Dominance Style of Female White-Faced Capuchins

Mackenzie L. Bergstrom* and Linda M. Fedigan

Department of Anthropology, University of Calgary, Calgary, AB T2N 1N4, Canada

ABSTRACT   Dominance style, the level of tolerance displayed by dominant individuals toward subordinate ones, is exhibited along a continuum from despotic to relaxed. It is a useful concept to describe the nature of dominance relationships in macaque species and it bridges among multiple features of dominance hierarchies, aggression, kinship and conflict resolution. Capuchins share many behavioral similarities with Old World monkeys and like macaques, may exhibit a suite of covarying characteristics related to dominance. Here, we provide an assessment of dominance style by examining measures of aggression and kin bias in 22 adult female white-faced capuchin monkeys (*Cebus capucinus*) in three social groups at Santa Rosa Sector, Costa Rica. We found that bidirectionality of aggression was low (mean = 6.9% ± SE 1.6). However, there were few significant correlations between kin relatedness and social behavior (approaching, grooming, proximity, and co-feeding), even though the intensity of kin bias in grooming was moderate and higher in the larger group. We conclude that patterns of aggression and kin-biased behavior in our study animals are dissimilar to the patterns of covariation observed in macaque species. While unidirectional aggression suggests a despotic dominance style, the moderate expression of kin bias suggests an intermediate to relaxed classification when compared with results from an analysis of 19 macaque species. Additional studies of capuchin species and behaviors associated with dominance style (i.e., conciliatory tendencies) would help to create a comparative framework for the genus *Cebus*, and allow for more detailed cross-species comparison of dominance relationships across all primates. Am J Phys Anthropol 150:591–601, 2013.   © 2013 Wiley Periodicals, Inc.

The socioecological basis for dominance style

Many hypotheses have been presented to determine selective pressures that shape the evolution of social systems in primates. One set of theories, focused on socioecological factors, postulates that predation pressure, resource availability, and inclusive fitness gains are key factors influencing the formation of primate social groups (Crook and Gartlan, 1966; Wrangham, 1980). Within-group competition is an inevitable consequence of group-living, and according to socioecological theory intraspecific competition for cost-effective food resources is the most important factor shaping social relationships among female primates (Wrangham, 1979, 1980). The distribution of desired resources is hypothesized to affect the type of female social relationships that form. When resources are ubiquitous, contest competition for acquisition is not necessary and egalitarian social systems without dominance hierarchies are predicted. When desirable resources are clumped and defendable, increased access through organization into kin groups (i.e., female-bonded groups) should outweigh the cost of competition (Wrangham, 1980; van Schaik, 1989). The level of between-group competition is predicted to affect the nature of dominance relationships among females in female-bonded groups. For example, when individuals rely on other group members for cooperative defense in response to high levels of intergroup competition or predator defense, a greater level of intragroup tolerance is expected between individuals of disparate rank (de Waal, 1989; van Schaik, 1989; Sterck et al., 1997). Some researchers have linked the variation in the nature of female social relationships proposed by socioecological theory to the concept of "dominance style". Dominance style is the level of tolerance displayed by dominant individuals toward more subordinate ones, and varies on a continuum from despotic to lenient (or relaxed) relationships (de Waal, 1989; Berman et al., 2004). It is a larger, more encompassing social construct than the dominance hierarchy that is formed within a group and depicts the "nature of the entire relationship between dominant and subordinate" in terms of dominance, competitiveness, and tension regulation (de Waal, 1986; de Waal, 1989). While some researchers predict that variation in dominance style is related to environmental pressures, including levels of intergroup and intragroup competition as well as predation, others stress that it is important for socioecological theory and dominance style to remain separate conceptual constructs.

Dominance style and behavioral covariation

A suite of measurable traits has been argued to covary (i.e., to be consistently related) in macaque species and has been used to classify the type of dominance style exhibited (Thierry, 1985; de Waal, 1989). These traits include the intensity and bidirectionality of aggression (i.e., the level of symmetry of aggressive interactions that occurs within a dyadic relationship), kin bias [i.e., "observable behavior favoring closer kin over more

TABLE 1. *Dominance style grading designed for macaque social organization adapted from Thierry (2000) to include additional species*

	1st Grade	2nd Grade	3rd Grade	4th Grade
Behavioral gradient	Low conciliatory tendency and social tolerance levels. High asymmetry of contests, dominance gradient and kin bias.	————————————→ ←————————————		High conciliatory tendency and social tolerance levels. Low asymmetry of contests, dominance gradient and kin bias.
Species	Rhesus macaque, Japanese macaque (Taiwan macaque)	Long-tailed macaque, Pigtail macaque, Tibetan macaque[a]	Stump-tailed macaque, Barbary macaque, Lion-tailed macaque, Bonnet macaque, (Toque macaque), (Assamese macaque)	Tonkean macaque, Moor macaque, Crested macaque, (*Gorontalo macaque*), (Heck's macaque), (Booted macaque), (Muna-Butung macaque)

Parentheses indicate least-known species.
[a] Berman et al. (2004).

distantly related or unrelated group members", (Berman, 2004)] in social behaviors such as approaching, grooming, proximity, and co-feeding (i.e., feeding within close proximity), as well as the presence or absence of post-conflict conciliatory behavior. The extent to which these behavioral traits are exhibited and influence social relationships provides a quantifiable way to classify the dominance style for each macaque species. Interspecific comparisons provide a means by which dominance style can be assessed across primate genera in relation to factors such as social organization and ecological pressures.

