



Male social bonds: strength and quality among co-resident white-faced capuchin monkeys (*Cebus capucinus*)

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Abstract

Social relationships among immigrant same-sex co-residents have received relatively little attention, particularly for species where males are the dispersing sex. White-faced capuchins (*Cebus capucinus*) are unusual in that immigrant males form cooperative alliances with co-resident males during intergroup encounters, and also have affiliative and tolerant intragroup relationships. We collected approx. 3341 h of focal animal data on 25 adult and subadult males in five groups of wild *Cebus capucinus* in the Santa Rosa Sector, Costa Rica, across three distinct field seasons. Using generalized linear mixed models, we examined the influence of number of co-resident males, group sociometric sex ratio, dominance status and age, and past parallel dispersal on social bond strength (i.e., proximity, contact rest, grooming, preferred grooming partners) and quality (i.e., grooming reciprocity) for 47 unique male–male dyads. Overall, dyads that included an alpha male had the weakest and least equitable bonds, while dyads composed of subordinate males had the strongest and most equitable bonds, with subordinate subadult peers being most likely to form preferred relationships. Several measures of bond strength and quality were highest among dyads in groups with few males and low sociometric sex (female-to-male) ratios. Dyad partners who had previously engaged in parallel dispersal had slightly better bonds than those that did not, suggesting that kinship and/or familiarity may be important. Our results indicate that within groups, male relationships are influenced by power asymmetry, partner availability, and dyad relationship history.

Keywords

male-biased dispersal, dominance, peers, partner availability, sex ratio, parallel dispersal, grooming equality.

1. Introduction

Socioecological models focus primarily on females and the factors that influence the acquisition and maintenance of resources, namely food and shelter (Emlen & Oring, 1977; Wrangham, 1980; van Schaik, 1989; Sterck et al., 1997; Clutton-Brock & Janson, 2012). Guided by this theoretical framework, much research has centered on explaining observed variability in affiliative social bonds among females (vervets, *Chlorocebus aethiops*: Seyfarth, 1980; rhesus macaques, *Macaca mulatta*: Widdig et al., 2001; savanna baboons, *Papio cynocephalus*: Silk et al., 2006a, b; hyenas, *Crocuta crocuta*: Smith et al., 2010; elephants, *Loxodonta africanus*: Archie et al., 2011; ring-tail coatis, *Nasua nasua*: Hirsch et al., 2012), while variation in males has been largely ignored.

In fact, early reports of male relationships stressed aggressive interactions and competition for access to females (e.g., Zuckerman, 1932). Building upon these observations, socioecological models predicted that male bonding (i.e., ‘coordination and mutual attraction’, van Hooff & van Schaik, 1994: 311) would be uncommon because male reproductive success is constrained by access to mates and non-divisible fertilizations (van Hooff & van Schaik, 1994; Kappeler, 1999; van Hooff, 2000). Thus, most research on male tolerance, affiliation, and cooperation has concentrated on philopatric males, where inclusive fitness benefits (Hamilton, 1964) can be accrued through cooperation with kin (e.g., chimpanzees, *Pan troglodytes*: Goodall, 1986; Watts, 2000a, b; Mitani, 2009; Costa Rican squirrel monkeys, *Saimiri oerstedii*: Boinski, 1994; muriquis, *Brachyteles arachnoides*: Strier, 1994; bottlenose dolphins, *Tursiops* sp.: Krützen et al., 2003; spider monkeys, *Ateles geoffroyi*: Schaffner et al., 2012; red colobus monkeys, *Procolobus* sp.: Pope, 1990; Starin, 1994; Struhsaker, 2010). While kinship does facilitate the formation of affiliative bonds, its role may be less influential than originally assumed (Langergraber et al., 2007; Mitani, 2009). Indeed, strong cooperative and sometimes affiliative bonds have been reported for a number of male dispersed species, such as manakins (*Chiroxiphia linearis*: Foster, 1977), lions (*Panthera leo*: Packer et al., 1991), ring-tailed lemurs (*Lemur catta*: Gould, 1997; Nakamichi & Koyama, 1997), South American squirrel monkeys (*Saimiri sciureus*: Mitchell, 1994), and several macaque species (review of *Macaca* sp. Hill, 1994; *M. assamensis*: Schülke et al., 2010; *M. radiata*: Adisheshan et al., 2011). Despite these findings, and in contrast to studies of females relationships that generally examine social bond strength (i.e., as-

sociation and grooming patterns, *sensu* Silk et al., 2006a) and quality (i.e., grooming equality, *sensu* Silk et al., 2006b), studies on male relationships have emphasized cooperative aggression and coalitionary support, rather than affiliation (Noë & Sluijter, 1995; Berman et al., 2007; Schülke et al., 2010).

In the present study, we examined social bond strength and quality among male white-faced capuchin monkeys (*Cebus capucinus*). Their highly social nature and longevity makes them an ideal species for examining factors influencing variation in male social bonds in a male-dispersed species. White-faced capuchins are medium-sized Neotropical primates that live in groups of related females, immigrant males, and immature offspring. They can live to at least 27 years in the wild (Fedigan & Jack, 2012). Previous research on white-faced capuchins has shown that while all group males — regardless of rank and age class — regularly affiliate with both male and female group members, social bonds among co-resident males are highly variable (Perry, 1997, 1998; Jack, 2003), some male dyads never or rarely interact while others are more affiliative with each other than they are with group females (Jack, 2003). Regardless of their level of affiliation, relationships among co-resident male capuchins are characterized by the formation and maintenance of group-level cooperative alliances against predators and extra-group males. At the intergroup level, severe and sometimes lethal male–male agonistic interactions occur in the context of intergroup encounters and group takeovers (Perry, 1996; Gros-Louis et al., 2003), and elevated glucocorticoid levels during periods of increased encounters suggest that they are stressful events (Schoof & Jack, 2013). In white-faced capuchins, groups takeovers are more likely to occur when groups have a lower number and proportion of males (Fedigan & Jack, 2004) and takeovers follow the emigration of male subordinates (Jack & Fedigan, 2004b). Thus, the size of the male coalition affects success in competition with extra-group males, and may influence the strength and quality of bonds among co-resident males. The relative importance of within and between group competition may be an important selective pressure for the evolution of strong social bonds among co-resident males (van Hooff, 2000; Ostner & Schülke, 2014, this issue). Indeed, the tolerant and often affiliative relationships observed among male white-faced capuchins are thought to be a consequence of high competition between groups and the importance of male cooperation during intergroup encounters (Rose & Fedigan, 1995).

Other individual and demographic factors can influence within-group male relationships. In groups with male-biased or fairly equal sex ratios, males may be more affiliative with one another because of a shortage of preferred female social partners (Hill, 1994). Similarly, small group size may also facilitate male bonding if partner choice is limited (Hill, 1994). Conversely, increased mating competition in groups with male biased sex ratios and groups with more males may limit the formation and maintenance of social bonds (Emlen & Oring, 1977). Males residing in larger groups may also face time constraints that can place upper limits on levels of association, affiliation, and grooming reciprocity due to the increased number of available partners (Lehmann et al., 2007). Published data on white-faced capuchins support the idea that group size is important; all measures of male affiliation were higher in smaller groups compared to larger groups (Jack, 2003), but the influence of the number of males *per se* has not been examined.

