

RESEARCH ARTICLE

Male Chimpanzees' Grooming Rates Vary by Female Age, Parity, and Fertility Status

DARBY P. PROCTOR^{1*}, SUSAN P. LAMBETH², STEVEN J. SCHAPIRO², AND SARAH F. BROSINAN^{1–3}¹Department of Psychology, Georgia State University, Atlanta, Georgia²Michale E. Keeling Center for Comparative Medicine and Research of the University of Texas,

M. D. Anderson Cancer Center, Houston, Texas

³Neuroscience Institute, Georgia State University, Atlanta, Georgia

Copulation preferences in our closest living relative, the chimpanzee, suggest that males prefer older females who have had previous offspring. However, this finding is counter to some behavioral models, which predict that chimpanzee males, as promiscuous breeders with minimal costs to mating, should show little or no preference when choosing mating partners (e.g. should mate indiscriminately). To determine if the preferences indicated by copulations appear in other contexts as well as how they interact, we examined how male chimpanzees' grooming patterns varied amongst females. We found that males' preferences were based on interactions among females' fertility status, age, and parity. First, grooming increased with increasing female parity. We further found an effect of the estrous cycle on grooming; when females were at the lowest point of their cycle, males preferentially groomed parous females at peak reproductive age, but during maximal tumescence, males preferred the oldest multiparous females. Nulliparous females received relatively little grooming regardless of age or fertility. Thus, male chimpanzees apparently chose grooming partners based on both female's experience and fertility, possibly indicating a two-pronged social investment strategy. Male selectivity seems to have evolved to effectively distribute costly social resources in a pattern which may increase their overall reproductive success. *Am. J. Primatol.* 73:1–8, 2011. © 2011 Wiley-Liss, Inc.

Key words: chimpanzee; male investment strategy; grooming; parity; age; estrus

INTRODUCTION

Darwin [1871] first suggested differing sex roles for male and female animals, whereby males were driven to mate as often as possible with any available female and females were selected to be choosier in their mating patterns. In a confirmatory study that shaped theories about mate selection in animals for decades, Bateman [1948] showed that male fruit flies mated opportunistically, whereas females were more selective about the males with whom they would mate. The logic behind this approach to mating was that males are, in theory, only limited in their reproductive potential by the number of females with whom they can mate. Females, however, have few opportunities to reproduce, and reproduction is biologically more costly than for males [i.e. more energetically expensive gametes, possible pregnancy or lactation costs; Bateman, 1948; Trivers, 1972; Williams, 1975]; thus, it was predicted, females should be choosier about their mates. However, this model does not account for either potential costs to males or females which differ in their reproductive potential and quality. If females have variable outcomes in reproduction and there is any cost to mating for males, then male selectivity toward

females with the highest reproductive success should evolve, as predicted by more recent theories [Parker, 1983; Ridley, 1983; Williams, 1975].

In chimpanzees (*Pan troglodytes*), there is variation in female reproductive success [Pusey et al., 1997], predicting some degree of male selectivity. Although the biological cost of sperm production is minimal [Clutton-Brock & Vincent, 1991], there can be other social costs to the males. Social dynamics limit copulations and copulation attempts, such that only higher ranking males routinely and reliably secure mating access [Klinkova et al., 2005; Muller & Mitani, 2005; Stumpf & Boesch, 2005; Tutin, 1979]. Moreover, male behavior indicates choosiness; there are anecdotal reports of

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*Correspondence to: Darby P. Proctor, Department of Psychology, Georgia State University, PO Box 5010, Atlanta, GA 30302. E-mail: dproctor3@student.gsu.edu

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male chimpanzees refusing a female solicitation [Allen, 1981; Goodall, 1986; Keddy-Hector, 1992; Small, 1993; Yerkes, 1939]. This suggests that males do not mate indiscriminately with any available female.

Context is also a factor in males' choices. Males prefer copulating with females in maximal tumescence, likely because this is the period in which fertilization is most likely [Deschner et al., 2004; Emery Thompson, 2005; Goodall, 1986; Nadler, 1995; Takasaki, 1985; Wallis, 1982, 1992; Yerkes, 1939; Yerkes & Elder, 1936]. Aside from copulations, males also show more interest in females during this time, as shown by association time, copulations, and interventions against other males' attempts to mate [Deschner et al., 2004]. Finally, males more frequently copulate or attempt to copulate with mature females who have had multiple offspring (multiparous females) [Muller & Mitani, 2005; Muller et al., 2006; Stumpf & Boesch, 2005], indicating that male preference is driven by more than current fertility.

