

Variation in Adult Male-Juvenile Affiliative Behavior in Japanese Macaques (*Macaca fuscata*)

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Abstract

Adult males of some primate species are known to positively interact with juveniles. In cases where paternal certainty is high, these behaviors have been largely attributed to the paternal investment hypothesis. Males have also been observed to interact with nonkin juveniles, which has often been explained in terms of mating effort. Here, we examined variation in adult male-juvenile affiliation in semi-free ranging Japanese macaques (*Macaca fuscata*) at the Oregon National Primate Research Center against possible influencing factors such as age, dominance rank, and female affiliation, and we also tested for fitness benefits. We conducted 154 h of focal observations of 14 adult males from June to September 2018. Males differed significantly in their rate of juvenile-directed affiliation, but not in their fitness in terms of number of offspring. There was a significant positive correlation between rank and age in the group, indicating that, in this group, rank does not conform to the classic inverted-U pattern observed elsewhere in this species. Although there was a significant positive correlation between rank and juvenile-directed affiliation, the highest-ranking male had few offspring and exhibited little juvenile-directed affiliation. These results suggest little to no preliminary support for either the paternal investment or mating effort hypotheses as explanations for juvenile-directed affiliation. This study suggests that there are multiple behavioral strategies for older males that may influence reproductive success.

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Introduction

In mammals, direct care of young by adult males occurs in approximately 5–10% of species [Clutton-Brock, 1991; Woodroffe and Vincent, 1994]. However, care by males is more common in primates than other mammals as this set of behaviors has been observed in 30–40% of primate genera [Clutton-Brock, 1991, and references therein]. Male care of immatures may be obligate or facultative, and has been explained by means of a number of evolutionary models including the paternal investment hypothesis and the mating effort hypothesis [Busse and Hamilton, 1981; Wright, 1990; Clutton-Brock, 1991; Smuts and Gubernick, 1992; Paul et al., 1996; Van Schaik and Paul, 1996; Mitani and Watts, 1997; Silk, 1999; Boose et al., 2018].

The paternal investment hypothesis predicts that (1) males should preferentially interact with related infants, and (2) these male-infant relationships should increase the infant's chances of survival and future reproductive success. It has been suggested that paternal investment can be positively associated with the degree of paternal certainty [Garber and Leigh, 1997; Fernandez-Duque et al., 2009]; however, the paternity certainty hypothesis is not adequate as an explanation for the evolution of male care of young in all nonhuman primate species [Smuts and Gubernick, 1992].

The mating effort hypothesis proposes that there is a mutually advantageous and reciprocal relationship between males and females in which male care of immatures occurs: (1) infants can benefit from male care, (2) females (or infants) can control and offer important benefits to males, and/or (3) females have opportunities to compare the behavior of different males and distribute mating benefits based on this comparison [Smuts and Gubernick, 1992]. For example, studies have reported that male vervet monkeys (*Chlorocebus pygerythrus*) were observed to be more affiliative with infants when that infant's mother was in visual contact [Van Schaik and Paul, 1996]. Another study of Assamese macaques (*Macaca assamensis*) found that females demonstrated preference, as measured through selective affiliation, for 2 particular male traits, i.e., dominance or access to resources and prior affiliation with immatures [Haunhorst et al., 2019]. Male care of infants has been observed to increase male reproductive success in several species [Clutton-Brock, 1991; Van Schaik and Paul, 1996; Silk, 1999; Rosenbaum et al., 2018]. According to this hypothesis, males that provide care to immatures are more likely to sire the female's subsequent offspring or have a generalized increase in reproductive success.

These hypotheses offer adaptive, but not mutually exclusive, explanations for this set of behaviors. It is important to note that, for example, a male could affiliate with its own biological offspring both as a form of paternal investment and as a strategy to gain reproductive access to the offspring's mother. In order to make inferences about support for these adaptive hypotheses, studies often evaluate individual factors (e.g., dominance rank, age, female affiliation, etc.) which may be highly correlated with male-juvenile affiliation. The age of the adult male has been observed to be highly correlated with the frequency of male care in multiple species of macaques, with older males more likely to affiliate with infants or immatures than younger males [Alexander, 1970; Langos et al., 2013]. Older males, past their physical peak and with a reduced likelihood of future reproductive opportunities, may look to enhance their own fitness by investing more in their own immatures or by using juvenile-directed affiliation as an alternative mating strategy to gain social contact with the mother [Langos et al., 2013].