Power asymmetries resulting from relative dominance status and age of social partners may influence social bonds. Several studies have found that younger and lower-ranking individuals groom up the dominance hierarchy, especially where the dominance hierarchy is steep, while males similar in age and dominance status are more affiliative and groom more reciprocally (*Macaca radiata*: Silk, 1994; *Lemur catta*: Nakamichi & Koyama, 1997; *Pan troglodytes*: Watts, 2000a; *Eulemur fulvus rufus*: Port et al., 2009; *Ateles geoffroyi*: Schaffner et al., 2012; meta-analysis of Old World primates: Lehmann et al., 2007; meta-analysis of female primates: Schino & Aureli, 2008). These patterns suggest that power asymmetry influences social relationships, such that subordinates may exchange grooming for tolerance from dominant individuals (e.g., Schino & Aureli, 2008; Port et al., 2009; Kutsukake & Clutton-Brock, 2010).

Male–male social relationships in white-faced capuchins may also be influenced by kinship, or at least long-term familiarity, despite the pattern of male dispersal. Parallel dispersal — which occurs when individuals emigrate together with peers or close kin, or immigrate into groups containing familiar or related individuals — provides dispersing individuals with the means to maintain long-term relationships (van Hooff, 2000; Schoof et al., 2009). Furthermore, in species such as white-faced capuchins, where male reproductive skew is high (Jack & Fedigan, 2006; Muniz et al., 2010), same-age cohorts may be paternally related (Altmann, 1979; van Hooff, 2000). In the Santa Rosa population, male natal dispersal occurs around 4.5 to 5.5 years of age (Jack et al., 2012; 7.6 years at Lomas Barbudal, Perry et al., 2012)

and males continue to change groups throughout their lives approximately every 4 years (Jack & Fedigan, 2004b). White-faced capuchins often engage in parallel dispersal through multiple immigration events (Jack & Fedigan, 2004a, b; Perry et al., 2012), a behavior that appears to be associated with stronger bonds (Jack, 2003) and which appears to maintain some degree of male kinship (Perry et al., 2012). Therefore, social bonds among same-age cohorts may be especially important where they are potential parallel dispersal partners, as a result of increased kinship and/or familiarity (*Saimiri sciureus*: Mitchell, 1994; *Cebus capucinus*: Jack, 2003).

In the present study, we expanded upon previous research on male relationships in white-faced capuchins by focusing not only on social bond strength, but also on the quality of those bonds. To this end, we evaluated variability in bond strength by examining the amount of time male dyads spent in proximity, resting in contact, grooming, and whether dyads were preferred grooming partners. We used multiple predictors to explore which factors affect bond strength, including number of co-resident males, sociometric sex ratio, dominance status and age, and the occurrence of past parallel dispersal. We further evaluated whether these same factors influence social bond quality, as assessed by grooming equality (i.e., reciprocity), and tested whether dyads characterized as preferred grooming partners groom more reciprocally.

2. Methods

2.1. Study site

Our study took place in the Santa Rosa Sector of the Área de Conservación Guanacaste (formerly Santa Rosa National Park). Located in the northwestern part of Costa Rica, Santa Rosa is approximately 108 km² protected area made up of a mosaic of dry deciduous, semi-evergreen and riparian forest fragments interspersed with regenerating pasture (Fedigan & Jack, 2012).

2.2. Subjects and behavioral data collection

We collected behavioral data on adult ($N = 16$; ≥ 10 years old) and subadult male ($N = 9$; 6–10 years old) white-faced capuchin monkeys residing in five social groups over three distinct field seasons (March 1998–March 1999, February–July 2007, and July 2008–November 2009; see Table 1). Alpha males were all adults and were clearly identifiable within each group based on physical appearance (i.e., more robust, Schoof et al., 2011) and

Table 1. Detailed information on sampling periods, including field season, social group identities, length of sampling period, group composition, and sex ratio.

Field season	Group ID	Days	♂♂	Male group composition details	♀♀	Juveniles	Sex ratio (range)
1998–1999 ^a	BH ^A	69	LO, GE, RE, KA, and male visitors	'unstable' group composition			
1998–1999	BH	163	LO, GE, RE, KA		3	2	0.75
1998–1999	BH	165	LO, RE, KA	GE emigrates from BH	2–3	3–4	0.93 (0.67–1.00)
1998–1999 ^a	CP ^{B,C}	17	NS				
1998–1999	CP	374	NS, TR		4	3–5	2.00
2008–2009	CP ^b	494	LE, BZ	TR immigrates into CP	7–9	13–15	4.15 (3.50–4.50)
1998–1999	CU	70	SK, GT		2	2	1.00
1998–1999 ^a	CU ^C	305	SK	GT emigrates from CU to CF			
1998–1999 ^a	CU/CF ^B	17	SK, GT, other males present	SK abandons CU and joins GT in CF group			
2007	EX	159	AT, AM		3	4	1.50
2007	GN	164	BG, MM, AD		9	7–12	3.00

Table 1.
(Continued.)

Field season	Group ID	Days	♂♂	Male group composition details	♀♀	Juveniles	Sex ratio (range)
2008–2009	GN	462	BG, MM, AD, GY, LF, MU, CR, MF	5 males immigrate to GN	10–11	14–17	1.27 (1.25–1.38)
2008–2009 ^a	GN ^B	20	BG, MM, GY, LF, MU, CR, MF	AD disappears			
1998–1999 ^a	LV ^B	20	DB, SD, PE, TR				
1998–1999	LV	262	DB, SD, PE	TR emigrates from LV to CP	4	7–8	1.33
1998–1999	LV	94	DB, SD	PE emigrates from LV	4	7–8	2.00
2007	LV ^c	163	CY, WW, MZ		5	7–10	1.67
2008–2009	LV ^c	491	CY, WW, MZ, NU	NU becomes subadult after 2007 field seasons	5–6	10–14	1.32 (1.25–1.50)

^a Not included in the final dataset: ^A male group membership was unstable due to visits from neighboring males or by resident males to neighboring groups ($N = 1$), or ^B they lasted 20 days or fewer (due to insufficient behavioral data, $N = 3$ periods), or ^C there was a single male in the group, and therefore interactions between pairs of males did not occur ($N = 2$).

^b Complete change in male group composition from the 1998–1999 field season to the 2008–2009 field season.

^c Complete change in male group composition from the 1998–1999 field season to the 2007 and 2008–2009 field seasons.

behavior (i.e., most active participant in intergroup encounters, Rose & Fedigan, 1995). Dominance relationships among subordinate males are difficult to identify given the rarity of aggression (Fedigan, 1993; Perry, 1998; Jack, 2003); therefore, we categorized subordinate males by their adult and subadult age class. Seven males were born into study groups and were of known ages; the remaining male ages were estimated based on comparisons with males of known ages. Following a detailed behavioral ethogram, we conducted focal animal follows (Altmann, 1974) of all study males lasting 10 min (2007, 2008–2009) or 15 min (1998–1999), and excluded any focal sessions in which the animal was out of sight for ≥ 1 or ≥ 2 min, respectively. The same basic behavioral ethogram was used in all study periods, with some research-specific additions in 2007 and 2008–2009. Between March 1998 and March 1999, we collected a total of 1198 h and 15 min of behavioral data on 11 males residing in four social groups (BH, CP, CU, LV). Between February–July 2007, we collected a total of 514 h and 20 min of behavioral data on eight males residing in three social groups (EX, GN, LV). Between July 2008–November 2009, we collected a total of 1629 h 10 min of behavioral data on 14 males residing in three social groups (CP, GN, LV).