A problem with exploring male mate choice is that male copulation attempts may be influenced by social pressures (e.g. interventions by other males) as well as their preferences. Thus, an important dimension is to investigate male mate preference in situations more removed from the immediate social pressures surrounding mating. One way to do this is to assess indirect measures of male preference, such as the degree of investment males make in individual females. For example, lower ranking males may exchange commodities, such as meat (from hunting) and grooming, as a way to gain access to females [e.g. Boesch & Boesch-Achermann, 2000]. Males both "show off" by obtaining difficult-to-catch or highly valuable foods as well as trading these limited resources for mating opportunities [de Waal, 1982; Kortlandt, 1972; Mitani & Watts, 2001; Moore, 1984; Nishida & Hosaka, 1996; Nishida et al., 1992]. For instance, despite a general lack of sharing of fruit among adult chimpanzees [Silk, 1979; Slocombe & Newton-Fisher, 2005], wild male chimpanzees share fruit acquired from raids on farms with fertile females, which the authors posit may reflect both showing off and provisioning of valuable resources by the males [Hockings et al., 2007]. Investments may be particularly relevant around the time of most likely conception, when males may spend additional time in proximity to [Newton-Fisher et al., 2010] or grooming [Hemelrijk et al., 1992; Wallis, 1992] estrous females. Males may also utilize consortships [Tutin, 1979], although these result in only a 10–20% increase in reproductive success [Boesch & Boesch-Achermann, 2000; Constable et al., 2001]. Aside from food sharing, grooming patterns across the reproductive cycle may indicate male preferences. Grooming is a particularly good measure in the context of male interest, as it is a costly investment

of time, promotes social bonding, has been suggested as a male reproductive tactic [Boesch & Boesch-Achermann, 2000; de Waal, 1982; Hemelrijk et al., 1992; McGinnis, 1979], and is one of the most common affiliative behaviors in nonhuman primates [Goosen, 1987]. Prior research has demonstrated that male-to-female grooming peaks during the onset of swelling and at menstruation, but this has not been correlated with any other demographic features of the females [Wallis, 1992].

We investigated how grooming patterns changed not only with current estimates of female fertility, but also with long-term reproductive potential. To measure the first, we used the estrous cycle as a proxy, as this period also corresponds with higher probabilities of conception [Emery & Whitten, 2003], despite not being a perfectly reliable cue [Deschner et al., 2003; Machatschke et al., 2006]. Regarding long-term reproductive potential, data from the wild indicate that female reproductive potential is not constant throughout the life cycle. Rather, reproductive potential follows an inverse U-shaped curve with peak reproductive years between 14 and 24 years, followed by a sharp decline between 25 and 30 years of age [Emery Thompson et al., 2007]. Following this, we considered females between 14 and 24 years of age to have the highest reproductive potential. Finally, we included female parity, which is known to influence male copulation decisions [Muller & Mitani, 2005; Muller et al., 2006; Stumpf & Boesch, 2005] and reflects past reproductive success. To assess this, we examined male chimpanzee grooming patterns of females in six stable, multimale, multi-female captive social groups. We hypothesized that male grooming patterns would vary depending on female age, rank, parity, and fertility, showing a pattern similar to that seen with copulations. Specifically, we predicted that males would spend more time grooming multiparous females in their peak reproductive years (i.e. 14–24), and that grooming would vary cyclically dependent upon the stage in the estrous cycle.

METHODS

The chimpanzees used in the study were housed at the Michale E. Keeling Center for Comparative Medicine and Research (Keeling Center) of the University of Texas M.D. Anderson Cancer Center (UTMDACC) in Bastrop, Texas. All chimpanzees had ad libitum access to water and primate chow and were fed enrichment meals four times a day. Subjects lived in large outdoor enclosures with climbing structures, material enrichment, and occupational enrichment multiple times per week. All procedures used in this research were in accordance with the American Society of Primatologists' Guidelines for the Ethical Treatment of Primates and the *Guide for the Care and Use of Laboratory Animals* and were

approved by the Institutional Animal Care and Use Committee of UTMDACC.