The bidirectionality of aggression refers to the type of interactions that dominants and subordinates exhibit in conflict situations. Aggression is intense and unidirectional when group-level cooperation is not necessary and dominant individuals do not tolerate subordinates as aggressors during within-group resource competition. Conversely, aggression tends to be mild (i.e., non-contact threats) and bidirectional when high ranking females tolerate some level of competition and aggression and when ecological pressures may promote the maintenance of a higher level of cohesion and cooperation among group members (de Waal, 1989).

In many species, the development of close social bonds is associated with a high degree of relatedness. There is also an association between the development of strong, linear dominance hierarchies and a high degree of nepotism in social behaviors. For example, dominance and kinship are linked in female rhesus macaques (*Macaca mulatta*) (Sade, 1972a). A high degree of kin bias in relation to rank is common in species with matrilineal dominance hierarchies, since maternally related females hold ranks adjacent to one another under these circumstances (Thierry, 1990). Kin bias is usually apparent in patterns of affiliation between closely related ($r \geq 0.25$) individuals (Chapais et al., 1997). Therefore, in order to determine the level of social bonding and tolerance exhibited towards distant or non-kin, it is important to determine the degree of kin bias associated with affiliation (approaching, grooming), and association (proximity, co-feeding), as well as whether the degree of kin bias changes as group size and the number of available social partners increases (Berman and Thierry, 2010).

The occurrence of reconciliation in primates has been proposed to represent an effort to pacify strained relationships in order to maintain strong bonds after agonis-

tic encounters. de Waal (1986) suggested that aggression and subsequent reconciliation may act to repair bonds disrupted by aggression in dyadic relationships. A species that exhibits frequent reconciliation may face socioecological pressures to maintain cooperative relationships. Reconciliation may function directly after a dispute as a means of resolving conflict, or similarly, tension may be reduced in relaxed species through means of ritualized behaviors that function to resolve conflict [e.g., soft biting in stump-tailed macaques (*Macaca arctoides*) (Thierry, 2000)].

The analysis of covariation of these social patterns allows us to assess dominance style along a continuum from despotic to relaxed. Factors that result in cooperative relationships and that work to counteract pressures such as intergroup competition, yield a more relaxed dominance style and include: a high proportion of bidirectional aggression between individuals, low levels of kin bias in social behaviors, and higher rates of reconciliation among dyads with greater rank disparity. On the other hand, intense and unidirectional aggression between individuals, high levels of kin bias in social behaviors, an increase in the intensity of kin bias in grooming with group size (Berman and Thierry, 2010), and infrequent reconciliation characterize a despotic dominance style. In despotic primate species, high ranking individuals display very little tolerance of subordinates in competitive and social situations.

Dominance style and Old World primates

Studies have begun to address the topic of dominance style in detail in Old World primate species, most thoroughly within the genus *Macaca*. Drawing from his own and previous research, Thierry (2000) investigated behavioral covariation of dominance characteristics for 19 species of macaques. He divided the continuum of characteristics described by de Waal (1989) into a 4-grade scale that categorizes different modes of conflict management (Table 1). While Thierry's graded scale provides categorization of macaque species, it does not provide behavioral cut-offs for each grade, leaving precise categorization (particularly between two adjacent grades) unclear. A number of studies have shown inconsistencies with the initially proposed covariation across traits even among macaques (reviewed by Balasubramaniam et al.,

2012). However, this graded scale still provides a useful framework of comparative measures among species. For example, Berman et al. (2004) was able to classify the dominance style of Tibetan macaques (*Macaca thibetana*) as despotic and place them within the second grade of Thierry's scale by comparing their behavioral patterns to those of other macaque species previously classified into dominance style grades. Research has recently extended beyond *Macaca*; e.g., captive studies have classified the dominance style of guereza colobus (*Colobus guereza*) as very relaxed (Grunau and Kuester, 2001). The behaviors reported for guereza colobus would likely fall into either grade 4 of Thierry's scale or into an even more relaxed category. Studies of dominance relationships among female chimpanzees (*Pan troglodytes*) have found both linear and non-linear hierarchies (Wittig and Boesch, 2003), that kinship is not likely to play an integral role in shaping social relationships since most females disperse and relatedness is low (although this requires further investigation, see Gilby and Wrangham, 2008; Langergraber et al., 2009). Finally, reconciliation and consolation are common (de Waal and Aureli, 1996), indicating that they exhibit a relaxed dominance style. Studies of dominance in bonobos (*Pan paniscus*) have produced conflicting results but generally classify dominance style as relaxed; direct measures associated with dominance style include hierarchical linearity (non-linear), formal submission (not present), and conciliatory tendencies (high at 50–60%) (Vervaecke et al., 2000; Palagi et al., 2004; Paoli et al., 2006).

Research questions and study species

This study investigates the dominance style of female white-faced capuchins (*Cebus capucinus*), a gregarious, female-bonded New World primate species (Fragaszy et al., 2004). Socioecological theory suggests that female fitness is more directly tied to resource competition than that of males, whose fitness relies more upon access to females (Wrangham, 1980). Consequently, dominance relationships and hierarchical structures may differ between sexes and we limited our analysis of dominance style to adult females. Similarities to cercopithecines in capuchin female social structure (i.e., patterns of social interactions; Kappeler, 2002) are likely to reflect similarities in many behaviors related to dominance. Here, we briefly review what is already known of female white-faced capuchins in terms of behaviors that have been found to be associated with dominance style in macaques: rank, nepotism, socialization and temperament, and aggression.