There is also evidence that the sex and age of the immature are both important for male affiliative attention. Males have been observed to preferentially direct attention towards male immatures rather than females [Langos et al., 2013]. A sex-preference towards females, if found, could lend support to the mating effort hypothesis. Furthermore, while the literature on the paternal investment and mating effort hypotheses have focused primarily on mother-dependent immatures, adult male primates have also been known to form long-term affiliative relationships with independent juvenile individuals, either kin or nonkin [Alexander, 1970; Horrocks and Hunte, 1993; Buchan et al., 2003; Moscovice et al., 2009; Rosenbaum et al., 2016]. For example, there is evidence in mountain gorillas (*Gorilla beringei beringei*) of long-term affiliative relationships between adult males and unrelated maturing group members [Rosenbaum et al., 2015, 2016]. In these cases, relationships between juveniles and adult male gorillas were found to be based on the adult male's rank rather than on paternity and were demonstrated to persist across both developmental classes and social upheaval. As such, it is important to consider male rank as a potential correlate to juvenile-directed affiliation and a possible factor to be incorporated into hypothetical models. Furthermore, there may be additional unexplored benefits of juvenile-directed affiliation for adult males. For example, the preferential focus on older male juveniles may serve to lay the foundation for future alliances, or a preferential focus on maturing female juveniles may allow males to begin cultivating future mating opportunities.

It has been suggested that the expression of paternal behavior may be group-dependent rather than species-specific, and that seasonal variation may play a role in the degree to which these behaviors occur [Itani, 1959; Berghänel et al., 2011]. Paternal behavior has largely been observed to take the form of grooming, playing, and carrying, with increases in the rate of these behaviors during the birthing season [Itani, 1959; Alexander, 1970]. Male affiliative bonds with juveniles have been reported repeatedly for a number of macaque species, and it may be a function of their high gregariousness and adaptability [Itani, 1959; Mitchell, 1969; Alexander, 1970; Maestripieri and Carroll, 1998; Berghänel et al., 2011; Minge et al., 2016]. As such, macaques present a uniquely well-suited model genus for examining juvenile-directed affiliative behavior. A study of male-immature relationships in *M. assamensis* suggested that these relationships extend beyond infancy and are primarily maintained by the immature [Minge et al., 2016]. However, it was unclear whether these male-immature relationships represent true paternal care. It is also important to note that while there are reports of these behaviors across the *Macaca* genus, with the frequency and intensity of juvenile-directed affiliation varying across both populations and species. However, these behaviors have been particularly reported in Japanese macaques (*Macaca fuscata*).

Japanese macaques live in large, multimale, multifemale social groups characterized by matrilineal hierarchies and male dominance (Itani et al., 1963; Watanabe, 1979). Male parental behavior has been repeatedly observed in this species. A study on seasonality of parental behavior in adult male Japanese macaques found that there was a significant increase in these behaviors during the birthing season [Alexander, 1970]. The authors concluded that >75% of sexually mature males exhibit an increase in affiliative behavior with juveniles (i.e., individuals 1–4 years of age) during the birthing season. Furthermore, this seasonal shift was consistent across all ages and ranks of adult males, and younger males (aged 5–7 years) were more likely

to engage in play behaviors with juveniles across seasons. It was also observed that some high-ranking males invested in specific juveniles. Some studies have suggested that this behavioral trend is a response by the adult males to the distress of juveniles abandoned by their mothers due to another birth [Itani et al., 1963]. Another study, which observed that dominant males maintained relationships with newborns, young juveniles, and their mothers following the birthing season, instead suggested that dominant males play a role in the socialization of the immatures [Alexander, 1970]. It is possible that early socialization does contribute to establishing and maintaining the authority of the dominant males in the next generation of troop members, thus offering an evolutionary explanation for the ability of male Japanese macaques to maintain authority after their physical peak [Imanishi, 1965; Yamada, 1966].