We observed six social groups (mean of ten individuals; range: 7–12), each with multiple adult males and females. The total sample included 62 chimpanzees (male: $N = 22$, age range: 6–42 years; female: $N = 40$, age range: 2–42 years). See Table I for a summary of female demographic characteristics. Each group was observed for 16–21 hr (mean of 19 hr per group, total 108 hr) over 11 months from 2004 to 2005. Observations consisted of 1 hr instantaneous scan samples of the group to record state behaviors [e.g. grooming, proximity, etc; Altmann, 1974]. Every 3 min, the behavior of each individual in

the group was noted and recorded. Observations cycled through the entire group in the same order for each sample. In cases in which an individual other than the target was involved (e.g. proximity or grooming), we recorded all partners with whom interactions took place. Additionally, rare behaviors, such as copulations and aggression, were recorded on an all occurrence basis. To minimize transcription errors, scan data were input directly into a computerized spreadsheet by the observer as the events occurred, thus no interrater reliability measures are available. These data were collected as part of a series of regular observations which contributed to a database of the behavior of the chimpanzees in this

TABLE I. Female Chimpanzee Demographic Features

Chimpanzee	Days at swelling size			Group	Observation days	Age	Parity	Rank
	Maximum	Medium	Minimum					
Abbey ^a	0	0	18	c4	17	43	2	Medium
April	0	1	6	c2	21	29	2	Medium
Bashful ^a	4	0	14	c3	16	43	2	High
Bernie ^a	9	0	10	c5	16	42	2	Low
Betsy ^a	0	0	21	c8	19	44	0	Medium
Betty	6	3	9	c3	16	35	2	High
Cassie	7	2	9	c4	17	20	0	Low
Cecelia	1	5	15	c8	19	18	0	Low
Coco	0	6	16	c2	21	25	0	Medium
Derma ^a	0	0	15	c8	19	42	0	Medium
Emily	5	3	10	c4	17	25	0	High
Gertrude ^a	1	0	20	c6	19	41	2	Medium
Glenda ^a	0	0	15	c4	17	42	2	Medium
Hannah	1	1	20	c2	21	19	0	Medium
Helga ^a	5	1	13	c5	16	43	0	Medium
Hodari	12	1	5	c3	16	16	0	Low
Jana	8	2	8	c3	16	21	2	Medium
Jane ^a	6	4	11	c6	19	38	2	Low
Jessie	6	2	10	c3	16	16	0	Low
Judy ^a	2	0	16	c3	16	41	2	High
Junie	4	1	17	c2	21	43	0	Medium
Karin ^a	0	0	0	c5	16	47	0	Medium
Kelley ^a	0	2	19	c8	19	41	2	Low
Lulu	10	1	7	c4	17	27	2	Medium
Mae ^a	5	3	14	c2	21	44	2	Medium
Martha ^a	3	2	16	c8	19	43	0	Medium
Mary ^a	0	0	21	c8	19	44	2	Medium
Michon	6	9	3	c3	16	27	2	High
Misty	7	0	12	c5	16	25	0	Low
Monique	4	4	10	c3	16	18	0	Medium
Nina	5	3	13	c6	19	26	0	Low
Pepper ^a	8	0	13	c6	19	42	2	Medium
Rhoda ^a	3	2	17	c2	21	46	2	High
Sandy ^a	8	2	8	c4	17	37	0	Medium
Sindee ^b	0	0	0	c2	21	10	0	Low
Tasha	6	2	13	c6	19	17	0	Low
Tinker	8	6	7	c8	19	26	0	Medium
Ursula	0	0	0	c5	16	45	2	Medium
Xena ^b	0	0	0	c3	16	10	0	Low
Zoe ^b	0	0	0	c8	19	7	0	Low

^aDenotes females whose ages are estimated.

^bDenotes noncycling juvenile female.

colony. This study was conducted as a post hoc analysis from this database.