White-faced capuchins live in multimale, multifemale social groups and share a variety of behavioral patterns with many Old World primate species, including female philopatry, male dispersal, and other characteristics of female-bonded species (Perry, 1996; Jack, 2007). In terms of dominance rank and acquisition, female white-faced capuchins, like macaques, form linear, strong and stable dominance hierarchies that can be constructed from clear interactions involving submission (Bergstrom and Fedigan, 2010). As illustrated in Table 2, many of the behavioral variables used to classify dominance style in macaque species are applicable to and have been independently investigated in white-faced capuchins. Since data are still scarce regarding dominance style in species outside of the subfamily Cercopithecinae, and particularly for New World primates, and since such data on

Cebus have yet to be synthesized under the conceptual umbrella of dominance style, we conducted this study of dominance patterns in white-faced capuchins to gain a more generalized understanding of dominance style in capuchins. Results can then be compared across species in relation to the macaque-specific dominance style grades.

In this study, we examined aggression and kin bias in order to assess the type of dominance style exhibited by female white-faced capuchins. Specifically, we measured the intensity and bidirectionality of aggression, as well as correlations between kin relatedness and approach, grooming, proximity, and co-feeding behaviors, and the intensity of kin bias in grooming. We compare the results obtained in our study to the large body of work published on macaque species.

We investigate two key research questions regarding the behavioral covariants of aggression and kin-biased social behavior, and make the following predictions.

What is the intensity and directionality of aggression among dyads of female white-faced capuchins?. Aggression is predicted to be intense and unidirectional when resources are monopolizable by few individuals and contest competition occurs. However, increased tolerance of lower ranking individuals during resource competition due to a need for intragroup cooperation in resource defense may lead to a higher proportion of bidirectional contests in some species (Sterck et al., 1997). White-faced capuchins are highly frugivorous and contest competition over monopolizable fruit patches is common (Vogel, 2005). Although intergroup encounters over resources occur, females rarely participate in these interactions in our study population. In captive capuchins, previous research has shown that contact aggression is common (Leca et al., 2002); however, because that study pooled all age and sex classes in analysis, we cannot draw firm conclusions from it regarding contact aggression among female-female dyads (i.e., contact aggression may be more common among other dyad types: female-male, male-male and adult-adult or adult-juvenile, but not necessarily among females). In the same study, bidirectionality of aggression (defined as counteraggression in dyadic conflicts among females, males, and juveniles) was high in physical encounters but low in non-physical encounters. However, a study of wild white-faced capuchins at a field site neighboring our own has shown that females primarily direct aggression down the hierarchy (i.e., unidirectional, Perry, 1996), which is typical of a despotic dominance style. Accordingly, we predicted that aggression among adult females in our wild population would be primarily unidirectional, which is characteristic of a despotic dominance style. Specifically, we made the following predictions regarding the intensity of aggression, and three measures of bidirectionality of aggression: 1) a high proportion of aggression will be intense (i.e., including contact). 2) There will be very few instances of aggressive events where lower ranking individuals direct aggressive signals towards dominant ones; 3) at the group level, the predominant direction of aggression will be down the hierarchy for all dyads; 4) in dyadic encounters between females, levels of counteraggression (i.e., instances where a lower ranking female responds and directs any type of aggression back at the aggressor within the same aggressive bout) will be moderate (e.g.,

TABLE 2. *Behaviors observed in Cebus capucinus are compared with similar behaviors cited in the macaque literature to evaluate the associated dominance style grade appropriate to capuchins*

Behavioral category	Observed behavior	*Cebus capucinus* citation	*Macaca* spp. citation	Associated dominance style grade
Dominance and kinship	Matrilineal hierarchies do not follow youngest ascendency. Rank reversal is uncommon.	Perry et al. (2008); Bergstrom and Fedigan (2010)	*M. sylvanus* (Paul and Kuester, 1987)	3
	Lack of formal submission to acknowledge status in the absence of conflict.	De Marco et al. (2008)	*M. sylvanus* (Preuschoft et al., 1998). *M. tonkeana* (Thierry et al., 1989)	3,4
Triadic behavioral patterns	Coalitionary behavior is common and partner choice is affected by power asymmetry.	Perry (1996); Perry et al. (2004)	*M. arctoides, M. mulatta, M. fascicularis* (Butovskaya, 1993). *M. sylvanus* (Preuschoft and van Schaik, 2000)	1,2,3
Conciliatory tendencies	Low among adult females (CCT: corrected conciliatory tendency of 0.09)	Manson et al. (2005)	*M. mulatta and M. fuscata* (CCT 0.04-0.12) reviewed in Thierry (2000)	1
Distribution of affiliative behavior (equal vs. kin- or rank-biased)	Permissive infant handling. Allonursing is present and its distribution is not kin- or rank-biased in capuchins.	Perry (1996); Carnegie et al., unpublished data	*M. sylvanus* (Small, 1990); *M. arctoides* (Maestripieri, 1994)	3,4
	Bond-strengthening and tension reduction mechanisms are present and equally distributed. 1) Capuchin handsniffing. 2) Macaque clasps and embraces	Perry 1996; Bergstrom & Fedigan 2012	*Macaca arctoides* (de Waal and Luttrell, 1989). *M. tonkeana* (Thierry, 1984)	3,4

10–30%), when we include encounters with both threats and contact aggression.

