RESEARCH ARTICLE

Paternal Kin Recognition and Infant Care in White-Faced Capuchins (*Cebus capucinus*)

ELIZABETH J. SARGEANT[1]*, EVA C. WIKBERG[1], SHOJI KAWAMURA[2], KATHARINE M. JACK[3], AND LINDA M. FEDIGAN[1]
[1]*Department of Anthropology and Archaeology, University of Calgary, Alberta, Canada*
[2]*Department of Integrated Biosciences, University of Tokyo, Kashiwa, Chiba, Japan*
[3]*Department of Anthropology, Tulane University, New Orleans, Louisiana*

Evidence for paternal kin recognition and paternally biased behaviors is mixed among primates. We investigate whether infant handling behaviors exhibit paternal kin biases in wild white-faced capuchins monkeys (*Cebus capucinus)* by comparing interactions between infants and genetic sires, potential sires, siblings (full sibling, maternal, and paternal half-siblings) and unrelated handlers. We used a linear mixed model approach to analyze data collected on 21 focal infants from six groups in Sector Santa Rosa, Costa Rica. Our analyses suggest that the best predictor of adult and subadult male interactions with an infant is the male's dominance status, not his paternity status. We found that maternal siblings but not paternal siblings handled infants more than did unrelated individuals. We conclude that maternal but not paternal kinship influence patterns of infant handling in white-faced capuchins, regardless of whether or not they can recognize paternal kin. Am. J. Primatol. 78:659–668, 2016.   © 2016 Wiley Periodicals, Inc.

Key words: infant handling; paternal kinship; kin selection

INTRODUCTION

Male-infant relationships range from intensive caretaking to abusive and exploitative behaviors [Whitten, 1987]. Positive behaviors that males direct toward infants can be divided broadly into two categories: direct care where males perform care-giving behaviors (e.g., carrying, holding, and grooming), and indirect care where males perform behaviors that may benefit infants (e.g., group defense against conspecifics or predators) [Whitten, 1987]. Mothers and infants may benefit from male care through increased predator protection [Janson, 1986], protection from conspecifics during inter-group encounters, and protection against infanticidal males [Altmann, 1980; Busse & Gordon, 1984; Smuts, 1985]. Males may themselves benefit in several ways from interacting with infants. When paternity certainty is high, males can provide intensive care to their offspring as a way to directly increase their fitness [Muller & Thompson, 2012]. In some species (e.g., Barbary macaques, olive baboons), males may also interact affiliatively with infants as a means to gain future reproductive access to their mothers [Smuts, 1985]. Additionally, males may preferentially interact with infants of dominant females in order to improve their social standing [Paul & Kuester, 1996; Small, 1990].

Part of the variation in male caretaking behaviors has been attributed to the degree of paternity certainty [Langergraber, 2012; Muller & Thompson, 2012]. Male care is more prevalent in species in which males have higher paternity certainty, which maximizes their chances of investing directly in their biological offspring [Whitten, 1987; Wright, 1984]. Therefore, we expect that male care should be prevalent in monogamous species or in one-male groups where males can monopolize all, or the majority of matings. For example, pair-bonded Callitrichid males participate in all infant care

activities, and will carry infants at higher rates than do mothers [MacKinnon, 2007]. Monogamous owl monkeys and titi monkeys also exhibit intensive male caretaking, including exclusive carrying of infants [Fernandez-Duque et al., 2012; Wright, 1984]. However, male savannah baboons are more likely to support their own infants in agonistic disputes, even though females mate with multiple males, thereby reducing paternity certainty [Buchan et al., 2003; Charpentier et al., 2008a,b]. This suggests that in certain circumstances, males are capable of distinguishing their offspring from non-offspring, possibly by the frequency of mating or the timing of mating with a female [Altmann, 1980; Widdig, 2007].

Paternity certainty does not account for all the observed patterns of male care in primates [Smuts & Gubernick, 1992]. Contrary to what is expected, some pair-bonded species exhibit only occasional care or tolerance of infants [*Hylobates* species, Whitten, 1987; *Indri Indri*, Wright, 1990]. Moreover, the somewhat intense and affiliative caretaking relationships between Barbary macaque males and infants are not closely tied to paternity, suggesting that factors, such as mother permissiveness, male rank or age, proximity to infants, and the relationship with the mother, influence patterns of male-infant interactions [Altmann, 1980; MacKinnon, 2007]. In general, when paternity is obscured, male care is typically described as being merely tolerant or occasionally affiliative; that is, males may inspect or touch infants but rarely provide direct and significant time or energy investments in infants [Smuts & Gubernick, 1992].

White-faced capuchins are characterized by poly-gynandrous groups, male dispersal, female philopatry, and a promiscuous mating system in which alpha males do not engage in overt mate guarding, thus providing subordinates with mating opportunities [Fedigan & Jack, 2013; Jack & Fedigan, 2006; Muniz et al., 2010; Perry, 2012; Rose, 1998]. In multi-male, multi-female groups such as these, are individuals capable of discriminating their paternal kin and more likely to direct affiliative behaviors toward infants to whom they are paternally related?

Two pertinent aspects of this question can be addressed when we have access to data on paternal kinship. First, do biological (i.e., genetic) fathers interact more frequently and more affiliatively with their infants as compared to "potential" fathers (fertile males resident in the group at the time of conception)? Theoretically, males may be able to assess the likelihood of having fathered an infant based on their previous mating access to the mother [Widdig, 2007]. It has been established that although alpha male white-faced capuchins do not hinder or harass subordinate capuchin males when they are mating, these alpha males still sire the majority of infants within their group [Jack & Fedigan, 2006; Muniz et al., 2010; Perry, 2012; Wikberg et al., 2015]. Thus, mating

opportunities for subordinates do not translate into reproductive opportunities equal to those of dominant males [Jack & Fedigan, 2006]. Nevertheless, the mating activities of subordinate males, as well as promiscuous mating on the part of females, may generate a high degree of paternity confusion; and thus we should expect a fairly equal investment in infant handling by potential and actual sires. Within the genus *Cebus*, no previous study has examined whether potential and genetic sires differ in care of infants.