For this study, the only behavior from the ethogram which we considered was grooming. Grooming was defined as “Picking through the hair, searching for and/or removing debris. May be accomplished with hand or mouth. Often accompanied by teeth clacking or lip smacking. May be self-groom or social groom. Social groom can be directed to another animal or received from another animal” (note: self-grooming was excluded from the current analysis). Whenever a grooming interaction was coded, the direction of the grooming interaction was indicated. Copulations were also recorded ad libitum. However, although copulation data would have been useful to include, copulations occurred too infrequently to analyze.

We considered the effect of four demographic factors, female age, rank, parity, and swelling status, on males’ grooming behavior. Females’ age and parity were collected from the long-term records kept for colony management purposes. These records extended back to the establishment of the colony. Ages for 20 females born in the wild were estimates; but the females had been captured when they were young juveniles or infants, so estimates were sufficiently reliable for the current analysis.

Female parity could be considered either as the number of offspring the female had remaining in her social group, which mimics attrition in the wild, or as the total number of offspring she had produced. We conducted the analysis using both measures. Due to the small number of chimpanzees that had more than two offspring, parity was coded as nulliparous (no offspring), primiparous (one offspring), or multiparous (two or more offspring). Note that the females who were born in the wild were caught when they were clearly nulliparous.

Swelling size, as an estimate of current fertility, was obtained from a database maintained by the facility for colony management purposes. Each females’ swelling status was collected daily by one of several members of the animal care staff at the Keeling Center. Swelling data were recorded daily for each female using a 0 (not swollen)–4 (fully swollen) scale. For the purposes of this analysis, we considered females either in peak estrus (4), moderately swollen (2–3), or not swollen (0–1).

Female chimpanzees have a nonlinear dominance hierarchy, making rank difficult to assess [Pusey et al., 1997]. Pusey et al. suggest that the most reliable indicators of female rank relationships are pant-grunts. However, there were not sufficient numbers of pant-grunts in our database for an analysis of rank. Instead, we coded individuals as “low,” “medium,” or “high” rank, based on the degree to which that individual exhibited the signs of rank, such as priority of feeding, access to social partners and other resources, and was the recipient

(or giver) of signals of subordination. Rank estimates were completed regularly by S.P.L., who has worked with this colony of chimpanzees for more than two decades. The rankings included here are from the same time period as the data collection.

One potential confound of any captive chimpanzee study is the widespread use of birth control. During the study period, chimpanzees at the Keeling Center were on either Mirena intrauterine devices or oral birth control. However, the females continued to cycle within the range of variation observed in wild chimpanzees [days per year of maximal tumescence; wild range from Deschner et al., 2003: 60.84–182.52; Keeling Center: $X = 78.2$]. Moreover, because these groups had been relatively stable since the early 1980s, before the frequent use of birth control, many of the females still had multiple offspring in their social group. Nonetheless, there were few juveniles under the age of 10 (total: six).

We used the general linear model to determine the effect of theoretically relevant female demographic factors on grooming bouts involving a male and female (mean: 7.45 bouts; range: 0–61). Our predictors were female age (mean: 25.6; range: 2–42), rank (high, $N = 6$; medium, $N = 21$, low, $N = 13$), parity (mean: 0.67), and swelling status (minimum swelling, $N = 34$; medium swelling, $N = 18$; maximum swelling, $N = 29$). Potential linear and quadratic effects of age were examined. Statistics were done using SPSS version 16 [2007]. All statistics are two-tailed and significance is considered $P < 0.05$.

RESULTS

Among female chimpanzees, age and rank tend to be correlated [Nishida, 1990; Pusey et al., 1997]. In order to avoid redundant variables in the regression model, a correlation between age and rank was run to determine if those variables were independent. Our correlation found a strong positive relationship between rank and age ($R = 0.477$, $P = 0.002$). This means that as age increases, there is typically an accompanying increase in rank. Given the strong correlation, only one of these variables could be used in the regression model at a time to avoid redundancy within the model [Cohen et al., 2003].

First, we ran a repeated measures general linear model using rank (rather than age), parity (based on the number of offspring currently residing in the group), and fertility status. Using this model, there were no significant interactions or main effects (main effect of rank; $F(2) = 0.179$, $P = 0.675$). We then ran the same analysis using age rather than rank. Using this model, there was a significant three-way interaction between female age, parity, and fertility ($F(2) = 3.388$, $P = 0.039$). This indicates that despite the strong correlation between rank and age, age accounts for variation that is not present within

the rank variable. Therefore, for the remainder of our analyses, we used age instead of rank.