Do female white-faced capuchins exhibit kin bias in affiliative social behaviors?. Socioecological theory predicts that female philopatric species facing within-group competition for monopolizable resources should form alliances with closely related females to increase access to food while maximizing inclusive fitness gains (Sterck et al., 1997). These kin-biased social relationships are often maintained through affiliative behavior such as grooming with alliance partners (Seyfarth, 1980). Association patterns (i.e., proximity) and rates of affiliation among female white-faced capuchins are very high (Fragaszy et al., 2004), particularly among females of similar rank who share a higher degree of kinship (Perry, 1996). Grooming is also more common between females in dyads with small rank differences (Manson et al., 1999) where a higher level of relatedness is expected, and is mostly directed towards dominant individuals. Additionally, females minimize the number of individuals in association while feeding (Phillips, 1995), which may increase bias while foraging (i.e., co-

feeding) with females of similar rank and/or higher relatedness. According to findings from earlier studies, overall levels of kin bias in social behaviors should be high [i.e., characterized by a positive and significant correlation between behavior and level of relatedness (Perry, 1996; Perry et al., 2008; Bergstrom and Fedigan, 2010)] and thus characteristic of a despotic dominance style. We made the following predictions regarding kinship and social behavior: 1) There will be a positive correlation between kin relatedness and rates of approaching, grooming, proximity, and co-feeding behaviors; 2) Intensity of kin bias during grooming will be high.

Given that a large proportion of behavioral patterns in white-faced capuchins suggest despotic relationships and that only a few behavioral indicators of relaxed dominance style have been reported, we predict that the overall dominance style among females will be despotic.

METHODS

Study subjects

This study is based on observational data collected on white-faced capuchins from a long-term (30 years) study

TABLE 3. *Group composition by age/sex class for each study group during 2007 (rainy) and 2008 (dry) data collection periods, including all individuals present at any time during each season (vs. minimum values)*

	LV		CP		GN	
Age/sex class	2007	2008	2007	2008	2007	2008
Adult female	5	5	7	7	10	10
Adult male	2	2	3	2	3	4
Subadult male	1	1	0	0	0	4
Juvenile female	4	4	4	4	2	2
Juvenile male	2	2	2	0	1	4
Infant female	2	2	4	5	2	2
Infant male	2	3	2	1	6	7
Total	18	19	22	19	24	33

TABLE 4. *Female group composition, age in years (as of May 2007) as well as known maternal relatedness for LV, CP, and GN groups of white-faced capuchins organized according to dry season rank within groups*

Group	ID	Rank	Birth date	Age	Mother
LV	KL	1	4/1/1989	18	GR
LV	DL	2	5/29/1991	16	GR
LV	BB	3	1/1/1983[a]	24[a]	Unknown
LV	SL	4	3/1/1996	11	BB
LV	CH	5	8/2/1999	7	BB
CP	SI	1	8/5/1998	8	LI
CP	SA	2	1/1/2001	6	LI
CP	ED	3	5/14/2000	7	PU
CP	TI	4	5/16/1996	11	SE
CP	KI	5	4/29/2002	5	PU
CP	SE	6	6/10/1989	17	P1
CP	ZA	7	2/2/1999	8	SE
GN	LY	1	1/1/1997[a]	10[a]	Unknown
GN	MX	2	1/1/1990[a]	17[a]	Unknown
GN	MV	3	1/1/1990[a]	17[a]	Unknown
GN	PT	4	1/1/2001[a]	6[a]	Unknown
GN	LL	5	1/1/1990[a]	17[a]	Unknown
GN	FL	6	1/1/2001[a]	6[a]	Unknown
GN	RS	7	1/1/2000[a]	7[a]	Unknown
GN	MW	8	1/1/1994[a]	13[a]	Unknown
GN	RM	9	1/1/1987[a]	20[a]	Unknown
GN	LV	10	5/1/2002[a]	5[a]	Unknown

[a] Estimated based on physical characteristics (e.g., brow length, scars, comparison with other females of known age).

population in Sector Santa Rosa (SSR) of the Area de Conservación Guanacaste (ACG), Costa Rica (Fedigan and Jack, 2012). All research protocols reported in this manuscript comply with the American Association of Physical Anthropologists Code of Ethics and were reviewed and approved by the Canadian Council for Animal Care through the University of Calgary Animal Care Committee (permit AC11-0082). This research project also received clearance from the Costa Rican governmental agency: Ministerio de (MINAE) as well as the Area de Conservación Guanacaste (ACG), Costa Rica. SSR is composed of 108 km^2 of seasonal tropical dry deciduous forest (Fedigan and Jack, 2001) and experiences two distinct seasons: the rainy season from mid-May through November and the dry season from December until mid-May. Data were collected during the rainy season from May to August 2007 (127.85 focal h; 345.57 h of observational contact) and during the dry season January to May 2008 (331 focal h; 714.27 h of observational contact) to control for possible seasonal differences in behavior. Fewer focal and observational hours were obtained during the rainy season due to a reduced ability to track and observe groups under more inclement weather conditions.

We excluded juveniles and infants (<5 years old) from data collection since their ranks are dependent upon their mother's until they reach sexual maturity. Behavior can also vary with group size since demographic factors such as the proportion of related social partners may differ (Berman et al., 1997; Chapais, 2001). We studied three habituated study groups of varying sizes: Los Valles (LV), Cerco de Piedra (CP), and Guanacaste (GN) that consisted of 5, 7, and 10 adult females (≥5 years old) respectively, totaling 22 females over both field seasons. Table 3 shows the number of individuals by age/sex class present in each study group during the rainy and dry seasons. Table 4 shows demographic information for focal females including rank (dry season), birth date, age at the beginning of the study, and mother. We used age, sex, body size, and distinguishing features (e.g., hair coloration and patterning, scars and physical injuries) to identify individuals and to estimate the age of individuals with inexactly known birth dates.