The second question relevant to infant handling that can be addressed with paternity data is whether paternal siblings exhibit kin biased behavior towards one another. That is, are there differences in the rates of interaction between infants and handlers who are paternal half-siblings, maternal half-siblings, full-siblings, or unrelated? Theoretically, individuals that share the same father should interact and exhibit the same suite of behaviors as do dyads that share the same mother, because the average estimated coefficient of relatedness is the same between paternal half-siblings and maternal half-siblings ($R = 0.25$) [Hamilton, 1964]. These half-sibling dyads in turn should interact less frequently and less affiliatively than do full sibling dyads, but more frequently than unrelated dyads. Using genetic data on paternal and maternal relatedness, we compare the rates of infant handling between paternal half-siblings, maternal half-siblings and full-siblings. Thus, in this study, we investigate the effects of paternity on infant handling behaviors by addressing the following questions:

1. Do biological fathers interact more frequently or differently with their infants than do potential sires?

   a. If biological fathers can distinguish their infants, then we would expect fathers to interact affiliatively at higher rates and aggressively at lower rates with their offspring than do males in the group who are only "potential sires."
   b. If biological fathers cannot distinguish their own infants directly, but can estimate their likelihood of siring a cohort of infants based on their own dominance rank, we would expect current alpha males to interact affiliatively at higher rates and aggressively at lower rates with infants than subordinate males.

2. Do paternal half-siblings infant-handler dyads interact more frequently or differently with one another than do maternal half-sibling dyads, full sibling dyads, or unrelated dyads?

   a. If kin selection was shaping patterns of interactions then we would expect that handlers to interact most frequently with infants who are

their full siblings, and handlers should interact at higher rates with half-sibling infants than with unrelated infants.

  b. If handlers can distinguish infants who are paternal half-siblings just as well as they distinguish maternal half-siblings, then we would expect that rates of infant handling would be similar for these two types of relatedness.

Maternal kin-biased social behaviors have been previously documented among female white-faced capuchins [Bergstrom & Fedigan, 2013], but the same has not been documented for paternal kin-biased behaviors [Perry et al., 2008]. Initial studies on other primate species have yielded mixed results, [Widdig, 2007], however, there is some evidence that paternity can affect infant-handler interactions even among individuals that live in multi-male groups [Buchan et al., 2003; Charpentier et al., 2007, 2008a,b]. Thus, white-faced capuchins (*Cebus capucinus*) present another opportunity to explore the gap in our understanding of how kinship, especially paternal kinship, may or may not influence patterns of infant handling.

METHODS
Study Site and Species

We conducted research on infant handling over the course of two study periods in Sector Santa Rosa in the Área de Conservación Guanacaste, Costa Rica. The first study period took place during the wet season (May through August of 2012) and focused on three habituated groups of capuchins (CP, LV, and GN). The second study period took place during the dry season (January through May of 2013), during which we followed five habituated groups of capuchins (CP-AD, CP-RM, LV, GN, and EX). In between the two field seasons, CP group fissioned along matrilines into CP-AD and CP-RM. And in the second season, we collected infant handling data on an additional habituated study group (EX) that is part of the larger Santa Rosa capuchin project [Fedigan & Jack, 2012]. Focal subjects comprised 21 infants in these study groups that were under the age of 17 months. We were able to individually identify all group members based on unique characteristics such as body-size, facial structure, scars, skin pigmentation, hair pattern, and coloration.

Female white-faced capuchins can be ranked into a stable linear dominance hierarchy and adult males can be categorized into "alpha" and "subordinate" positions. It is easy to distinguish alpha males by their behaviors and permanent state of piloerection, but more difficult to place subordinate males into a dominance hierarchy [Schoof & Jack, 2014]. Therefore, we consider them here simply as subordinate males. Adult females are capable of giving birth year round (i.e., they are not strict seasonal breeders),

however the majority (~44%) of infants are born between May and July, with a distinct peak in May [Carnegie et al., 2011]. This corresponds to the early-wet season in Santa Rosa. Male dispersal is often done in parallel, that is, they transfer between groups in cohorts or selectively join groups containing familiar, previously dispersed, males [Jack & Fedigan, 2004a,b; Wikberg et al., 2014]. Male capuchins change groups throughout their lives, with complete change-over of adult male residents occurring approximately every 4 years [Fedigan & Jack, 2004]. Aggressive group takeover by male coalitions is the most common mode of male immigration, though infant mortality in association with all types of male replacements is significantly higher than during years of group stability [Jack et al., 2014].

Data Collection

Study groups were followed on a 3-day rotational basis and behavioral data were collected 10–12 hr/day for 5–6 days/week. We collected behavioral data using a PSION Workabout hand-held computer and conducted 10-min continuous focal animal sampling of infants [Altmann, 1974]. We followed 8 focal infants during the first study period and 13 focal infants during the second. We have 121 data collection days with 1,075 contact hours and an average of 17.8 focal hours per infant (range: 3.8–40.5 hr) (Supplemental Data, Table SI). Focal order was randomly determined each day, and a minimum period of 20 min separated the same focal infant so as not to sample the same focal infant in back-to-back focal sessions. During 10-min continuous focal follows, we recorded all behavioral events and states, as well as the identity of those individuals who interacted with the focal infant. Bouts of grooming and carrying were considered separate within the same focal if the behavior ceased for more than 30 sec.

The research reported in this study adhered to protocols approved by the Canada Council for Animal Care through the University of Calgary's Life and Environmental Animal Care Committee (LESACC, protocol numbers: AC11-0082, BIO8R-03, BI 2008-03, BI 2005-07, BI 2002-08) and the University of Alberta's Biosciences Animal Care Committee (protocol numbers: 610151, 151804, 319104). Our research also adhered to the laws of Costa Rica and was conducted with permission from the administrators of the Àrea de Conservación Guanacaste and the National Park Service of Costa Rica (ACG-PI-060-2015). Finally, the research adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non Human Primates.

Genetic Analysis

We attempted to collect at least two fecal samples from all group members for subsequent genotyping.