Based on the propensity of male Japanese macaques to form affiliative bonds with juveniles, this study used the Japanese macaque population at the Oregon National Primate Research Center, Beaverton, OR, USA, to investigate if (1) there is variation between adult males in juvenile-directed affiliative behaviors, (2) age and/or dominance rank influence variation in juvenile-directed affiliation, and (3) there is any significant relationship between reproductive success and variation in juvenile-directed affiliation. We tested the correlation between rates of juvenile-directed affiliation, affiliation received from females, fitness, age, and dominance rank. This group included both natal and nonnatal juveniles. Nonnatal individuals were introduced to the group as weaned yearlings. We also investigated, where possible, the variation in direction of affiliative behavior towards natal or nonnatal juveniles, so as to assess the potential kin-bias. The presence of nonnatal juveniles offered an opportunity to preliminarily exclude paternity as the sole explanation for this behavior. Our two lines of inquiry allowed us to explore whether this behavior is an expression of the paternal investment hypothesis or the mating effort hypothesis.

We would expect that if adult males who have higher rates of juvenile-directed affiliation also have higher rates of received affiliative behavior from adult females and greater fitness, then this would be consistent with a female preference for males that affiliate with juveniles. This would support male affiliation with juveniles as a potential mechanism of mating effort. In addition, we would expect that if adult males preferentially affiliated with natal juveniles who are more likely to be their own offspring or a genetic relative, this would be consistent with the notion that affiliation with juveniles is a form of paternal investment.

Materials and Methods

Housing

The study group was located at the Oregon National Primate Research Center (ONPRC) and housed in a 1-acre outdoor enclosure with steel walls and open access to an indoor feeding room (approx. 3 × 12 m in size). The corral included a number of platforms and other structures for play and enrichment. The group was fed a diet of commercial monkey chow provided twice daily, and supplementary fruits, vegetables, and grains. Water was available ad libitum. The housing area also included 2 observation towers, outside but overlooking the corral, from which observations were conducted. As part of the general animal husbandry practice of the ONPRC, animals were given unique markings on their backs, thereby allowing for individual identification of all members of the group from the observation tower.

Table 1. Japanese macaque focal group demographics as of June 2018

| | Infant | Juvenile | Subadult | Adult | Aged | Total |
|---------|--------|----------|----------|-------|------|-------|
| Females | 4 | 70 | 12 | 31 | 17 | 134 |
| Males | 1 | 62 | 8 | 11 | 5 | 87 |
| Total | 5 | 132 | 20 | 42 | 22 | 221 |

Table 2. Individual Subject identification, age class, age, rank, fitness, and number of mothers

| ID | Age class | Age, years | Rank | Fitness, <i>n</i> of offspring | Mothers, <i>n</i> |
|-----|-----------|------------|--------|--------------------------------|-------------------|
| M1 | aged | 25 | high | 4 | 4 |
| M2 | aged | 21 | high | 3 | 3 |
| M3 | aged | 20 | high | 2 | 2 |
| M4 | aged | 18 | high | 6 | 6 |
| M5 | aged | 17 | high | 5 | 5 |
| M6 | adult | 9 | low | 4 | 4 |
| M7 | adult | 10 | middle | 6 | 6 |
| M8 | adult | 8 | middle | 11 | 11 |
| M9 | adult | 8 | middle | 5 | 4 |
| M10 | adult | 8 | low | 4 | 4 |
| M11 | adult | 8 | low | 2 | 2 |
| M12 | adult | 9 | low | 10 | 10 |
| M13 | adult | 8 | low | 2 | 2 |
| M14 | adult | 7 | low | 2 | 2 |

Study Subjects and Age Classifications

Data were collected on the semi-free ranging group of Japanese macaques at the ONPRC. At the outset of the study, the focal group included 134 females and 87 males in an age range of 0–25 years (Table 1).