We constructed dominance hierarchies using the I&SI method and dyadic interactions that included supplantation, cower, avoid, grimace and flee behaviors (de Vries, 1998; Bergstrom and Fedigan, 2010). We limited analyses involving maternal relatedness to LV and CP groups on which long-term data have been collected since 1990 and 1986, respectively; two matrilines were present in

LV and three in CP during the study period. GN has been studied since 2007 and kinship of the adult females is unknown.

Data collection

We collected behavioral data for 10 to 12 h per day, 5 days per week using a PSION Workabout hand-held computer but noted rapidly occurring interactions such as intense aggression using a digital voice recorder, when needed. Monthly data collection varied with group size (i.e., larger groups were followed longer than smaller groups) to attain similar focal data hours per individual.

We conducted 10-min continuous-time focal animal follows to record all social behaviors that involved the focal and IDs of interactants (Altmann, 1974). We recorded instantaneous scan samples at 2.5-min intervals during follows and included the activity of the focal animal as well as all individuals within close proximity [i.e., in contact, <1 body length, 1–5 body lengths, and 5–10 body lengths (Perry, 1996)]. We collected ad libitum data opportunistically for vocalizations, intragroup agonism, and intergroup encounters. To sample individuals as equally and independently as possible, we randomly selected available focal subjects who had not interacted with, or been in proximity of, the previously sampled individual within the last 2.5 min scan interval of the follow. Data were collected by two individuals and always dictated by MLB and monitored and recorded by her field assistant to avoid inter-observer reliability issues.

Variables and analyses

Bidirectionality of aggression. We measured the rate of aggression per female as the number of aggressive events per hour collected during focal samples and

compared average rates per female across groups using a between-subjects ANOVA. We also calculated from focal samples at the group level, the proportion of threat aggression (i.e., behaviors lacking physical contact: swipe at, tooth grind, bounce, snap at, lunge, glare, or open-mouth threat) versus contact aggression [i.e., behaviors involving escalation (e.g., chase) or physical contact: bite, hit, pull, push, pounce on, or wrestle]. We included ad libitum data in all measures of aggression other than rate calculations.

Following Berman et al. (2004), we used three group-level measures to test the bidirectionality of aggression among females. First, the degree of bidirectionality was determined using the directional inconsistency index (de Waal, 1977). This index calculates the asymmetry of aggression as the percentage of all interactions that were directed in the less frequent direction during dyadic aggression. Second, we measured the direction of aggression using the dyads-up index to calculate the percentage of dyads for which the main direction of aggression was up the dominance hierarchy of the dyads that interacted. Third, we measured counteraggression as the percentage of bouts of dyadic aggression of any kind that included one or more aggressive responses from the subordinate target. We did not include counteraggression by dominant individuals toward subordinates in this measure since this type of aggression likely indicates enforcement/reinforcement of dominance status by higher ranking individuals when challenged. A bout was defined as an aggressive sequence between two individuals that included one or more aggressive events. All aggressive events within the same dyad were considered the same bout until 10 min without aggression elapsed. Although these measures are not mutually exclusive, they provide different perspectives from which to analyze the bidirectionality of aggression (i.e., at the level of the dyad or the whole group).

Kin bias. Relatedness, measured via the coefficient of relatedness (r), represents the percentage of genes that two individuals share by common descent. Values used in this study reflect known relatedness through maternal lines in LV and CP groups. Paternity is only partially documented. However, Jack and Fedigan (2006) found that alpha males father 70 to 90% of the young during their tenure in the group. Therefore, we assumed that maternal siblings born during the tenure of the same alpha male were full-siblings whereas maternal siblings born during the tenure of different alpha males were assumed to be half-siblings. We assessed the degree of kin bias for approach, grooming, proximity, and co-feeding behaviors to determine whether preference varied among maternal kin (two categories) and distant/non-kin. We categorized females based on the degree of relatedness through matrilineal lines as $r \geq 0.5$ for mother-daughter and full-siblings, $r \geq 0.25$ for half-siblings, and $r < 0.125$ for distant and non-kin; a standard cut-off for kin bias in primate studies is $r \leq 0.25$ (Chapais et al., 1997).

We measured approach rate as the frequency per hour that the focal animal approached another individual within 2.5 m. We measured rate of grooming as the frequency per hour that a focal subject initiated a bout of grooming with another individual. To calculate the proportion of time spent within 1 m of another individual, we measured the percentage of scan samples in which the focal subject was within 1 m of another specific individual out of the total scan samples taken for that dyad. To determine whether individuals preferentially co-feed with close kin, we recorded the frequency of co-feeding bouts per hour that a focal subject and another individual fed within 5 m of one another.

We used matrix correlations from partial Kendall's (Kr) row-wise tests with 2,000 permutations (Hemelrijk, 1990) to determine kin bias in rates of approach, grooming, and co-feeding as well as the percentage of time spent within 1 m. This nonparametric method of correlation analysis tests for a relationship between each social factor and the relatedness of individuals while controlling for possible effects of rank distance, since females rank adjacent to maternal kin (Noldus Information Technology, 2003). Kr coefficients range between −1 and 1, with positive values categorized as weak (0–0.5), moderate (0.5–0.8), and strong (0.8–1.0) positive correlations between datasets. We only used groups with known maternal relatedness (LV and CP) for these analyses.

Intensity of kin bias. We also used the intensity of kin bias (KBI) as a measure of kin preference among group members. To determine the intensity of kin bias, we used a method described by Berman et al. (2004). Here, we only analyzed grooming, as there are no comparative data for the intensity of other behavioral categories (i.e., approaching, proximity and co-feeding) from macaques. We compared the amount of observed grooming to the null hypothesis that there was an equal number of grooming bouts among all females in the group. Expected grooming was calculated as the total number of grooming bouts given and received by a female during her focal follows multiplied by the proportion of females in the group that were related by ≥ 0.25. Since we were only comparing two social groups, we could not extensively test the impact of group size on this measure. We report the rate of increase in KBI per female and we used a Mann-Whitney U test to determine whether there was a significant difference in KBI between groups.