Six of 21 focal infants were excluded from the analyses on paternal kinship because we did not obtain DNA samples from them (Supplemental Data, Table SI). Samples were collected using sterile techniques, dissolved in RNAlater, and then stored in a freezer ($-20°C$) for several months before being shipped to the laboratory for analysis. We used these samples to extract and genotype DNA at 20 short tandem repeat loci: Apm01, Ceb01, Ceb02, Ceb03, Ceb04, Ceb07, Ceb08, Ceb09, Ceb10, Ceb11, Ceb105, Ceb115, Ceb119, Ceb120, Ceb127, Ceb128, Ceb130, d3s1210, d7s794, and pepl4 [Cortés-Ortiz et al., 2010; Escobar-Páramo, 2000; Jack & Fedigan, 2006; Muniz & Vigilant, 2008]. Heterozygote genotypes were confirmed with two replicates while the number of replicates required to confirm homozygote genotypes depended on the extract concentration and drop-out rates [Morin et al., 2001]. Laboratory protocols are further described in Wikberg et al. [2014].

We constructed pedigrees for each group using known maternal kinship from long-term census data on births and parentage assignments in CERVUS. For all infants and most of the juveniles and adult females, maternal kinship was known from long-term census data on births and we confirmed that these mother-offspring dyads known from the demographic record shared at least one allele per locus. We assigned sires (for individuals whose mothers were known from the demographic record) or parent pairs (for individuals whose mothers were unknown) in CERVUS using trio likelihood ratios (delta) and a 95% confidence level [Kalinowski et al., 2007; Marshall et al., 1998]. The proportion of sampled candidate sires (or mothers) was set to the proportion of sampled males (or females) at least 6-years old that were resident in the group at the time of conception. The genotyping error rate was set to the recommended 1%. The paternity of three additional infants (HU, EA, and CD) could be estimated with a high degree of certainty despite the lack of DNA samples because of the presence of only one adult male in the group at the time of conception, the lack of observed extra-group copulations, and the lack of assigned extra-group parentage. From this parentage information, we created pedigrees to determine kinship between handlers and infants (see below for categories used).

Terminology

Only behaviors directed by handlers towards focal infants were considered part of the *infant handling* repertoire. Infant handling behaviors include: *Touch*, *Oral Inspect*, *Visual Inspect*, *Genital Inspect*, *Sniff*, *Groom*, and *Carry* (Supplemental Data, Table SII). Individuals were classified into age category ranges because we do not have exact dates of birth on some individuals within the study population (e.g., males who have immigrated, recently habituated groups). We classified sub-adult (7–10 years) and adult males (≥10 years) into two relatedness categories: *Genetic Sires* are the genetically determined father of the focal infant. *Potential sires* include any sub-adult and adult male present in the group during the time of conception (which excludes the genetic sire of the focal infant). The time of conception was narrowly estimated to be 157.83 ± 8.13 days prior to the first sighting of the newborn infant [Carnegie et al., 2011; Fragaszy et al., 2004]. However, because the exact day of some infants' births had to be estimated (within a week or two), we expanded the definition of potential sires to include any male present in the group 1-month prior and 1-month after the estimated conception date. Based on partial pedigrees and parentage assignments, we classified immature handlers (18 months–7 years) into four kinship categories: *full-siblings*, *maternal half-siblings*, *paternal half-siblings*, and *unrelated dyads*. We classified dyads with a theoretical dyadic relatedness $r < 0.25$ as unrelated because dyads with a lower degree of relatedness no longer show kin-bias in several species of primates, including white-faced capuchins [Chapais, 2001; Kapsalis & Berman, 1996; Perry et al., 2008]. Only dyads for which we determined paternal relatedness were used in this analysis, because some individual's paternal kinship is yet to be fully resolved. We have provided the number of available dyads in each kin category (*genetic sires*, *potential sires*, *full-siblings*, *maternal half-siblings*, *paternal half-siblings*, and *unrelated dyads*; Table I).

Analysis of Data

Analyses were conducted using Linear Mixed Models (LMM, Genlinmixed in SPSS v. 21.0) with a normal distribution and an identity link function. For each model, infant and handler identifications were nested within study groups and incorporated as random factors. Random factors allowed us to take into account repeated measures on individuals.

The following fixed effects were treated as discrete categorical independent variables: paternity (sire/potential sire), current male rank (alpha/subordinate) (i.e., current rank rather than rank during conception), and sibship (full siblings, maternal half-siblings, paternal half-siblings, and non-kin where non-kin was our baseline level against which the other types of kin categories were compared). In order to examine the effects of these categories on infant handling, the following dependent variables were analyzed: the rate of each infant handling behavior, the rate of all infant handling behaviors combined, the duration of carrying bouts in seconds, and the duration of grooming bouts in seconds for each infant-handler dyad. Both of the latter were treated as continuous variables. Rates of each infant

TABLE I. Number of Focal Infants With the Number Available Handlers in Each Handler Category Per Group

Season	Group	Number of infants	PS	FS	MHS	PHS	UN
1	CP	3	6	3	0	45–48	20–21
1	LV	1	2–4	2	0	3	5
1	GN	5	3–4	1	8	8	88–90
2	AD	4	2–6	3	0	10–11	6
2	RM	3	2–6	1	4	3	19–22
2	LV	1	2–4	1	1	0	3
2	GN	4	3–4	1	0	8	86–89
2	EX	3	3	1	4	0	9

PS, potential sires; FS, full siblings; MHS, maternal half-siblings; PHS, paternal half-siblings; UN, unrelated dyads.
A range is indicated where individuals died or emigrated.

handling behavior were calculated as: (the number of bouts/the number of observed focal infant hours) per infant-handler dyad. Since handler availability varied through the season, the *number of observed focal infant hours* took into account only those hours for which the handler was present in the group. In all analyses involving rate, we included potential infant-handler dyads that we did not observe to interact as having a rate of zero. Initially, we included interaction effects between the fixed effects but removed non-significant interaction effects from the final model. We performed Tukey HSD pairwise comparisons when trying to determine whether there were significant differences between all combinations of kinship categories. The number of handlers available to each infant changed as the season progressed and these changes were not consistent across groups or categories. When accounting for the number of handlers available, we calculated the available handler proportions to each infant for each focal session. Handler proportions were included as continuous covariates in the LMM models as an interaction effect with the appropriate fixed effect variable. Mothers of the infant being sampled were not included in the calculations of the proportion of available handlers. Mother–infant dyads were not considered to be an infant-handler dyad; however mothers could be handlers if they were interacting with infants that were not their own.