The following age classifications were provided by the ONPRC [K. Coleman, pers. comm.]: infants (<1 year), juveniles (>1 to 4 years), subadults (>4 to 7 years), adults (>7 to 15 years), and aged (>15 years).

Juveniles were easily visually distinguished from infants by their given markings, as well as by their decreased nursing and increased independence at 1–2 years of age [Coleman et al., 2011; personal observ.]. Additionally, there were juveniles of approximately 1 year of age, born in extra-troop harem groups, that had been introduced into the group. These juveniles may have had distant biological relatives within the larger group, but they had not been raised with these genetic relatives nor integrated into the maternal hierarchies. There was a total of 6 of these juveniles at the beginning of the study, 5 males and 1 female in an age range of 11–17 months. They were easily identified by black dye on their heads. While they were successfully accepted into the existing group, they were nonnatal and thus had no genetic parents or strong kin alliance system within the group.

For this study, 14 males classified as either aged or adult individuals were the subjects of focal follows. Table 2 lists gender, age class, age, fitness, and rank. Rank was classified as high, middle, or low, based upon the observation of priority-of-access to enrichment food. The average age of a male classified as “aged” was 20.25 (± 3.02) and that of a male classified as “adult” was 8.44 (± 0.78) years.

Table 3. Ethogram of recorded behaviors and modifiers

| Behavioral class | Behavior | Definition |
|--------------------|--|---|
| Other social (SOC) | Groom (GM) | Manipulation of the hair of another individual with the hand and/or mouth |
| | Play (PL) | Social interactions that are characterized by apparently low tension may be accompanied by a “play face” (a facial gesture in which the mouth is open and the features are relaxed); these may include any of the following: grunting, wrestling, sham-biting, jumping on, jumping over, chasing, fleeing, and hiding |
| | Tolerant contact (TO) | Subject is in physical contact with another individual(s) |
| | Ventral social (VS) | Huddling and/or close stationary contact other than grooming, with another individual(s) |
| | Other (OT) | Subject is engaged in behavior not listed in the ethogram; describe in comments section of observation sheet |
| Aggressive (AGG) | Chase (CH) | Behavior that involves pursuit past the location the recipient maintained at the start of the interaction |
| | Threat (TH) | Expression containing facial, vocal, or physical components (may include head-thrusting, open-mouth threat, scream, raised eyebrow, ground beating, and lunge) |
| | Bite (BI) | During which the skin/limb of another animal is grasped with the teeth; may be accompanied by head-shaking |
| | Contact (CO) | May include nipping, grabbing, kicking, pulling, pushing, poking, slapping, pulling hair, butting, and shoving |
| | Other (OT) | Subject is engaged in other form of aggressive behavior not covered by the above categorizations |
| Sociosexual (SOS) | Mount | Subject mounts another individual |
| | Grab (GR) | Subject physically grabs another individual (usually female) in sexual approach. Scored as receptive if the individual is female |
| | Copulate (CO) | Subject engages in copulation with another individual |
| | Proceptive approach (PA) | Subject receives sexual approach, sexual grab, or display of genitalia/sexual swelling from a female individual |
| Solitary (SOL) | Abnormal (AB) | Subject is engaged in atypical behavior which may include any of the following: stereotype, self-bite, coprophagy, floating limb |
| | Eat (EA) | Subject is ingesting liquid (drinking) or solid food material (common usage) |
| | Explore (EX) | Subject inspects or manipulates an object other than food |
| | Forage (FO) | Subject is searching through grass or other substrate material, presumably for food |
| | Locomotion (LO) | Subject engages in movement from one location to another while using its entire body |
| | Self-groom (SG) | Picking through and/or slowly brushing aside own hair with hands and/or mouth |
| | Self-play (SP) | Subject engages in independent play with active movement; this may include swinging, running, or spinning on objects |
| | Sleep (SL) | Subject appears to be sleeping; is stationary with eyes closed |
| | Stationary (ST) | Subject is inactive without motile movement; may still involve head or arm movement |
| Other (OT) | Subject is engaged in behavior not listed in the ethogram; describe in comments section of observation sheet | |
| Out of view (OV) | Individual is out of observer view; do not record partner | |