2.3. Dataset

For each social group, behavioral data were divided into periods when the adult or subadult male group membership changed. Thus, a new sampling period started when (1) a male immigrated, emigrated, or disappeared, or (2) a male advanced into a new age category (i.e., large juvenile to subadult, or subadult to adult). We identified 18 such sampling periods, ranging in length from 17–494 days (Table 1). Sampling periods were excluded if (A) male group membership was unstable due to transient visits from neighboring males or by resident males to neighboring groups ($N = 1$ period), (B) they lasted 20 days or less and behavioral data were insufficient, ($N = 4$ periods), or (C) there was a single male in the group, and therefore within-group male dyadic interactions did not occur ($N = 2$ periods). Our resulting dataset contained 13 sampling periods ranging from 41–494 days in length. The final dataset included 58 dyads, 11 of whom we had two repeated measures for due to multiple sampling periods; therefore, our dataset includes 47 unique dyads.

2.4. Dependent variables

We used male dyads as the unit of analysis. For each male–male dyad, we calculated multiple relationship measures that we used as proxies for the strength and quality of social bonds.

2.4.1. Strength of social bonds

The relationship measures of interest were time spent in non-aggressive proximity (within 2 body lengths but not in contact), resting in contact, and grooming. We used multiple, separate measures of bond strength, in lieu of a composite index, because these may represent different aspects of affiliative behavior (Berman et al., 2007; Lehmann et al., 2007; Hirsch et al., 2012). Behavioral rates were calculated in seconds/focal hour for each dyad. We also evaluated if dyads were preferred grooming partners. Since the number of available male grooming partners varied across phases (both within and across groups), we standardized grooming time by calculating a z -score. Although groups also varied by size and number of females, we chose to standardize grooming effort based on the number of group males because we are specifically interested in male–male relationships. Following Lehmann & Boesch (2009), we considered dyads with grooming z -scores larger than 1 to be preferred grooming partners.

2.4.2. Quality of social bonds

We used directed and received grooming among dyad members to calculate Silk's grooming equality index (Silk et al., 2006b). The index was calculated as 1 minus the absolute value of grooming asymmetry between dyad partners. Grooming asymmetry was measured as $((G_{M1 \rightarrow M2} / G_{M1, M2}) - (G_{M2 \rightarrow M1} / G_{M1, M2}))$, where $G_{M1 \rightarrow M2}$ represents the amount of time Male 1 groomed Male 2, $G_{M2 \rightarrow M1}$ represents the amount of time Male 2 groomed Male 1, and $G_{M1, M2}$ represents the total amount of grooming between dyad partners. Therefore, a grooming index of 1 indicates perfectly reciprocal (i.e., equitable, bidirectional) grooming relationships, and values less than one indicate unequal relationships, with a minimum value of 0 representing completely unidirectional grooming.

2.5. Predictor variables

We included number of co-resident males, group sociometric sex ratio, dominance status, age, and past parallel dispersal as predictors of dyadic bond strength and quality. For group sex ratio, we calculated the average monthly adult female-to-adult/subadult male ratio for each sampling period. We com-

bined dominance status and age into a single ‘status/age’ variable because (i) alpha males are always adults, (ii) subadult males are invariably subordinate, non-alpha males, (iii) subadult males rank below subordinate adult males and (iv) dominance ranks below alpha cannot be discerned in a linear fashion (Perry, 1998; Jack, 2003; Schoof, unpublished). As a result, dyads were characterized as being composed of an adult alpha male and a subordinate adult male (‘alpha-adult’), an adult alpha male and a subordinate subadult male (‘alpha-subadult’), two subordinate adult males (‘adult peers’), a subordinate adult male and a subordinate subadult male (‘non-peers’), or two subordinate subadult males (‘subadult peers’). Using long-term data from the Santa Rosa Capuchin Project (co-directed by L.M. Fedigan, K.M. Jack and A.D. Melin; see Fedigan & Jack (2012) for more details on the project), we used the presence or absence of past parallel dispersal as a measure of relationship history and possible proxy for male relatedness. We tested for multicollinearity among all predictors using a conservative variance inflation factor (VIF) threshold of $VIF \leq 4.0$ (Chatterjee et al., 2000) as opposed to the more liberal threshold of $VIF \leq 10.0$ that is frequently employed (Myers, 1990). We did not include group size as a predictor variable because the VIF was > 50 ; once excluded, the remaining predictor variable VIF values were < 4.0 .

2.6. *Statistical analysis*

We used repeated measures generalized linear mixed models (GLMMs) to examine which predictor variables were associated with measures of bond strength and quality. These models have several advantages over other regression models, namely: (1) GLMMs can handle nested or hierarchal data structures (dyads nested within social groups) and (2) they account for the non-independence of repeated measures (by nesting sampling periods within dyads). We log transformed all measures of social bond strength except for preferred grooming (the latter follows a binomial distribution). Since some dyads had a value of zero for contact rest and/or grooming, these variables were transformed by adding one second to the behavioral rate for all dyads before they were log transformed. We examined residual plots to detect non-linearity and the scatterplots of residuals for all combinations of dependent and predictor variables.

Each model was fitted with one social bond measure as the response variable using a linear identity link function (for continuous variables, i.e., non-aggressive proximity, contact rest, grooming, grooming equality) or a

binary logit link function (for the binary response variable, i.e., preferred grooming partners). Number of males (categorical: 2, 3, 4 or 8), group socio-economic sex ratio (continuous: range 0.75–4.15), dyad status/age category (categorical: alpha-adult, alpha-subadult, adult peers, non-peers, or subadult peers), and past parallel dispersal (categorical: no or yes) were included as fixed effects. The sampling period (for each dyad, range 1–2) was set as the repeated measure. Dyad identity was nested within group identity as a random factor for the three continuous measures of bond strength (i.e., proximity, contact rest, grooming) but not for preferred grooming partners nor for grooming reciprocity because the Hessian matrix was not definite positive (this often the case when there is a lack of variability within the random factor, and is easily resolved by removing it). For social bond quality, we used Silk's grooming equality index as the response variable; we used the same structure as described above for the continuous variables, but also included 'preferred grooming partners' as a fixed effect (categorical: yes or no).

For all GLMMs, we used a scaled identity covariance matrix for the repeated measure, which had slightly better AICc values than models run with other covariance matrices (e.g., AR1). We used robust estimation to handle violations of model assumptions and the Satterthwaite method allowing degrees of freedom to vary between tests because of the small sample size. We conducted pairwise comparisons for the categorical predictors (i.e., number of co-resident males, dyad status/age, and past parallel dispersal) only for models in which these were statistically significant predictors. We report antilog-transformed estimated means and SEMs as these are more intuitive than the log values used in the analyses. For continuous measures of bond strength and quality, we also conducted Spearman rank tests to assess the correlation of these different relationship measures.