RESULTS

Infant Handling by the Genetic Sire and Potential Sires

The genetic sire was known for 15 infants; however, corresponding behavioral interaction data were only available for 12 infants because three of the sires were not present in the infant's group during our study. Ten of the fifteen infants (67%) were sired by alpha males who maintained the alpha position for at least 1-month prior to and after the conception of the infant. The rate of interaction directed towards infants by genetic sires or potential sires, as well as

by alpha and subordinate males varied across different behaviors.

When analyzing the interaction rates of all types of affiliative behaviors combined, infant handling did not significantly differ between genetic and potential sires ($F_{4,394} = 2.458$, $P = 0.361$). We also analyzed the infant handling behaviors separately (Fig. 1). Although fathers directed four out of five of the behaviors toward infants more often than did potential sires, the rates did not differ significantly for any of the behaviors tested: oral inspect ($F_{4,69} = 1.539$, $P = 0.249$); touch ($F_{4,69} = 1.919$, $P = 0.170$); genital inspect ($F_{4,69} = 1.312$, $P = 0.320$); sniff ($F_{4,69} = 6.907$, $P = 0.677$); inspect ($F_{4,69} = 0.910$, $P = 0.346$); and groom ($F_{4,69} = 7.262$, $P = 0.315$). There was no significant difference in the duration of grooming bouts by fathers and by potential sires ($F_{2,4} = 0.011$, $P = 0.968$). There was not enough data to carry out a separate statistical analysis on rates or duration of carrying behavior.

We then examined whether or not the male handlers were the alpha male (A) or a subordinate male (S) within the group. When all behaviors were analyzed together, the rank status of the male, not his genetic relation to the infant, was the best
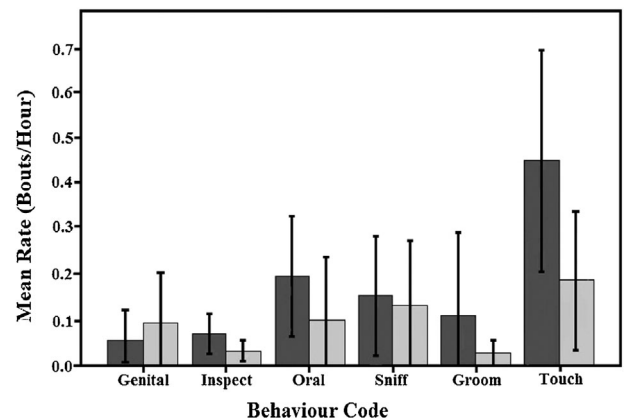

Fig. 1. Rates (bouts/hour ± SE) of interaction between genetic sires (dark gray) and potential sires (light gray) for all infant-handling behaviors, except carry.

predictor of whether or not a male interacted with an infant (A: bouts/hr = 0.34 ± SE 0.07; S: bouts/hr = 0.05 ± SE 0.02; $F_{4,201}$ = 9.376, P = 0.002). When we analyzed behaviors separately, we found that alpha males touched (A: bouts/hr = 0.60 ± SE 0.17, S: bouts/hr = 0.09 ± SE 0.05, $F_{4,68}$ = 4.914, P = 0.030), sniffed (A: bouts/hr = 0.47 ± SE 0.14, S: bouts/hr = 0.02 ± SE 0.02, $F_{4,69}$ = 26.314, P = 0.000), inspected (A: bouts/hr = 0.11 ± SE 0.03, S: bouts/hr = 0.02 ± SE 0.01, $F_{4,69}$ = 32.823, P = 0.000), and groomed (A: bouts/hr = 0.16 ± SE 0.06, S: bouts/hr = 0.01 ± SE 0.01, $F_{4,69}$ = 18.021, P = 0.001) infants at significantly higher rates than did subordinate males (Fig. 2). There was no significant difference for genital inspect ($F_{4,69}$ = 2.314, P = 0.087) and oral inspect ($F_{4,69}$ = 3.746, P = 0.179). Due to small sample sizes, there was not enough data to carry out a separate statistical analysis on rates or duration of carrying behavior by alpha versus subordinate males. Moreover, we were also unable to analyze whether alpha males groomed infants for longer than did subordinate males.

Infant Handling by Siblings

When analyzing the interaction rates of all types of affiliative behaviors combined, full-siblings and maternal half-siblings (but not paternal half-siblings) interacted with infants at significantly higher rates than did non-kin (FS: bouts/hr = 0.80 ± SE 0.4; MHS: bouts/hr = 0.84 ± SE 0.33; PHS: bouts/hr = 0.18 ± SE 0.08; UN: bouts/hr = 0.26 ± SE 0.10; $F_{3,2076}$ = 8.550, P = 0.000; Fig. 3, Table II). Tukey HSD pairwise comparisons also showed that the interaction rates were higher for full-siblings and maternal half-siblings than paternal half-siblings while full-siblings and maternal half-siblings did not differ (Table II).

When behaviors were analyzed separately, we found that it was only full siblings that carried infants at significantly higher rates than non-kin (FS: bouts/hr = 0.57 ± SE 0.06; MHS: bouts/hr = 0.13 ± SE 0.05; PHS: bouts/hr = 0.06 ± SE 0.03; UN: bouts/hr = 0.06 ± SE 0.02; $F_{3,156}$ = 6.606, P = 0.000, Table II). Pairwise comparisons between the other kinship categories showed that full-siblings also carried infants at higher rates than maternal and paternal half-siblings, while there was no difference between the two types of half-siblings (Table II).

We also found that full siblings and maternal half-siblings touched infants at higher rates than did non-kin (FS: bouts/hr = 0.36 ± SE 0.08; MHS: bouts/hr = 0.33 ± SE 0.06; PHS: bouts/hr = 0.08 ± SE 0.04; UN: bouts/hr = 0.09 ± SE 0.03; $F_{3,156}$ = 5.664, P = 0.003, Table II). Pairwise comparisons also showed that full-siblings and maternal half-siblings touched infants at higher rates than did paternal half-siblings, while there was no different between full-siblings and maternal half-siblings (Table II).