Behavioral Observations

Observations were conducted between June and September 2018 from 08:30 to 16:00 on Monday to Friday. The data collection period largely overlapped with the birth season of Japanese macaques which ranges from May to August at the ONPRC, with the largest number of births usually occurring in June and July. This is the aforementioned peak for male-juvenile affiliative behavior [Alexander, 1970; Coleman et al., 2011]. We collected 154 h of data with equal effort (11 h) per male. The subjects are frequently observed by staff and public visitors and so were behaviorally acclimated to human presence.

Focal follows of individuals were conducted using 30-s instantaneous scans [Altmann, 1974]. Approximately 20 focal follows were conducted per day, with breaks in observation between follows (i.e., 1–2 follows/subject/day). The order of subjects for focal follows was randomly selected, such that each individual was the subject of at least 1 follow per day. K.N.G. collected all data.

We recorded social and solitary behaviors (Table 3). All social behaviors included partner classification where possible. It was not always possible to reliably identify individuals aside from the 14 study subjects. Thus, unless the social partner was another adult male study subject, potential partners were coded according to classes rather than individual identifiers. These classes included adult female, subadult individual, juvenile individual, infant, and unknown individual. Where possible, we recorded whether a male was interacting with a natal or nonnatal juvenile. Directionality (recipient vs. instigator) was recorded for social behaviors when possible.

Data Analyses

We calculated hourly rates of juvenile affiliation per adult male based on the number of affiliative events observed divided by the number of observation hours. We calculated rates based exclusively on juvenile-directed affiliation. Affiliative events were all events in which an adult male was observed engaged in grooming, play, tolerant contact, ventrosocial contact, or other social behaviors (e.g., as carrying) where the social partner was a juvenile (Table 3). The study period encompassed 4 equal observation time blocks, resulting in 4 affiliation rates per focal male ($n = 56$).

The original intention was to create a dominance hierarchy based on aggressive interactions between the adult males. However, the resulting matrix was largely empty, with many males not having been observed interacting with each other. As a result, we were unable to create a reliable linear dominance hierarchy for use in statistical analyses. Therefore, we opted to categorize individuals as having a high, middle, or low rank. These rank categorizations were based on opportunistic observations, including priority-of-access to enrichment food and the frequency with which individuals became involved in settling aggressive encounters within the group.

We ran a one-way ANOVA of the rate of juvenile-directed affiliation, again using individual identification as a random factor, to ascertain whether males differed significantly in their rate of affiliative behavior towards juveniles. We then used Spearman nonparametric correlations ($p < 0.05$) for the following pairs of variables: (1) dominance rank and age, (2) dominance rank and the rate of juvenile-directed affiliation, and (3) the rate of affiliative behavior received from adult females and the rate of juvenile-directed affiliation.

We used a G-test of goodness-of-fit to equal fitness, to examine whether males differed in their observed number of offspring (Sokal and Rohlf, 2012). Fitness was measured as the total number of offspring per male. The number of offspring ranged from 2–11 from an average of 4.64 mothers (Table 2). We reported the number of different females with which a male sired offspring (Table 2). The number of sired offspring was determined from genetic data for each male provided by the ONPRC. The oldest identified offspring was approximately 17 years old and the youngest approximately 1 year old. The youngest male recorded in this study sample as siring offspring was 5 years old and the oldest was 25 years old. As such, these data are presumably a reasonable estimate of fitness for this group. Variation in access to females was not included as a tested variation as the number of females in the group has remained consistent over time. Finally, to see whether fitness was determined by age, we ran a linear regression of fitness on age. All analyses were conducted using SAS v9.4 (Cary, NC, USA).