Statistical analysis was performed using SPSS 20.0. We considered all results of statistical tests significant at $P \leq 0.05$.

RESULTS
Bidirectionality of aggression

We recorded a total frequency of 329 dyadic female-female aggressive behaviors (during focal animal sampling only) over both study periods (2007: 130, 2008: 199) to calculate the rate of aggression per female and means for each group. Rates of aggression differed significantly across the three groups ($F_{(2,19)} = 3.873$, $P = 0.039$) (see Fig. 1). Tukey post hoc comparisons of the three groups indicate that rates of aggression increased with group size and were statistically different between the smallest (LV) and largest (GN) groups ($P = 0.031$). When aggression did occur, the majority was threat ($X = 73.6\%$, SD = 1.2%) rather than contact aggression ($X = 25.9\%$, SD = 1.4%).

Table 5 shows results for the three measures of bidirectionality of aggression (directional inconsistency index, dyads-up index, and percentage counteraggression) among females for both study periods across LV, CP, and GN groups. We recorded a total of 438 aggressive interactions (focal and ad libitum sampling) across all three groups (2007: 148, 2008: 290). The directional inconsistency index
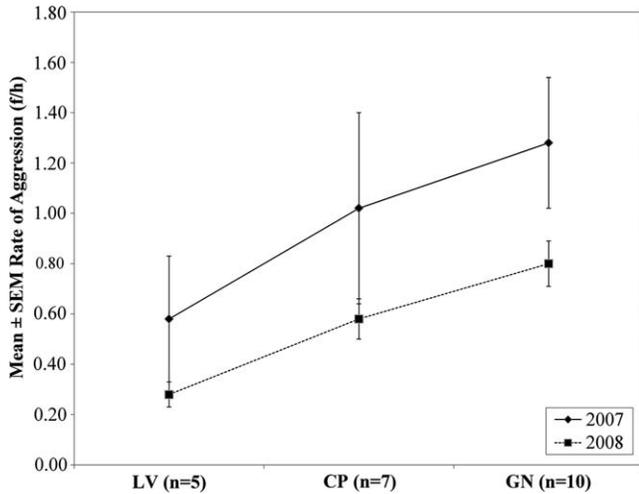
Fig. 1. Rates of dyadic aggression (freq/h) among female white-faced capuchins are shown for LV ($n = 5$), CP ($n = 7$), and GN ($n = 10$) for 2007 and 2008 study periods.

TABLE 5. *Bidirectionality of aggression among adult female white-faced capuchins across both data collection periods for LV, CP, and GN groups (as per Berman et al.,)*

	2007	2008
Directional inconsistency index		
LV	3/20 (15.0%)	1/29 (3.4%)
CP	8/45 (17.8%)	8/85 (9.4%)
GN	15/83 (18.1%)	17/176 (9.7%)
Dyads up index		
LV	1/7 (14.3%)	0/9 (0.0%)
CP	1/14 (7.1%)	0/19 (0.0%)
GN	4/25 (16.0%)	1/31 (3.2%)
Counteraggression (%)		
LV	0/13 (0.0%)	0/19 (0.0%)
CP	1/25 (4.0%)	1/55 (1.8%)
GN	1/39 (2.6%)	1/93 (1.1%)

reports the highest bidirectionality in aggressive interactions of the three measures. Scores fell between 15.0 and 18.1% for all three groups in 2007 and between 3.4 and 9.7% for two of three groups in 2008, indicating that on average, females directed aggression up the hierarchy in approximately one of eight behavioral interactions.

Low dyads-up scores indicate that although some aggressive interactions were directed up the hierarchy, the majority of aggression at the dyad level among females was directed downward from dominant toward subordinate individuals. In 2007, dyads-up scores were 14.3% and 7.1% and 16.0% for LV, CP, and GN respectively. Scores were lower (0–3.2%) for all three groups in 2008. Changes in the direction of aggression in twelve of the 76 dyadic relationships (1 in LV, 1 in CP, and 10 in GN) accounted for the seasonal variation in dyads-up scores across sampling periods. The apparent changes may have resulted from the very low number of behavioral interactions (one or two per dyad) and more data are needed to confirm whether they reflect a true change in the direction of aggression for those relationships.

We recorded a total of 244 dyadic bouts of aggression (i.e., a sequence of at least one aggressive behavior) during both study periods across all three study groups. The overall percentage of counteraggression was low

TABLE 6. *Kin bias among adult female white-faced capuchins over both seasons for LV and CP groups: partial Kr correlation coefficients (P value) between maternal relatedness coefficients and approach rate, grooming rate, percentage of time spent within 1 m, and co-feeding rates, while controlling for rank difference*

Group	Year	Approach	Groom	% Time in 1 m	Co-feed
LV	2007	0.41 (0.12)	0.03 (0.53)	0.22 (0.16)	N/A
	2008	0.62 (0.09)	0.57 (0.07)	0.52 (0.10)	0.10 (0.38)
CP	2007	0.24 (0.08)	0.52 (0.00)	0.32 (0.05)	N/A
	2008	0.24 (0.09)	0.19 (0.13)	0.21 (0.12)	0.13 (0.27)

(1.6%) indicating that contests between white-faced capuchin females are asymmetric. Only four bouts included an aggressive response from the subordinate target female.