We found no difference between any dyads for the remaining handling behaviors (Grooming [$F_{3,156}$ = 1.641, P = 0.182], inspect [$F_{3,156}$ = 5.161, P = 0.102], genital inspect [$F_{3,156}$ = 1.576, P = 0.198], oral inspect [$F_{3,156}$ = 1.388, P = 0.249], and sniff [$F_{3,156}$ = 4.858, P = 0.113]).

DISCUSSION

In general, resident adult and subadult male capuchins have relationships with infants that can be described as affiliative or tolerant [MacKinnon, 2007; Perry, 2012; Rose, 1998]. Males approach and inspect newborn infants, and continue to associate and interact with them throughout infancy. Infants actively engage with males by approaching them, climbing on them, playing with them, resting in proximity, or by directing "gargle" vocalizations towards the male [Gros-Louis et al., 2008]. Moreover, males are tolerant of infants visually inspecting,
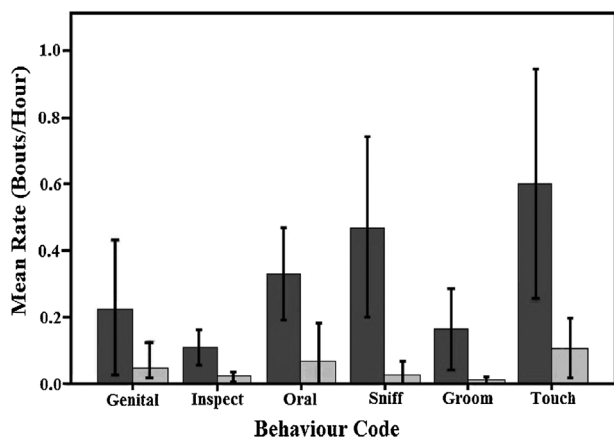

Fig. 2. Rates (bouts/hour ± SE) of interaction between alpha males (dark gray) and subordinate males (light gray) for all infant handling behaviors, except carry.
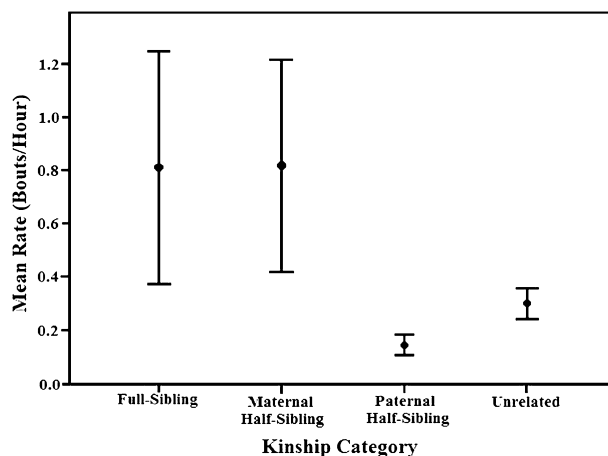

Fig. 3. Rate (bouts/hour ± SE) of the interaction rates of all types of affiliative handling behaviors combined between different sibling groups (full-sibling, maternal half-siblings, paternal half-siblings, and unrelated dyads).

TABLE II. *P*-Value Results for the Pairwise Comparison for Combined Behaviors, Carry, and Touch Behaviors for Each Possible Dyad Combination

	FS-MHS	FS-PHS	FS-UN	MHS-PHS	MHS-UN	PHS-UN
Combined	0.212	$\leq0.001^*$	$\leq0.001^*$	0.004^*	0.002^*	0.977
Carry	$\leq0.001^*$	$\leq0.001^*$	$\leq0.001^*$	0.237	0.193	0.933
Touch	0.119	0.002^*	$\leq0.001^*$	0.002^*	0.001^*	0.841

FS, full siblings; MHS, maternal half-siblings; PHS, paternal half-siblings; UN, unrelated dyads.
Significant differences are indicated with an asterisk (*).

touching, or collecting discarded food items from them [Pers. obs.; Fragaszy et al., 2004]. We never observed an infant incur a serious injury from a resident male. However, infanticidal attacks by nonresident males have been observed during group takeover events within this study population and in studies of other *Cebus* species [Fedigan, 2003; Fragaszy et al., 2004; Perry, 2012].

Paternal Kinship and Male Rank

Evidence for paternal kin-bias among primate species is mixed [Rendall, 2004]. For example, adult female rhesus macaques and juvenile mandrills were significantly more likely to exhibit affiliative behaviors towards paternal half-siblings as compared to unrelated individuals [Charpentier et al., 2007; Widdig et al., 2001, 2002]. Evidence suggests that mandrill and chimpanzee males spend more time with infants that they have sired [Charpentier et al., 2007; Lehmann et al., 2007]. However, paternal kin are treated like non-kin in many studies [Charpentier et al., 2008a,b; Langergraber et al., 2007; Perry et al., 2008]. A main hypothesized mechanism of maternal kin recognition among primates is familiarity, in that there is a high correlation between maternal relatedness and social association [Rendall, 2004; Widdig, 2007]. Paternal kin familiarity could occur when infants fathered by the same sire are born within the same age cohort [Altmann et al., 1996]. However, age proximity may not be the most successful mechanism if reproductive skew is imperfect or if male tenure extends beyond one breeding season [Widdig, 2013], as is the case with white-faced capuchins [Jack & Fedigan, 2004b]. Phenotypic matching is another mechanism by which paternal kin can distinguish each other, but evidence for this is not widely supported in primates [Widdig, 2007].

Paternal relatedness through the father does not appear to have a strong effect on infant handling behaviors in our study, since we found no significant results of fathers preferentially interacting with their offspring. Although there was not a significant difference, actual sires showed on average higher interaction rates than did potential sires, and it is possible that there would be a small but significant

positive effect of sire status in a larger sample. In some monogamous species, (e.g., *Aotus*) where males might be able infer paternity with a high degree of certainty, resident males partake in direct caretaking activities such as carrying the infant, sharing food, or guarding against predators. These resident males are able to preferentially direct affiliative behaviors towards their biological infants and may increase their fitness [Wright, 1984, 1990]. Conversely, a resident male in a multi-male group who is able to distinguish paternity might be more likely to harm or kill a dependent infant within his group that is not his own offspring in order to bring the mother into estrus more quickly and thus increase his own reproductive success [Palombit, 2012]. However, resident male capuchins do not monopolize receptive females, and in the absence of cues as to paternity, selection for infanticide by resident males would run the risk of killing all the infants in the group, including genetic offspring.