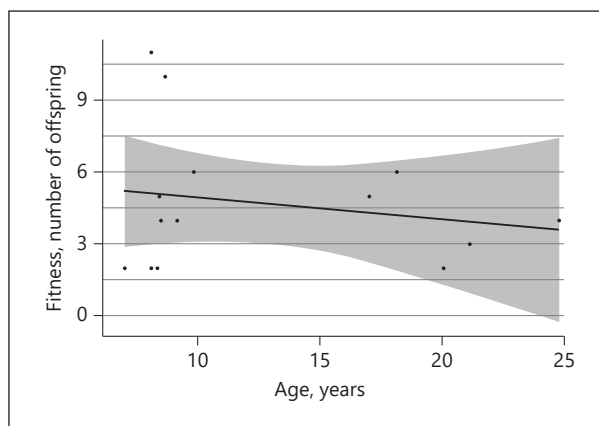


Fig. 1. Linear regression of fitness and age.

Results

We observed 1,342 male-juvenile affiliative interactions by the 14 study subjects. Males displayed significant variation in the rate of affiliation directed at juveniles ($F = 10.81$; $df = 1, 54$; $p < 0.01$). On average, males engaged in approximately 9 (mean 8.64 ± 1.89) affiliation events with juvenile partners per hour; 36% ($n = 483$) of the interactions were confirmed to be with nonnatal juveniles. M2 and M4 exhibited 86% of the total nonkin interactions, interacting exclusively with nonnatal juveniles and comprising 31% ($n = 154$) and 55% ($n = 267$) of these interactions, respectively. The remaining 14% of nonnatal interactions were by 6 other males. We could not identify the remaining 64% of interactions ($n = 859$) as either natal or nonnatal.

We did find that dominance rank was significantly correlated with age ($r = 0.803$; $n = 14$; $p < 0.001$). We found a significant positive correlation between rank and the rate of juvenile-directed affiliation ($r = 0.594$; $n = 14$; $p < 0.05$). There was no significant correlation between affiliation with adult females and the rate of juvenile-directed affiliation ($r = 0.178$; $n = 14$; $p = 0.543$), or between fitness and the rate of juvenile-directed affiliation ($r = 0.237$; $n = 14$; $r = 0.414$). However, males did not differ significantly in fitness ($G = 19.53$; $p = 0.108$, ns), and we found no significant relationship between age and fitness ($F = 0.43$; $p = 0.522$, ns) (Fig. 1).

Discussion

In this study, we found a dominance structure in which rank was significantly positively correlated with age. Takahashi [2002] reported an age-rank relationship in dominance tenure in Japanese macaques, such that both younger and aged males were either ranked lower or held a high rank for a shorter term. However, the acquisition of a long-term higher rank was also impacted by the continued tenure of previously dominant males, with incoming males experiencing a dominance plateau if current dominant individuals did not emigrate or disappear from the troop. However, this particular study also represented a departure from the inverted-U dominance structure [Cowlshaw, 1991; Takahashi, 2002].

Contrary to the traditional model in which dominant males have the greatest reproductive success, this has not been consistently observed in Japanese macaques [Eaton, 1974; Inoue et al., 1993; Takahata et al., 1999]. The lack of a significant correlation between age, rank, and fitness match what has been previously observed. Both genetic data and personal communications with ONPRC staff demonstrated that young males (approx. 8–10 years of age) have the greatest fitness. While rank appears to translate to priority-of-access to food within this group, as is typical, it does not appear to translate into priority-of-access to females. This implies that female choice may override the male priority-of-access model, allowing females to preferentially mate with younger males.

We did not find any significant correlation between affiliation with females and age or dominance rank. This would appear to suggest that females in this group do not have a statistically demonstrable preference for more dominant or older males. Similarly, the lack of a significant correlation between juvenile-directed affiliation and affiliation from adult females suggests that females do not prefer more highly affiliative males. These results are in direct contrast to the observed female preference for both dominance and affiliation with immatures demonstrated in Assamese macaques (Haunhorst et al., 2019), which may indicate a species-level variation within the larger genus *Macaca*. We conclude that, while there may be some degree of female preference operating within this group, this is not consistently a preference for high-ranking males. This is consistent with previously discussed Japanese macaque studies.