Patterns of kin bias

Table 6 shows results for partial Kr correlation matrix analysis of kin relatedness and social behaviors. There was no correlation between kin relatedness and affiliative (approach and grooming) or associative (proximity and co-feeding) behaviors during either study period among females in LV group, although there were nonsignificant tendencies for females to approach and groom kin more than non-kin in 2008. Females in CP group showed a significant moderate correlation ($0.5 \leq \tau \leq 0.8$) between kin relatedness and grooming and a significant but weak correlation ($\tau < 0.5$) between kin relatedness and time spent within close proximity (1 m) in 2007. There were nonsignificant tendencies for females to approach more closely related females during both sampling periods. However, there were no significant correlations between kin relatedness and grooming, proximity or co-feeding behavior among CP females in 2008. We also investigated the intensity of the kin bias expressed in grooming behavior among females. To measure intensity, we compared the frequency of observed grooming among kin to the amount of expected grooming based on the number of available kin within the groups following Berman et al. (2004). Females in LV group lacked kin bias in grooming in 2007 (mean intensity = 0.95 ± 0.31, $n = 5$) but groomed female kin at an intensity of 1.51 ± 0.09 ($n = 5$) in 2008 (i.e., kin spent 1.5 times as much time as expected by chance with kin). Females in CP group showed a similar bias for maternal kin as grooming partners in 2007 and groomed kin 1.4 times the expected amount given maternal relatedness within the group ($m = 1.40 \pm 0.27$), but lacked kin bias in grooming in 2008. Kin bias increased at a rate of 0.384/female as group size increased between groups. Kin bias was significantly higher in CP, the larger of the two groups (Mann-Whitney $U = 4.00$, $P = 0.03$). Overall, females showed few significant correlations between kinship and approaching and grooming behavior but the intensity of kin bias in grooming increased significantly with group size.

DISCUSSION

In this study we attempt to synthesize research focusing on behavior related to dominance style with our investigation of the bidirectionality of aggression and kin bias in social behavior among female white-faced

capuchins. Our aim is to provide an initial assessment of dominance style and to make behavioral comparisons with Old World species in which dominance behavior is better understood. Based on behavioral patterns of white-faced capuchins associated with aggression and kin relatedness published in previous studies, we had predicted that females in our study population would exhibit behavioral patterns that are more indicative of a despotic dominance style, including intense and unidirectional aggression and strong correlations between kin relatedness and social behavior. However, the patterns of social behavior documented in this study suggest that aspects of dominance style among female white-faced capuchins may not covary as they do in some species of macaques. Certain aspects of capuchin female social behavior seem indicative of a despotic dominance style, whereas others resemble a more relaxed style, when compared with macaque species. Thus, our results suggest that an intermediate classification of dominance style may be more appropriate.

Levels of aggression significantly increased with group size, and were similar overall (approximately one or fewer interactions per hour) to rates reported previously among female white-faced capuchins in this population (Fedigan, 1993; Rose, 1994). Aggressive encounters mostly consisted of mild, non-contact interactions. However, all three measures of bidirectionality of aggression suggest that the majority of aggression is unidirectional among females, which is characteristic of a despotic dominance style and is supportive of our first set of predictions about bidirectionality of aggression. The unidirectionality of overall aggression (directional inconsistency index) and the direction of aggression within dyads (dyads-up index) indicate few attempts by low ranking individuals to challenge higher ranking ones. Subordinate females responded with counteraggression in only 1.6% of aggressive bouts.

However, contrary to our predictions, there were few correlations between kin relatedness and affiliative social behavior, which is suggestive of a more relaxed dominance style. Females only showed significant correlations between kin relatedness and grooming and proximity in CP group during the 2007 study period. However, the intensity of kin bias in grooming behavior was 1.4 times greater than expected in CP in 2007 and 1.5 times greater in LV in 2008. Additionally, the intensity of kin bias in grooming was significantly higher in the larger group. Since kin bias has been found to increase with group size in both despotic and tolerant macaque species (Berman and Thierry, 2010), it would be beneficial to look at the rates of change in intensity in relation to group size as well. This would provide a more thorough evaluation of whether this measure of kin bias is more indicative of despotic or relaxed dominance styles since despotic macaques exhibited faster rates than relaxed species. These findings, in addition to the few correlations we found among kin relatedness and social behavior, suggest that capuchins may be intermediate in their dominance style in terms of kin bias.

Comparison with macaque species

Although measures of dominance style for macaque species are often calculated across all male and female partner combinations, broad comparisons can be drawn from behavioral interaction patterns of female white-faced capuchins (see Table 2). Published results for despotic species of macaques classified within grades 1 and 2 of Thierry's (2000) scale [Long-tailed (*Macaca fascicularis*), Japanese, rhesus, and Tibetan macaques; reviewed by Berman et al. (2004)] display low percentages of bidirectional aggression across the directional inconsistency index (0–4%), dyads-up (0–5%), and counteraggression measures (0–30%). Female white-faced capuchins display percentages that are characteristic of grades 1 and 2 for the dyads-up index and counteraggression measures during the dry season, although directional inconsistency index scores are somewhat higher (mean = 12.2% ± 2.3% SEM) than scores reported for all (despotic and relaxed) macaque species. Considering all three measures of bidirectional aggression, a grade 2 or 3 categorization seems fitting.