If paternity confusion is created by the promiscuous mating patterns of adult females, then all resident males could be sires and therefore would be less likely to commit infanticide against infants within their group, and more likely to help defend the group from invading males. Indeed, evidence suggests that the function of non-conceptive mating behavior by adult female white-faced capuchins is to confuse paternity and is the primary adaptive counterstrategy of females to infanticide [Carnegie et al., 2006; Fedigan & Jack, 2013; Manson et al., 2004]. Among white-faced capuchins, infanticide risk is highest from invading males during the processes of immigration and male take-over events [Fedigan, 2003].

From an infant's point of view, establishing the identity of their biological father may be of little consequence, especially, if due to dispersal or death, the father is not likely to remain within the group during the entire infancy period. Male tenure length varies between age classes; adult males (median: 48.9 months) remain within a group for longer than do subadult males [median: 22.7 months; Jack & Fedigan, 2004b]. Despite these relatively long tenure periods, during this study, only about 54% of potential sires (including the father) remained in the groups long enough for us to observe them interacting with the infants. Moreover, 5 of the 15

genetically determined fathers were no longer resident in their infant's group during the study period. Given the frequent dispersal of males, as well as the variability in male tenure length, it may not be productive for infants to establish bonds solely with their biological father.

It would, however, be beneficial for infants to establish strong bonds with their group's alpha male, irrespective of his genetic relationship to the infant, as there may be direct and indirect advantages to associating more closely with the alpha male [Jack & Fedigan, 2006; Perry, 2012; Rosenbaum et al., 2015]. From the infant's perspective, infants may gain some protection from invading infanticidal males, aggressive group members, or predators by associating closely with the alpha male who is the most vigilant group member and may be better able to rescue or drum up the support of other males [Rose, 1998]. However, both infants and alpha males are centrally located and, therefore, may spend more time in proximity to one another than with subordinate males who sometimes maintain a more peripheral group position [Rose, 1998]. This would suggest that infants and alphas are not necessarily more likely to interact because of some adaptive benefit, but rather simply because they more often find themselves in close proximity.

Alpha males themselves may benefit from associating more closely with infants. Dependent infants spend the majority of their time with their mothers, and interacting with the infant may allow males to establish stronger bonds with the infant's mother [Altmann, 1980]. Future studies should examine the formation or maintenance of social bonds or alliances between adult males and females within the context of infant handling. In addition, subordinate males may increase their fitness by supporting the alpha male in the care and protection of infants, if, owing to mating opportunities, some of the infants have been sired by them rather than the alpha male. Alternatively, subordinate males may increase their inclusive fitness, if, owing to the high rates of parallel dispersal by brothers and cousins, these subordinates are in fact related to the alpha male and his offspring [Perry, 2012; Wikberg et al., 2014].

Paternal Kinship Recognition and Siblings

According to kin selection theory, full-siblings should handle infants at higher rates compared to half-siblings, who in turn should handle infants at higher rates compared to unrelated dyads. When all handling behaviors were considered together, maternally related kin (full-siblings and maternal half-siblings) interacted with infants at higher rates than did paternal half-siblings and unrelated dyads. This suggests that some behaviors are maternally kin-biased, and that kin-recognition may be limited to maternal kin. After examining each behavior

separately, we found that only carrying and touch behaviors showed a significant bias towards full-siblings and maternal half-siblings, suggesting that only certain behaviors may be governed by kin-selection mechanisms [Hamilton, 1964]. High-cost behaviors, such as carrying, may come under stronger kin-selective pressure than do more energetically inexpensive behaviors such as inspect and sniff. That is, even though all white-faced capuchin group members carry infants, they may be more motivated to carry a closely related infant because of the increased costs.

Furthermore, in our analyses of the individual handling behaviors, we did not find a statistical difference between the rates of touch for paternal half-siblings versus unrelated dyads. Perry et al. [2008] found in a neighboring population of *C. capucinus* that adult female full-sisters and maternal half-sisters interacted more often with each other than with paternal half-sisters and unrelated females suggesting that white-faced capuchins bias behaviors towards maternal rather than paternal kin. Maternal kin can be distinguished based on mother-mediated familiarity while paternal kin discrimination possibly requires a more error-prone kin recognition such as age-mediated proximity, father-mediated proximity, or phenotype matching [Schulke et al., 2013].

We also need to consider that white-faced capuchins may be able to recognize paternal kin, but do not exhibit biases towards them. For example, experimental research has shown that Japanese macaques do not always discriminate related individuals from unrelated individuals despite being able to recognize kin [Chapais et al., 1997]. Moreover, yellow baboons exhibit stronger bonds towards paternal sisters when maternal kin are absent [Silk et al., 2006]. Therefore, the motivation to interact with different kinds of kin may be influenced by the availability of kin-types within the group. Maternal kin may be more familiar than paternal kin despite both having the same theoretical inclusive fitness benefits. Familiar kin may be more reliable social partners, and as a consequence, maternal kin are favored over paternal kin [Chapais, 2001].

CONCLUSION

Given that fathers do not preferentially interact with their offspring nor do paternal half-siblings interact with infants in a manner distinct from unrelated individuals, our analyses do not indicate that white-faced capuchins distinguish paternal kin. However, carrying shows a distinct bias towards full-siblings that may be the result of individuals distinguishing paternal kin, or perhaps of having greater familiarity with both their paternal and maternal kin, than with unrelated group members. Alpha males are more likely to

interact with infants and this may be driven by their attempt to maintain or establish closer bonds with adult females. There may also be selection on infants to establish bonds with the alpha male to gain increased protection against conspecifics or predators. Even though it may be possible for our study animals to distinguish paternal kin, the handling behaviors we examined are not strongly influenced by paternal relatedness patterns.