To test the hypothesis that males were time constrained, we also examined the total amount of time each male spent engaged in grooming with co-resident males. We used non-parametric Kruskal–Wallis analyses and pairwise comparisons to test for differences in individual male grooming rate across groups differing in the numbers of co-resident males. For males studied during two sampling periods (Table 1, $N = 11$), we used a paired t -test to examine whether they spent more time engaged in male–male grooming when more males were present in the group. All analyses were run in IBM SPSS Statistics for Mac, version 20.0, and statistical significance was set to $\alpha < 0.05$.

3. Results

3.1. Non-aggressive proximity

Male dyads spent an average of 58 ± 13 s/focal h in non-aggressive proximity. Time spent in proximity was significantly associated with the number of co-resident males ($F_{3,26} = 30.759$, $p < 0.001$), while sex ratio ($F_{1,1} = 0.182$, $p = 0.739$), status/age ($F_{4,10} = 2.195$, $p = 0.141$), and the occurrence of past parallel dispersal were not significant predictors ($F_{1,25} = 0.991$, $p = 0.329$). Dyads in groups with 2, 3 or 4 males spent more time in proximity than dyads in the group with 8 males, but there was no difference among dyads in groups with 2, 3 or 4 males (Figure 1, Table 2).

3.2. Contact rest

Male dyads spent an average of 20 ± 6.5 s/focal h in resting in contact. Time spent resting in contact was significantly associated with the number of co-resident males ($F_{3,5} = 26.623$, $p = 0.002$), sex ratio ($F_{1,6} = 9.281$, $p = 0.024$), status/age category ($F_{4,9} = 8.377$, $p = 0.004$), and with the occurrence of past parallel dispersal ($F_{1,23} = 13.837$, $p = 0.001$). Dyads in groups with fewer males spent more time resting in contact than dyads in the group with 8 males (Figure 2a, Table 2). Dyads in groups with 2

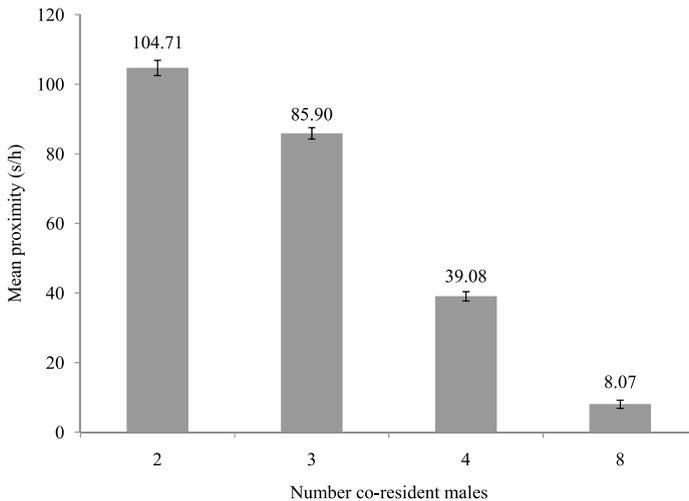


Figure 1. Role of number of co-resident males in predicting time spent resting in contact in seconds per focal hour. Means represent antilog estimated means generated by GLMMs, and error bars represent robust SEM.

Table 2.

Pairwise comparisons: Number of co-resident males was a significant predictor of male dyad time spent in proximity, resting in contact, grooming, preferred grooming status, and grooming equality.

Pairwise comparison	Coefficient (SE)	<i>t</i> (df)	<i>p</i>
Proximity			
2 vs. 3	0.086 (0.394)	0.218 (3)	0.844
2 vs. 4	0.428 (0.388)	1.102 (8)	0.301
2 vs. 8	1.113 (0.367)	3.034 (9)	0.014*
3 vs. 4	0.342 (0.260)	1.318 (2)	0.326
3 vs. 8	1.027 (0.225)	4.559 (2)	0.049*
4 vs. 8	0.685 (0.097)	7.088 (7)	<0.001*
Contact rest			
2 vs. 3	0.472 (0.263)	1.797 (3)	0.178
2 vs. 4	0.977 (0.304)	3.214 (3)	0.051
2 vs. 8	1.339 (0.288)	4.642 (3)	0.020*
3 vs. 4	0.505 (0.118)	4.282 (23)	<0.001*
3 vs. 8	0.866 (0.098)	8.845 (18)	<0.001*
4 vs. 8	0.362 (0.105)	3.460 (35)	0.001*
Grooming			
2 vs. 3	0.288 (0.167)	1.725 (17)	0.103
2 vs. 4	0.277 (0.216)	1.279 (13)	0.223
2 vs. 8	0.761 (0.193)	3.949 (17)	0.001*
3 vs. 4	-0.012 (0.139)	-0.082 (12)	0.936
3 vs. 8	0.473 (0.109)	4.348 (19)	<0.001*
4 vs. 8	0.485 (0.104)	4.647 (35)	<0.001*
Preferred grooming			
2 vs. 3	0.982 (0.008)	123.166 (48)	<0.001*
2 vs. 4	0.997 (0.004)	259.386 (39)	<0.001*
2 vs. 8	0.997 (0.004)	234.587 (31)	<0.001*
3 vs. 4	0.015 (0.009)	1.626 (48)	0.110
3 vs. 8	0.015 (0.009)	1.606 (48)	0.115
4 vs. 8	0.000 (0.001)	0.104 (48)	0.917
Grooming equality			
2 vs. 3	-0.007 (0.155)	-0.042	0.966
2 vs. 4	-0.108 (0.225)	-0.482	0.633
2 vs. 8	0.161 (0.194)	0.831	0.411
3 vs. 4	-0.102 (0.142)	-0.719	0.477
3 vs. 8	0.168 (0.100)	1.673	0.102
4 vs. 8	0.270 (0.089)	3.044	0.005*

GLMM coefficients are reported with their standard errors (SE).

* Significant difference.

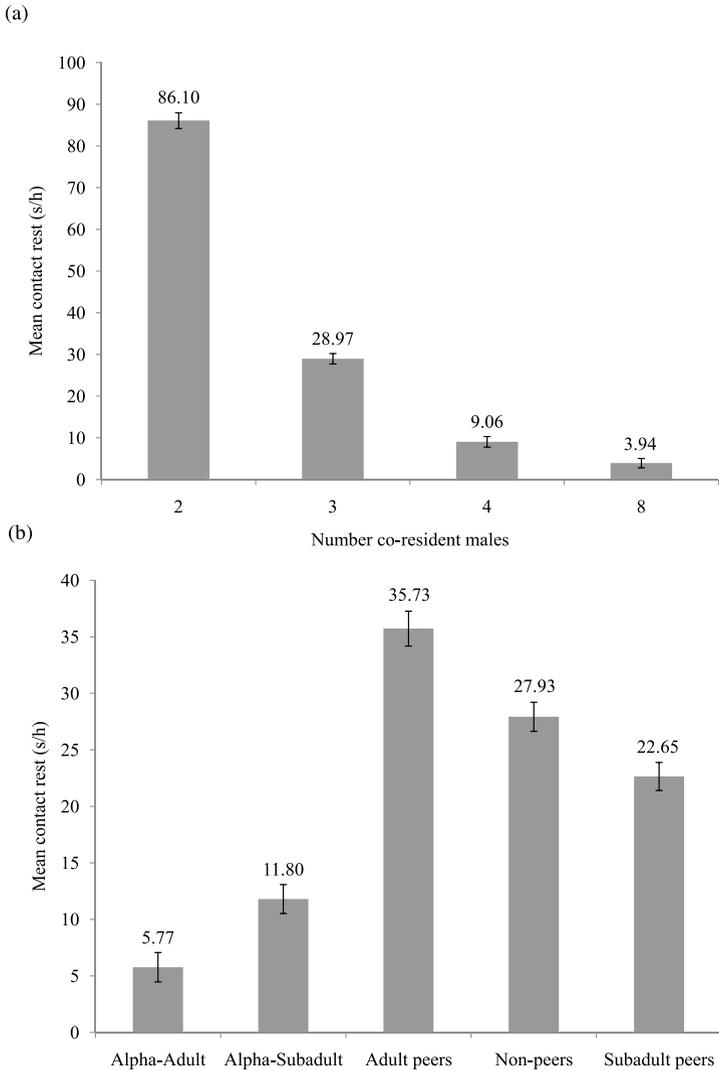


Figure 2. Role of (a) number of co-resident males and (b) dominance status/age in predicting time spent resting in contact in seconds per focal hour. Means represent antilog estimated means generated by GLMMs, and error bars represent robust SEM.