Female white-faced capuchins showed few moderate correlations between kin relatedness and social behavior in comparison to grade 2 Tibetan macaques (for which the most extensive kin bias results have been published). Capuchin results were significant for grooming and proximity behavior in one of two groups. While this difference between capuchins and macaques may reflect a difference in social behavior, it may also be the outcome of smaller group sizes in capuchins (mean of 18, Fragaszy et al., 2004) versus macaques (mean of 15–50 across all species but as high as 70–90; Thierry, 2007) and reduced maternal kin availability, in turn leading to reduced amounts of social behavior with more closely related individuals (Chapais, 2001). Indeed, Perry et al. (2008) found that the influence of kinship on grooming and proximity patterns increased as group size increased, mean relatedness decreased, and interdyadic variation in relatedness increased in capuchin females at Lomas Barbudal Biological Reserve, Costa Rica. Female group sizes ($n = 5$ and 7) in our study groups were comparable to the smaller group sizes in their study. Taking into account variation in female group size as well as the presence of correlations between kinship and social behavior across our study groups and neighboring populations, kin bias in affiliative interactions among female capuchins seems characteristic of intermediate (grade 2 and 3) macaques, since grade 1 species show strong kin bias, whereas grade 4 typically do not show a strong relationship between kinship and affiliative behaviors (Thierry, 2000). Kin bias, as indicated by the strong intensity of grooming among female capuchins (LV: 1.5; CP: 1.4) fell nearest to published data on grade 3 macaques (stump-tailed macaques: 1.3, Berman et al., 2004). This suggests that capuchins could fall in either grade 2 or grade 3 based on kin bias and grooming behavior. However, because both despotic and tolerant macaques may show kin bias (Berman and Thierry, 2010), our findings might be expected as a result of group size regardless of dominance style. A more detailed analysis with multiple groups of capuchins comparing the rate (i.e., slope) at which KBI increases with female group size, and compared with published data for macaques, would give greater insight into how the level of kin bias varies in relation to macaque species (Berman and Thierry, 2010), independent of the availability of social partners.

Evidence for low-grade conciliatory tendencies has been published for another white-faced capuchin population (Manson et al., 2005) and the presence of alloparenting and social rituals suggests that cooperation exists among adult females, which is again, suggestive of an intermediate dominance style classification. These

behavioral patterns are comparable with macaques in grades 2 and 3 of Thierry's (2000) scale.

Dominance style and predictive theory

Our results do not fully support predictions of dominance style based on socioecological theory. While the largely frugivorous diet of white-faced capuchins seems to promote unidirectional contest competition, the lack of intensity in aggressive encounters, as well as the moderate to low kin bias in social behavior, was not predicted. It is possible that the nature (i.e., size and distribution) of resources within the environment of our study population does not make it advantageous for close kin to form alliances that are maintained and expressed through kin bias in social behavior during resource competition, or that we are not accurately estimating the degree of predation pressure and intergroup competition necessary to promote tolerance in dominance style. Or it may be that nepotism in affiliation and association does not play a significant role in the maintenance of dominance at the relationship level (i.e., dominance style), once rank has been established at sexual maturity. Rather, affiliation and association with non-kin may be equally important for adults in maintaining hierarchical stability and power relations (Chapais et al., 1991; Perry et al., 2004). Indeed, Thierry et al. (2008) found that kin bias in reconciliation may be a stronger more relevant indicator of dominance style than kin bias in affiliative and associative behaviors when investigating dominance style and the covariation of traits expressed in relation to conflict. Alternatively, aspects of capuchin social life aside from those associated with conflict, such as the need for cooperative relationships in infant rearing and the resulting unbiased distribution of alloparental care may be affecting the nature of social relationships and lowering expression of kin bias from levels predicted by resource competition to a more balanced overall expression.

Hypotheses other than those proposed by socioecological theory, such as phylogenetic inertia, must also be considered. Recent genetic analysis of capuchin species has revealed two distinct monophyletic lineages, *Cebus* and *Sapajus* (gracile and robust radiations, respectively) (Lynch Alfaro et al., 2012). Additional studies of capuchin species within these two genera, or sister taxa *Saimiri*, will help to elucidate the possible impact of phylogenetic inertia on dominance style among the platyrrhines, as well as create a comparative framework from which we can begin to expand our knowledge of behavioral variation and possible covariation and assess dominance style among New World primates.

CONCLUSIONS

Studies of macaques provide an excellent base from which to compare behavioral data from species with similar behavioral patterns, such as capuchins. Evidence from this study and previous investigations of social behavior support the classification of an intermediate dominance style for female white-faced capuchins. However, our results argue against the universal application of covariation of behavioral traits characteristic of many species of macaques to classify dominance style (see also Berman, 2004; Thierry et al., 2008; Balasubramaniam et al., 2012). Capuchins exhibit behavioral patterns indicative of both despotic and relaxed macaque societies, and patterns of aggression and kin bias did not positively covary. Nepotism may be a less useful indicator of dominance style than aggression and conciliatory tendencies, or we may need to focus on specific aspects of kin bias, such as how it differentially varies across species as within-species group size changes, to more accurately assess whether notable changes are caused by variation in demographics versus a true difference in dominance style (Berman and Thierry, 2010). Further analyses of capuchins that assess additional behavioral components, such as the recent work on social networks in four species of macaques published by Sueur et al. (2011), may help to support behavioral patterns found in this study. More comparable data on female-female dyads is needed across seasons, populations and species to confirm the style of dominance exhibited by female capuchins. A wider range of dominance style indicators should also be examined, such as detailed measurement and analysis of conciliatory tendencies, including the use of specific behaviors to reconcile as well as kin bias in reconciliation (Thierry et al., 2008). Detailed studies of other species within the family Cebidae, and across other primate families, will help us to expand our understanding of dominance style, clarify behavioral differences between grades of the continuum, and assess whether the despotic to relaxed continuum of dominance style, designed for macaque species, represents the full spectrum of variation possible across the primate order.

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