ACKNOWLEDGMENTS

REFERENCES

Altmann J. 1980. Baboon mothers and infants. Cambridge: Harvard University Press.

Altmann J. 1974. Observational study of behaviour: sampling methods. Behaviour 49:227–267.

Altmann J, Alberts SC, Haines SA, et al. 1996. Behaviour predicts genetic structure in a wild primate group. Proceeding of the National Academy of Science USA 93:5797–5801.

Bergstrom ML, Fedigan LM. 2013. Dominance style of female white-faced capuchins. American Journal of Physical Anthropology 150:591–601.

Buchan JC, Alberts SC, Silk JB, Altmann J. 2003. True paternal care in a multi-male primate society. Nature 425:179–181.

Busse CD, Gordon TP. 1984. Infant carrying by adult male mangabeys (*Cercocebus atys*.). American Journal of Primatology 6:133–144.

Carnegie SD, Fedigan LM, Melin AD. 2011. Reproductive seasonality in female capuchins (*Cebus capucinus*). International Journal of Primatology 32:1076–1090.

Carnegie SD, Fedigan LM, Ziegler TE. 2006. Post-conceptive mating in white-faced capuchins, *Cebus capucinus*: hormonal and sociosexual patterns of cycling, noncycling, and pregnant females. In: Estrada A, Garber PA, Pavelka MSM, Luecke L, editors. New perspectives in the study of mesoamerican primates: distribution, ecology, behavior, and conservation. New York: Springer. p 387–409.

Chapais B. 2001. Primate Nepotism: what is the explanatory value of kin selection. International Journal of Primatology 22:203–229.

Chapais B, Gauthier C, Prud Homme J, Vasey P. 1997. Relatedness threshold for nepotism in Japanese macaques. Animal Behaviour 53:1089–1101.

Charpentier MJE, Deubel D, Peignot P. 2008a. Relatedness and social behaviors in *Cercopithecus solatus*. International Journal of Primatology 29:487–495.

Charpentier MJE, Van Horn RC, Altmann J, Alberts SC. 2008b. Paternal effects of offspring fitness in a multimale primate society. Proceedings of the National Acadamy of Sciences USA 105:1988–1992.

Charpentier MJE, Peignot P, Hossaert-McKey M, Wickings JE. 2007. Kin discrimination in juvenile Mandrills (*Mandrillus sphinx*). Animal Behaviour 73:37–45.

Cortés-Ortiz L, Mondragón E, Cabotage J. 2010. Isolation and characterization of microsatellite loci for the study of Mexican howler monkeys, their natural hybrids, andother Neotropical primates. Conservation Genetics Resources 2:21–26.

Escobar-Páramo P. 2000. Microsatellite primers for the wild brown capuchin monkey *Cebus apella*. Molecular Ecology 9:107–108.

Fedigan LM. 2003. Impact of male takeovers on infant deaths, births, and conceptions in *Cebus capucinus* at Santa Rosa, Costa Rica. International Journal of Primatology 24:723–741.

Fedigan LM, Jack K. 2004. The demographic and reproductive context of male replacements in *Cebus capucinus*: how, when and why do male white-faced capuchins take over groups? Behaviour 141:755–775.

Fedigan LM, Jack KM. 2012. Tracking neotropical monkeys in Santa Rosa: lessons from a regenerating Costa Rican dry forest. In: Kappeler PM, Watts DP, editors. Long-term field studies of primates. Berlin Heidelberg: Springer Verlag. p 165–184.

Fedigan LM, Jack KM. 2013. Sexual conflict in white-faced capuchins: it's not whether you win or lose. In: Fisher ML, Garcia JR, Chang RS, editors. Evolution's empress: darwinian perspectives on women. New York: Oxford University Press. p 281–303.

Fernandez-Duque E, Di Fiore AW, Hauk M. 2012. The behavior, ecology and social evolution of New World monkeys. In: Mitani JC, Call J, Kappeler PM, Palombit RA, Silk JB, editors. The evolution of primate societies. Chicago: University of Chicago Press. p 43–64.

Fragaszy DM, Visalberghi E, Fedigan LM. 2004. The complete capuchin: the biology of the genus cebus. Cambridge: Cambridge University Press.

Gros-Louis JJ, Perry SE, Fichtel C, et al. 2008. Vocal repretoir of *Cebus capucinus*: acoustic structure, context, and usage. International Journal of Primatology 29:641–670.

Hamilton WD. 1964. The genetical evolution of social behaviour. Journal of Theoretical Biology 7:1–51.

Jack KM, Fedigan LM. 2004a. Male dispersal patterns in white-faced capuchins (*Cebus capucinus*). Part 1: patterns and causes of natal emigration. Animal Behaviour 67:761–769.

Jack KM, Fedigan LM. 2004b. Males dispersal patterns in white-faced capuchins (*Cebus capucinus*). Part 2: patterns and causes of secondary dispersal. Animal Behaviour 67:771–782.

Jack KM, Fedigan LM. 2006. Why be alpha male? Dominance and reproductive success in wild white-faced capuchins (*Cebus capucinus*). In: Estrada A, Garber M, Pavelka M, Luecke L, editors. New perspectives in the study of Mesoamerican primates: distribution, ecology, behavior, and conservation. New York: Springer. p 367–386.

Jack KM, Brasington LF, Ritchotte K, et al. 2014. Bide your time: method of alpha male replacement, infant deaths, and time to conception in *Cebus capucinus*. American Journal of Physical Anthropology 153:150.

Janson CH. 1986. Ecological and social consequences of food competition in brown capuchin monkeys [dissertation].

Washington: University of Washington. Available from: ProQuest Dissertations & Theses Global. 8521604.

Kalinowski ST, Steven T, Taper ML, Marshall TC. 2007. Revising how the computer program cervus accommodates genotyping error increases success in paternity assignment. Molecular Ecology 16:1099–1106.

Kapsalis E, Berman CM. 1996. Models of affiliative relationships among free-ranging rhesus monkeys (*Macaca mulatta*) 1. Criteria for kinship. Behaviour 133:1209–1234.