males did not differ from dyads in groups with 3 or 4 males, but dyads in groups with 3 males spent more time resting in contact than dyads in groups with 4 males. Sex ratio was negatively associated with time spent resting in contact, such that dyads in groups with relatively fewer females

per male spent more time resting in contact than groups with relatively more females per male ($\beta \pm \text{SE} = -0.340 \pm 0.112$, $t = -3.047$, $p = 0.004$). Alpha-adult dyads spent significantly less time resting in contact than all other status/age categories except adult peers. Alpha-subadult dyads spent significantly less time resting in contact than subordinate dyads containing at least one adult male, but there was no difference with subordinate subadult peer dyads. No significant difference in time spent resting in contact was found among subordinate dyads, regardless of whether they were peers or non-peers (Figure 2b, Table 3). The occurrence of past parallel dispersal was associated with greater time spent resting in contact (mean \pm SEM: no parallel dispersal = 10.8 ± 1.2 , past parallel dispersal = 27.6 ± 1.3 ; $\beta \pm \text{SE} = 0.407 \pm 0.110$, $t = 3.720$, $p = 0.001$).

Table 3.

Pairwise comparisons: Dyad dominance status/age category was a significant predictor of time spent resting in contact, grooming, preferred grooming partners, and grooming equality.

Pairwise comparison	Coefficient (SE)	<i>t</i> (df)	<i>p</i>
Contact rest			
Alpha-adult vs. Alpha-subadult	-0.311 (0.136)	-2.285 (10)	0.045*
Alpha-adult vs. Adult peers	-0.792 (0.193)	-4.107 (21)	0.001*
Alpha-adult vs. Non-peers	-0.685 (0.127)	-5.384 (11)	<0.001*
Alpha-adult vs. Subadult peers	-0.594 (0.141)	-4.222 (10)	0.002*
Alpha-subadult vs. Adult peers	-0.481 (0.188)	-2.556 (25)	0.017*
Alpha-subadult vs. Non-peers	-0.374 (0.126)	-2.976 (14)	0.010*
Alpha-subadult vs. Subadult peers	-0.283 (0.119)	-2.373 (5)	0.060
Adult peers vs. Non-peers	0.107 (0.170)	0.631 (22)	0.535
Adult peers vs. Subadult peers	0.198 (0.178)	1.110 (14)	0.286
Non-peers vs. Subadult peers	0.091 (0.105)	0.867 (5)	0.427
Grooming			
Alpha-adult vs. Alpha-subadult	-0.309 (0.126)	-2.444 (16)	0.027*
Alpha-adult vs. Adult peers	-0.329 (0.179)	-1.837 (31)	0.076
Alpha-adult vs. Non-peers	-0.344 (0.102)	-3.372 (6)	0.015*
Alpha-adult vs. Subadult peers	-0.546 (0.123)	-4.442 (10)	0.001*
Alpha-subadult vs. Adult peers	-0.020 (0.181)	-0.111 (38)	0.912
Alpha-subadult vs. Non-peers	-0.036 (0.109)	-0.328 (17)	0.747
Alpha-subadult vs. Subadult peers	-0.237 (0.114)	-2.070 (11)	0.064
Adult peers vs. Non-peers	-0.016 (0.150)	-0.103 (26)	0.919
Adult peers vs. Subadult peers	-0.217 (0.177)	-1.225 (27)	0.231
Non-peers vs. Subadult peers	-0.201 (0.113)	-1.776 (14)	0.097

Table 3.
(Continued.)

Pairwise comparison	Coefficient (SE)	<i>t</i> (df)	<i>p</i>
Preferred grooming			
Alpha-adult vs. Alpha-subadult	-0.396 (0.274)	-1.444 (48)	0.155
Alpha-adult vs. Adult peers	0.000 (0.000)	-0.917 (33)	0.366
Alpha-adult vs. Non-peers	-0.745 (0.192)	-3.878 (48)	<0.001*
Alpha-adult vs. Subadult peers	-0.949 (0.036)	-26.459 (48)	<0.001*
Alpha-subadult vs. Adult peers	0.396 (0.274)	1.443 (48)	0.156
Alpha-subadult vs. Non-peers	-0.349 (0.266)	-1.311 (48)	0.196
Alpha-subadult vs. Subadult peers	-0.553 (0.274)	-2.019 (48)	0.049*
Adult peers vs. Non-peers	-0.745 (0.192)	-3.875 (48)	<0.001*
Adult peers vs. Subadult peers	-0.949 (0.036)	-26.451 (48)	<0.001*
Non-peers vs. Subadult peers	-0.204 (0.188)	-1.083 (48)	<0.001*
Grooming equality			
Alpha-adult vs. Alpha-subadult	0.142 (0.114)	1.242 (38)	0.222
Alpha-adult vs. Adult peers	-0.072 (0.142)	-0.508 (38)	0.614
Alpha-adult vs. Non-peers	-0.270 (0.163)	-2.131 (38)	0.040*
Alpha-adult vs. Subadult peers	-0.242 (0.163)	-1.483 (38)	0.146
Alpha-subadult vs. Adult peers	-0.214 (0.122)	-1.753 (38)	0.088
Alpha-subadult vs. Non-peers	-0.412 (0.095)	-4.349 (34)	<0.001*
Alpha-subadult vs. Subadult peers	-0.384 (0.126)	-3.056 (38)	0.004*
Adult peers vs. Non-peers	-0.198 (0.143)	-1.382 (38)	0.175
Adult peers vs. Subadult peers	-0.170 (0.178)	-0.954 (38)	0.346
Non-peers vs. Subadult peers	0.028 (0.145)	0.192 (38)	0.849

GLMM coefficients are reported with their standard errors (SE). Dominance status/age categories include dyads with an adult alpha male and a subordinate adult male ('alpha-adult'), an alpha male and a subordinate subadult male ('alpha-subadult'), two subordinate adult males ('adult peers'), a subordinate adult male and a subordinate subadult male ('non-peers'), or two subordinate subadult males ('subadult peers').

* Significant difference.