In the model using age (see Table II for the summary of the regression results), we first examined fertility status and parity, including only offspring who were present in the group as the measure of parity (statistic reported above). We then repeated the analysis considering each female's total offspring, without regard to whether they were currently in the group. In this latter case, no significant effect of offspring was found ($F(1) = 2.350$, $P = 0.134$). All subsequent statistics are done using only offspring present in the group as the measure of parity.

In order to explore the interaction of these three characteristics, we examined the effects of age and parity on grooming bouts at each level of fertility. For females that were minimally swollen, or in their least fertile state, there was a significant effect of parity on males' grooming behavior ($B = 3.282$, $SE = 1.194$, $T = 2.749$, $P = 0.009$). Among minimally swollen chimpanzees, multiparous females were involved in the most grooming bouts, followed by primiparous, and then nulliparous females (Fig. 1). The grooming bouts for these minimally swollen females, regardless of parity, followed a quadratic function with the peak number of grooming bouts occurring in females in their early 20s, with fewer grooming bouts seen among younger and older chimpanzees.

Among females in maximal tumescence, there was a significant interaction of age and number of offspring living in the group ($B = -0.266$, $SE = 0.086$, $T = -3.103$, $P = 0.039$). Primiparous and multiparous females were groomed the most and the grooming bouts increased linearly as age increased. Nulliparous females were groomed the least, and unlike for females with offspring living in the group, the rate of grooming did not differ depending upon their age (Fig. 2).

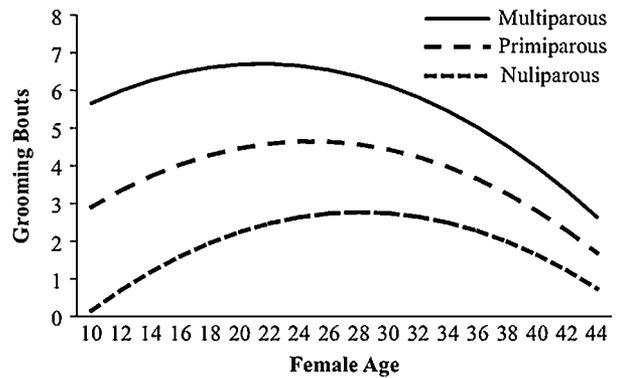


Fig. 1. During periods of minimal fertility, males preferred to groom females with greater parity over those who had fewer offspring. Within each level of parity, males spent the most time grooming females who were in their peak reproductive years.

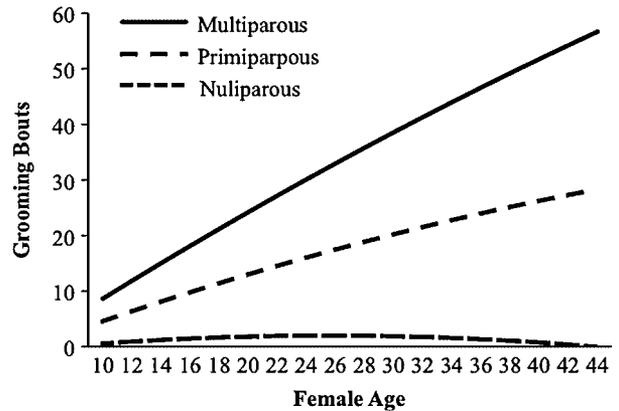


Fig. 2. During the highest fertility periods, as measured by the estrous cycle, males preferred to groom females with greater parity; but in this case, the frequency of grooming increased linearly with increasing female age. Males rarely groomed females with no offspring in the group, regardless of age.