Langergraber K. 2012. Cooperation among kin. In: Mitani JC, Call J, Kappeler PM, Palombit, RA, Silk JB, editors. The evolution of primate societies. Chicago: University of Chicago Press. p 491–513.

Langergraber K, Mitani J, Vigilant L. 2007. The limited impact of kinship on cooperation in wild chimpanzees. Proceedings of the National Acadamy of Sciences USA 104:7786–7790.

Lehmann J, Fickenscher G, Boesch C. 2007. Kin biased investment in wild chimpanzees. Behaviour 143:931–955.

MacKinnon KC. 2007. Social beginnings. The tapestry of infant and adult interactions. In: Campbell CJ, Fuentes A, MacKinnon KC, Bearder S, Stumpf RM, editors. Primates in perspective. New York: Oxford University Press. p 440–455.

Manson JH, Gros-Louis J, Perry S. 2004. Three apparent cases of infanticide by males in wild white-faced capuchins (*Cebus capucinus*). Folia Primatologica 75:104–106.

Marshall TC, Slate J, Kruuk LEB, Pemberton JM. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. Molecular Ecology 7:639–655.

Morin P, Chambers K, Boesch C, Vigilant L. 2001. Quantitative polymerase chain reaction analysis of DNA from noninvasive samples for accurate microsatellite genotyping of wild chimpanzees (*Pan troglodytes verus*). Molecular Ecology 10:1835–1844.

Muller MN, Thompson ME. 2012. Mating, parenting and male reproductive strategies. In: Mitani JC, Call J, Kappeler PM, Palombit RA, Silk JB, editors. The evolution of primate societies. Chicago: University of Chicago Press. p 387–411.

Muniz L, Vigilant L. 2008. Isolation and characterization of microsatellite markers in the white-faced capuchin monkey (*Cebus capucinus*) and cross-species amplification in other New World monkeys. Molecular Ecology Resources 8:402–405.

Muniz L, Perry S, Manson JH, et al. 2010. Male dominance and reproductive success in wild white-faced capuchins (*Cebus capucinus*) at Lomas Barbudal, Costa Rica. American Journal of Primatology 72:1118–1130.

Palombit RA. 2012. Infanticide: male strategies and female counterstrategies. In: Mitani JC, Call J, Kappeler PM, Palombit RA, Silk JB, editors. The evolution of primate societies. Chicago: University of Chicago Press. p 432–468.

Paul A, Kuester J. 1996. Infant handling by female Barbary macaques (Macaca sylvanus) at Affenberg Salem: testing functional and evolutionary hypotheses. Behavioral Ecology and Sociobiology 39:133–145.

Perry S, Manson JH, Muniz L, Gros-Louis J, Vigilant L. 2008. Kin-biased social behavior in wild adult female white-faced capuchins, *Cebus capucinus*. Animal Behaviour 76:187–199.

Perry S. 2012. The behavior of wild white-faced capuchins: demography, life history, social relationships, and communication. Advances in the Study of Behavior 44:135–181.

Rendall D. 2004. Recognizing kin: mechanisms, media, minds, modules, and muddles. In: Chapais B, Berman CM, editors. Kinship and behavior in primates. Oxford: Oxford University Press. p 295–316.

Rose LM. 1998. Behavioral ecology of white-faced capuchins (*Cebus capucinus*) in Costa Rica [dissertation]. Washington: Washington University. Available from: ProQuest Dissertations & Theses Global. 9918668.

Rosenbaum S, Hirwa JP, Silk JB, Vigilant L, Stoinski TS. 2015. Male rank, not paternity, predicts male-immature relationships in mountain gorillas, *Gorilla beringei beringei*. Animal Behaviour 104:13–24.

Schoof VAM, Jack KM. 2014. Male social bonds: strength and quality among coresident white-faced capuchin monkeys (*Cebus capucinus*). Behaviour 151:963–992.

Silk JB, Altmann J, Alberts S. 2006. Social relationships among adult female baboons (*Papio cynocephalus*): variation in the strength of social bonds. Behavioral Ecology and Sociobiology 6:183–195.

Small MF. 1990. Alloparental behavior in Barbary macaques, *Macaca sylvanus*. Animal Behavior 39:297–306.

Smuts B. 1985. Sex and friendship in baboons. New York: Aldine.

Smuts B, Gubernick D. 1992. Male-infant relationships in nonhuman primates: paternal investment or mating effort? In: Hewlett B, editor. Father-child relations, cultural, and biosocial contexts. New York: Aldine. p 1–30.

Whitten PL. 1987. Infants and adult males. In: Smuts B, Cheney DL, Seyfarth RM, Wrangham RW, Strusaker TT, editors. Primate societies. University of Chicago Press, Chicago. p 343–357.

Wikberg EC, Jack KM, Campos FA, et al. 2014. The effect of male parallel dispersal on group composition in white-faced capuchins (*Cebus capucinus*). Animal Behaviour 96:9–17.

Wikberg EC, Jack KM, Campos FA, et al. 2015. Alternative routes to reproductive success may explain male cooperation in a primate population (*Cebus capucinus*) with high reproductive skew. American Journal of Physical Anthropology 156:324.

Widdig A. 2007. Paternal kin discrimination: the evidence and likely mechanisms. Biological Reviews 82:319–334.

Widdig A. 2013. The impact of male reproductive skew on kin structure and sociality in multi-male groups. Evolutionary Anthropology 22:239–250.

Widdig A, Nuernberg P, Krawczak M, Streich WJ, Bercovitch FB. 2001. Paternal relatedness and age proximity regulate social relationships among female rhesus macaques. Proceedings of the National Academy of Sciences of the USA 98:13769–13773.

Widdig A, Nuernberg P, Krawczak M, Streich WJ, Bercovitvh F. 2002. Affiliation and aggression among adult female rhesus macaques: a genetic paternal cohorts. Behaviour 139:371–391.

Wright PC. 1984. Biparental care in *Aotus trivigatus* and *Callicebus moloch*. In: Small M, editor. Female primates: studies by women primatologists. Alan R. Liss, New York. p 59–75.

Wright PC. 1990. Patterns of paternal care in primates. International Journal of Primatology 11:89–102.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.