3.3. Grooming

Mean grooming rate for male-male dyads was 5.5 ± 1 s/focal h. Dyad grooming time was significantly associated with the number of co-resident males ($F_{3,19} = 13.479$, $p < 0.001$), status/age category ($F_{4,10} = 5.523$, $p = 0.013$), and with the occurrence of past parallel dispersal ($F_{1,12} = 6.083$, $p = 0.030$), but not with sex ratio ($F_{1,14} = 2.873$, $p = 0.112$). Dyads in groups with 2, 3, or 4 males spent more time grooming than dyads in the group with 8 males, but there was no difference among dyads in groups with 2, 3, or 4 males (Figure 3a, Table 2). Alpha-adult dyads spent the least

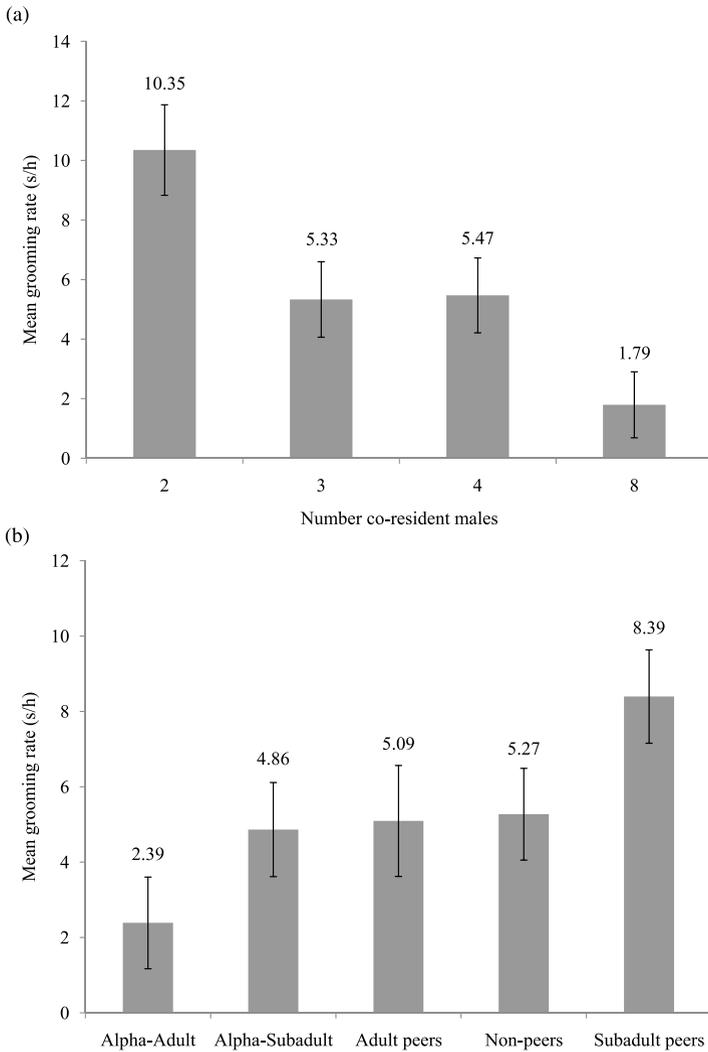


Figure 3. Role of (a) number of co-resident males and (b) dominance status/age in predicting time spent grooming in seconds per focal hour. Means represent antilog estimated means generated by GLMMs, and error bars represent robust SEM.

amount of time grooming, while subadult peers spent the most amount of time grooming (Figure 3b). Alpha-adult dyads groomed significantly less than alpha-subadult dyads, non-peers, and subadult peers. No significant differences in grooming time among alpha-subadult dyads, adult peers, subordinate non-peers, and subadult peers were found (Figure 3b, Table 3). The

occurrence of past parallel dispersal was associated with greater time spent grooming (mean \pm SEM: no parallel dispersal = 3.8 ± 1.2 , past parallel dispersal = 6.1 ± 1.2 ; $\beta \pm SE = 0.209 \pm 0.085$, $t = 2.446$, $p = 0.017$).

To test the hypothesis that males were time constrained, we examined the total amount of time each male spent engaged in grooming with co-resident males. Mean male grooming rate was 5.9 ± 3.0 , 9.4 ± 2.7 , 33.4 ± 10.2 and 9.5 ± 2.4 s/focal h for groups with 2, 3, 4 and 8 males, respectively, and differed between groups (Kruskal–Wallis: $H = 9.328$, $df = 3$, $p = 0.025$). Post-hoc pairwise comparisons indicate that there was a slight increase in male grooming rate as the number of males increases from 2 to 4 males ($t = -15.950$, $p = 0.015$), but there was no difference between any other groups (2 vs. 3: $t = -5.617$, $p = 1.000$; 2 vs. 8: $t = -7.450$, $p = 0.945$; 3 vs. 4: $t = -10.333$, $p = 0.250$; 3 vs. 8: $t = -1.833$, $p = 1.000$; 4 vs. 8: $t = 8.500$, $p = 0.756$). When we limited our examination to the 11 males who were sampled across study phases (i.e., when male group membership changed), time engaged in social grooming with co-resident males was not higher when more males were present in the group (Wilcoxon signed rank test: $Z = -0.711$, $p = 0.477$).

3.4. Preferred grooming partners

We identified nine dyads that fit our definition of preferred grooming partners. The model including all four predictor variables was statistically significant and the overall percentage of cases correctly assigned was high (87.7%). Correct assignment to the non-preferred grooming category was high (47 of 49 dyads; 97.9%), but only three of the nine preferred grooming partner dyads (33.3%) were correctly categorized. Given that we were interested in what factors predicted a preferred grooming relationship, we reran the model with different combinations of predictor variables. The model with the highest correct assignment of preferred grooming partners (7 of 9 dyads; 77.7%) included the number of co-resident males, status/age category, and past parallel dispersal as predictor variables; this was also the model with the highest overall percent of correctly assigned cases (89.5%). In this latter model, only the number of co-resident males ($F_{3,48} = 27.906$, $p < 0.001$) and dominance/age category ($F_{4,48} = 42.200$, $p < 0.001$) were significant predictors of preferred grooming dyads, but past parallel dispersal was not ($F_{4,49} = 16.489$, $p = 0.171$). Dyads in groups with 2 co-resident males were more likely than dyads in groups with 3 or more males to form preferred grooming partnerships (Table 2). Overall, dyads containing at least

one subadult male were more likely to be identified as preferred grooming partners (Tables 3). However, more than half of all subadult peer dyads were characterized as preferred grooming partners (6 of 11), and they made up 66% of all preferred grooming partnerships.

3.5. *Grooming equality*

Eight dyads were never observed to groom; seven of these dyads contained an alpha male. Mean grooming equality across the remaining dyads was low (Silk's grooming index: 0.41 ± 0.05), but was highly variable (range: 0–0.99). The number of co-resident males ($F_{3,38} = 4.514$, $p = 0.008$), sex ratio ($F_{1,38} = 5.506$, $p = 0.024$), and dyad status/age category ($F_{4,38} = 6.620$, $p < 0.001$) were significant predictors of grooming equality. Grooming equality was not associated with past parallel dispersal ($F_{1,38} = 1.712$, $p = 0.199$) nor with the likelihood of being preferred grooming partners ($F_{1,38} = 1.057$, $p = 0.312$). Grooming equality was slightly but significantly higher among dyads in groups with 4 males than in the group with 8 males, but none of the other comparisons were significant (Figure 4a, Table 2). Sex ratio also negatively predicted grooming reciprocity ($\beta \pm SE = -0.146 \pm 0.062$, $t = -2.347$, $p = 0.024$), such that dyads in groups with relatively fewer females per male groomed more reciprocally than those in groups with more females per male. For dyads containing an alpha male, grooming reciprocity did not differ depending on whether the partner was a subordinate adult or subadult. Grooming reciprocity also did not differ among subordinate only dyads (Figure 4b, Table 3). However, subordinate non-peers groomed more reciprocally than dyads containing at least one alpha male (i.e., alpha-adult and alpha-subadult) and subadult peers groomed more reciprocally than alpha-subadult dyads.