Many studies have related the variation in affiliation with juveniles by adult males to potential fitness benefits. The only significant correlation we found was between the rate of juvenile-directed affiliation and rank. However, there was no significant correlation between the rate of juvenile-directed affiliation and fitness. The lack of a significant correlation between rank (or age) and fitness is surprising, as the reproductive access conferred upon individuals by attaining high dominance rank has been well-recorded in the previous literature [Cowlshaw, 1991; Bulger, 1993; de Ruiter, 1993; Alberts et al., 2003; Watts, 2010; Majolo et al., 2012; Sukmak et al., 2014]. This evidence suggests a complex relationship between fitness, age, rank, and juvenile-directed affiliation.

Animal care technicians and behavioral staff consistently identified M3 as the most dominant male. It is interesting to note that the top-ranking male (M3) had both a low rate of affiliation events with juveniles and a low reproductive success, in comparison with the other older males. This reaffirms similar findings from studies of males in enclosed and semi-free ranging groups, in which dominance was not correlated with the number of offspring, or reproductive activity followed predictions based on the priority-of-access model but was interrupted by elements of female preference for lower-ranking males [Inoue et al., 1993; Takahata et al., 1999]. However, as this study was heavily influenced by the behavior of 2 specific males, it will be important to examine behavioral changes as males get older and whether these results remain consistent when examining other individuals.

Similar to Alexander [1970], we observed that more dominant adult males affiliated most with juveniles, and that 2 of these adult males each invested intensely in 1 particular juvenile. This suggests that these relationships are differentiated bonds and not a pattern of generally directed behavior. We observed that 2 males engaged in the highest rates of juvenile-directed affiliation (M2 and M4) and were observed

interacting exclusively with nonnatal juveniles. As these juveniles were born to parents outside of the group, and then introduced at approximately 1 year of age, they can be eliminated as being the offspring of the affiliating males. This would suggest that paternal investment is not a strong evolutionary driver of this behavior in this population. While this behavior has clear benefits for the juvenile partner, such as protection and access to better resources, the lack of a genetic relationship between the juveniles and adult males makes identifying the functional benefits for the adult males not immediately obvious. It is also possible, following a previously established theory of infant-directed behavior in females [Silk, 1999], that the general low cost of juvenile-directed affiliation by males is outweighed by the potential benefits, despite the probability of the male having either sired the immature or gaining future mating opportunities. The benefits of these behaviors may have been diluted by low paternal certainty, but the behaviors themselves could still be functionally selected for as a by-product of past selection for paternal or mating strategies. This should be a focus in further studies.

Reports by animal care technicians at the ONPRC and other national primate research centers have confirmed that these juvenile-directed behaviors are not unique to the ONPRC Japanese macaque troop. There have been multiple observations of similar carrying and affiliative behaviors in Rhesus macaque groups resident at the ONPRC and other institutions. While these observations have yet to be confirmed, the reported prevalence of such behaviors is of great interest from an evolutionary perspective. A long-term study would enable an examination of the longevity of male-immature affiliative bonds and a seasonal comparison. Furthermore, the inclusion of multiple species would allow for an investigation of variation in behavioral patterns between species.

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Statement of Ethics

This study was approved by the ONPRC Institutional Animal Care and Use Committee (IP00001766) and followed the guidelines outlined in both the Animal Welfare Act (1966–2002) and the *Guide for the Care and Use of Laboratory Animals* (1996). The ONPRC is accredited by the Association for the Assessment and Accreditation of Laboratory Animal Care, International.

Conflict of Interest Statement

The authors have no conflicts of interest to declare.

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Author Contributions

Conceived and designed the study: K.N.G., L.R.U., and F.J.W. Performed data collection: K.N.G. Analyzed the data: K.N.G., C.M.B., and F.J.W. Wrote the paper: K.N.G., C.M.B., L.R.U., and F.J.W.

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