–167.
- Strier KB (1994b). Myth of the typical primate. *Yearbook of Physical Anthropology* 37: 233–271.
- Strier KB (1999). Why is female kin bonding so rare? Comparative sociality of neotropical primates. In *Comparative Primate Socioecology*, (Lee PC, ed.), pp. 300–319. Cambridge, Cambridge University Press.
- Struhsaker TT (1985). Infanticide in a patrilineal society of red colobus monkeys. *Zeitschrift für Tierpsychologie* 69: 89–132.
- Symington MM (1990). Fission-fusion social organization in *Ateles* and *Pan*. *International Journal of Primatology* 11: 47–61.
- Zar JH (1999). *Biostatistical Analysis*, ed 4. New York, Prentice-Hall.
- Zuckerman S (1932). *The Social Lives of Monkeys and Apes*. London, Kegan.