3.6. *Correlation of behavioral measures*

The rates of all three measures of social bond strength (non-aggressive proximity, contact rest, and grooming) were strongly and positively correlated with another (Table 4). These measures were also positively correlated with social bond quality (grooming equality), though the relationships were not as strong.

4. Discussion

Male white-faced capuchins formed differentiated relationships with co-resident males in this female philopatric species. The number of group males

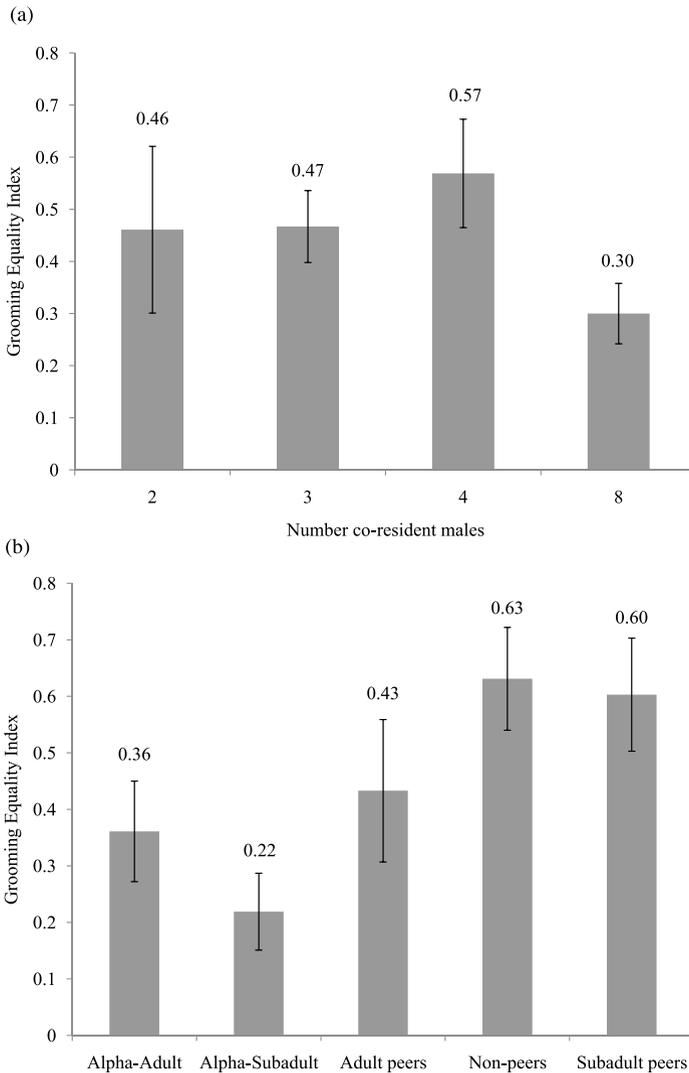


Figure 4. Role of (a) number of co-resident males and (b) dominance status/age in predicting grooming equality. Means represent antilog estimated means generated by GLMMs, and error bars represent robust SEM.

was the most important variable influencing the strength and quality of male–male bonds, with increased affiliation and grooming reciprocity and a greater likelihood of being preferred grooming partners in groups with fewer males. We found that group sociometric sex ratio and a history of parallel dispersal

Table 4.

Correlation between all continuous behavioral measures of social bond strength and quality.

	Proximity	Contact rest	Grooming	Grooming equality
Proximity	–	0.682 ^a	0.679 ^a	0.379 ^b
Contact rest	$p < 0.001$	–	0.810 ^a	0.300 ^b
Grooming	$p < 0.001$	$p < 0.001$	–	0.493 ^b
Grooming equality	$p = 0.007$	$p = 0.036$	$p < 0.001$	–

Spearman rank correlations between behavioral measures are shown in the top half of the matrix, while associated two-tailed p -values are shown in the bottom half of the matrix.

^a $N = 57$ dyads.

^b $N = 48$ dyads.

also influenced several measures of social bonding. In contrast to previous research (Jack, 2003), we found that the dominance status and age of dyad partners was also an important predictor of male–male social bonds.

Male dyads in groups with fewer males had the strongest social bonds as measured by time spent in proximity, resting in contact, grooming, and preferred grooming partnerships. Dyads in groups with 2 males were the most likely to be preferred grooming partners. There was limited difference in the strength of social bonds among male dyads in groups with 2–4 males, but a significant decrease in groups containing 8 co-resident males. Bond quality, as measured by grooming reciprocity, was also lowest among dyads in groups with 8 males. Our results suggest that the number of co-resident males influences bond strength and quality. Several factors could influence this association. Time spent affiliating with other males may simply reflect partner availability. Previous research on white-faced capuchins found that males in smaller groups are more affiliative (Jack, 2003), and similar results have been reported for macaques (Hill, 1994). In white-faced capuchins, the number of group males and group size covary, making it difficult to distinguish the driving factor influencing affiliation. The potential importance of partner availability is supported by the observation that male dyads in groups with higher sex ratios (i.e., more females per male) spent less time resting in contact and groomed more equitably. Female-biased sex ratios are associated with an increase in the availability of female social partners and males may prefer to affiliate with females rather than males (Hill, 1994). In groups with relatively few females, however, males may form relationships with other males due to a shortage of potential female partners. It may simply be that

partner availability is naturally limited in small groups with fewer males and low sex ratios so that co-residents have the time to invest in social relationships with all group members, or with males in particular in the absence of available female group members. Alternatively, increased affiliation could reflect the adaptive benefits of building and maintaining strong bonds when there are few co-resident males. In species where co-resident males form coalitions against extra-group males, such bonds may be especially important if the number of participants influences the outcome of between-group competition (van Hooff, 2000) or the occurrence of group takeovers (Pope, 1990; Ostner & Kappeler, 2004). In white-faced capuchins, groups takeovers are more likely to occur when groups have a lower number and proportion of males (Fedigan & Jack, 2004) and takeovers occur shortly after an alpha male loses all of his co-resident males via emigration (Jack & Fedigan, 2004b). Therefore, in groups with few males, the participation value of each co-resident male is relatively high.

The adaptive benefits of male social bonds (i.e., enhanced cohesiveness of the male coalition) could be equally important in groups with many males, but time and energy constraints may place upper limits on investment in males bonds. Among chimpanzees, males groom less equitably as the number of males in the community increases, but there is only a slight difference in the number of male grooming partners (Watts, 2000b), which is consistent with the idea that there are upper limits on grooming time as the number of males or total group size increases (Lehmann et al., 2007; Kutsukake & Clutton-Brock, 2010). We found little evidence that white-faced capuchins engage in more male–male grooming as the number of group males increases. Combined with the observation that dyads in the group with 8 males spent the least amount of time grooming (and affiliating in general), we suggest that time constraints limit the ability of co-resident males to form and maintain strong bonds, at least via affiliative interactions (i.e., cooperative group aggression may be a strong indication of allegiance when greater numbers of co-resident males are present). There may be a tipping point, in terms of the number of co-resident males, at which social bonds become increasingly difficult to maintain. In our white-faced capuchin study groups, this appears to be somewhere between 4 and 8 co-resident males.

Alternatively, weaker social bonds in groups with more males may reflect the costs of increased resource competition among co-resident males. For females, absolute group size may be especially important since they may

compete with all group members for access to food or water (Clutton-Brock & Janson, 2012). Among males, however, competition is expected to be most intense for access to females, such that the most important variable is the number of co-resident males, rather than group size *per se* (Rose & Fedigan, 1995; Scarry & Tujaque, 2012). An increase in the number of male competitors, and thus within-group competition, could lead to increased social monitoring and a breakdown in male social bonds. This hypothesis is supported by the observation that in two of three groups, male social vigilance decreased after the emigration of a co-resident male (Jack, 2001). In the present study, however, dyads in groups with lower sex ratios (i.e., fewer females per male) spent more time resting in contact, grooming, and groomed more equitably, which is inconsistent with the idea that increased male competition for fewer females leads to a breakdown in male bonding.

Males may compete for resources other than females. Specifically, subordinate males may compete with one another for access to the group's alpha male. In red-fronted lemurs, grooming inequality between dominant and subordinate males increased as the number of subordinates increased (Port et al., 2009; see Kutsukake & Clutton-Brock, 2010 for similar results in meerkats). Previous research on white-faced capuchins indicated that male age, but not dominance status, was a significant predictor of some measures of social bond strength (Jack, 2003). In our expanded dataset, we found that dyads containing an alpha and a subordinate male spent the least amount of time resting in contact and grooming, though alpha-subadult dyads were slightly more affiliative than alpha-adult dyads. Although grooming reciprocity was non-significantly lower in alpha-subadult dyads compared to alpha-adult dyads, we found that all 10 of the alpha-subadult dyads in which grooming was observed, subordinate males groomed alpha males more than they were groomed by them (compared to three of the nine alpha-adult dyads). Greater grooming time and lower reciprocity may reflect a large power imbalance between alpha and subordinate subadult males, while lower grooming time and higher reciprocity between alpha and subordinate adult males may reflect reduced power asymmetry among same aged males who may have more established relationships. In other words, subadult males could be actively seeking out and attempting to forge bonds with alpha males while bonds between alpha and adult subordinates may require less maintenance. Several studies have shown that rank disparity is associated with unequal grooming, with lower ranking individuals grooming up the dominance hierarchy (*Macaca*

radiata: Adiseshan et al., 2011; see Silk, 1994 for similar results among captive bonnet macaques; *Pan troglodytes*: Watts, 2000a; Mitani, 2009). Subordinate males may groom dominant males in exchange for benefits such as increased tolerance (Port et al., 2009), and subadults may be especially eager to gain the alpha male's favor. However, Schülke et al. (2010) report that high-ranking male Assamese macaques (*Macaca assamensis*) who invested in social bonds, often with lower ranking males, maintained their high dominance status, whereas those males who failed to form strong bonds dropped in rank; thus, dominant males can also benefit from forming strong social bonds with lower-ranking co-resident males. However, it is interesting that seven of the eight dyads that were never observed to groom involved three of the eight alpha males in our study. Future research should examine if alpha male white-faced capuchins that have stronger bonds with their co-resident males have longer tenure lengths.

Among male philopatric spider monkeys, affiliative behaviors were reciprocated more among same-age males (Schaffner et al., 2012). Similarly in this study, subordinate peers were generally more affiliative, and subadult peers were especially likely to be preferred grooming partners. Elevated affiliation among peers may be due in part to kinship ties, because same age cohorts have an increased likelihood of being paternally related when male reproductive skew is high (Altmann, 1979; van Hooff, 2000). Parallel dispersal from the natal group and during secondary dispersal is common in white-faced capuchins (Jack & Fedigan, 2004a, b), and may function to maintain kinship even among immigrant males (van Hooff, 2000). In a previous study on male dispersal in capuchins, 80% of subadult males engaged in parallel dispersal (slightly higher than adult males, 74%, and juveniles, 63%; Jack & Fedigan, 2004b). However, it is not known if these events involved same-age cohorts (i.e., adult–adult or subadult–subadult) or age-graded groups (i.e., adult–subadult). The present study indicates that bonds among subordinates are strong, but that adult peers spent the most time resting in contact and subadult peers spent the most time engaged in grooming. These data are consistent with the idea that subordinate males, especially peers, may form and maintain bonds with another for future parallel dispersal and aggressive takeovers of conspecific groups.

Given that parallel dispersal is common in white-faced capuchins, and relationships can last through multiple dispersal events, we predicted that males who had previously immigrated together would have stronger and

more equitable social bonds. In support of our prediction, we found that males spent more time resting in contact and grooming if they had a history of parallel dispersal. However, dyads with a history of parallel dispersal were not more likely to be preferred grooming partners, nor did they groom more equitably; continued observation of these study subjects may indicate that preferred grooming partners are more likely to be future dispersal partners. In ring-tailed lemurs, immigration partners formed preferred associations (i.e., proximity, Nakamichi & Koyama, 1997; affiliation: Gould, 1997), and among squirrel monkeys, males who immigrated together supported one another in agonistic interactions (Mitchell, 1994). Strong equitable bonds among males may occur from increased familiarity and predictability, or could represent kin-bias in selecting social partners and potentially increased inclusive fitness benefits through cooperation with kin (reviewed in Schoof et al., 2009). However, evidence for recognition of and preference for paternal kin is limited (Langergraber et al., 2007; Perry et al., 2008; Schülke et al., 2010) and is difficult to disentangle from familiarity (Widdig, 2007). The challenge in studying the dispersing sex lies in following individuals through dispersal events and knowing the history of immigrant males. In Jack's study (2003), the males with the longest relationship duration were born in the same study group and subsequently immigrated to another study group and several were known or suspected siblings. In the expanded dataset analyzed here, several males immigrated into study groups together as cohorts — and may have been born into the same social group — but evidence of this is not available until genetic analyses are completed.

5. Conclusion

The formation of strong social bonds may be especially important among long-lived animals, such as primates, because their lives are often characterized by repeated interactions with the same individuals (Clutton-Brock, 2009). Male relationships, beyond the competitive aspect, have received little attention, especially among species characterized by female philopatry and male dispersal. In our study, we found that co-resident males form affiliative social bonds, and that the strength and quality of these bonds are highly variable. Overall, dyads that included an alpha male had the weakest and least equitable bonds, while dyads composed of subordinate males, especially peers, had the strongest and most equitable bonds. Number of co-

resident males and group sex ratio also influenced bond strength and quality, with stronger and more equitable bonds among dyads residing in groups with fewer males and with lower socioeconomic sex ratios (i.e., fewer females per male). The formation and maintenance of male bonds may be especially important in white-faced capuchins, where the number of co-resident males influences the outcome of intergroup encounters and takeover risk. This may be a particularly important consideration for co-resident male white-faced capuchins since the pervasive pattern of parallel dispersal provides them with opportunities to maintain bonds over long periods despite the frequency with which males change groups throughout their lifetime

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