TABLE II. Parameter Estimates of the Regression Model

Dependent variable	Parameter	B	SE	t	Sig.
Grooming bouts when minimally swollen	Intercept	2.663	1.942	1.371	0.179
	Age	-0.058	0.130	-0.446	0.659
	Offspring	3.282	1.194	2.749	0.009*
	Age squared	-0.008	0.010	-0.849	0.402
	Age*offspring	-0.053	0.124	-0.431	0.669
Grooming bouts when medium swollen	Intercept	1.105	0.969	1.140	0.262
	Age	-0.054	0.065	-0.832	0.411
	Offspring	0.920	0.596	1.543	0.132
	Age squared	-0.006	0.005	-1.217	0.232
	Age*offspring	-0.043	0.062	-0.705	0.486
Grooming bouts when fully swollen	Intercept	1.778	1.349	1.318	0.196
	Age	-0.074	0.090	-0.813	0.422
	Offspring	3.107	0.829	3.746	0.001
	Age squared	-0.006	0.007	-0.927	0.360
	Age*offspring	-0.266	0.086	-3.103	0.004*

*Denotes significant result at $P < 0.05$.

There were no significant effects of any of the factors among females with medium swellings. This is likely owing to the transitional nature of this phase in the estrous cycle (i.e. females would be approaching or leaving maximal tumescence). Finally, looking at age and parity independent of swelling cycle, we found that for each level of parity (nulliparous, primiparous, multiparous), the most grooming bouts occurred among females in their early to mid-20s (37% grooming bouts observed included females aged 20–27 years while those females make up only 23% of our sample).

To rule out the possibility that older females were simply more frequently swollen than younger females, a correlation was run between age and level of estrus swelling. There was no significant correlation between age and being maximally swollen ($R = -0.289$, $P = 0.069$). This indicates that older and younger females did not differ in the frequency with which they were swollen. However, if the noncycling juvenile females were excluded, a significant negative correlation emerged between age and being maximally swollen ($R = -0.408$, $P = 0.012$). Thus, in our sample, younger individuals were more often maximally swollen than older individuals. Therefore, if males were choosing grooming partners based on swelling alone, they would be preferentially grooming younger females, rather than the pattern that we saw of males grooming older females.

DISCUSSION

As predicted, males' grooming patterns varied based on interactions among female parity, age, and swelling status. Overall, males preferred to groom females with multiple offspring currently living in the group. There was a more complex interaction between the other two factors—females' current fertility (as determined by swelling status) and reproductive potential (as determined by her age). Females' age had a strong effect on males' grooming rates, but this varied across swelling status. Among minimally swollen females who are unlikely to conceive, males groomed females during their peak reproductive years (14–24) more frequently than those who were older or younger (e.g. an inverse *U*-shaped preference; Fig. 1). On the other hand, among maximally swollen females who are likely to conceive, males' preference for grooming primiparous and multiparous (counting only offspring currently living in the group) females increased linearly with the females' age, with males showing the strongest preference for grooming the oldest multiparous females (Fig. 2). These data demonstrate a pattern similar to what is found for male preferences in mating contexts, in which females with no offspring are least often solicited as mating partners [Muller & Mitani, 2005; Muller et al., 2006; Stumpf & Boesch, 2005; Tutin, 1979]. These data

also support the recent finding that males spent more time with females who were the most likely to be able to conceive [Newton-Fisher et al., 2010].

The interaction we found between females' age and swelling status may reflect a tradeoff between future investment and immediate mating access. During minimal tumescence, although female parity remains important, males nonetheless spent more time grooming females at the peak of their reproductive years rather than consistently preferring the oldest females. Thus, during females' least fertile periods, chimpanzee males may prefer to groom females that will be of interest in the future, possibly as a long-term investment strategy, as similar behaviors have been seen in other primate species as well [for example, friendships in baboons; Smuts, 1985]. On the other hand, during periods of maximal tumescence, when females are more likely to conceive, males preferentially groomed females with the most offspring living in the group (that is, the highest proven levels of reproductive success). Additionally, within each parity category, males spend more time grooming older females. Thus, when females are maximally fertile, grooming may be used as a short-term strategy to gain access to the most reproductively successful females.

Interestingly, despite the strong correlation between age and rank, using rank in the model accounted for less variance than did age. This suggests that while rank and age are correlated [see also Pusey et al., 1997], the biological feature of age has more impact than socially determined rank when used as a predictor for which females males groom most frequently. This may imply that chimpanzee males are paying greater attention to biological factors when considering distributing services amongst chimpanzee females. However, our sample size was fairly small, particularly for high-ranking females. In a larger sample that included more high-ranking females, a different pattern might emerge. Alternatively, our sample could be an accurate representation for smaller groups of chimpanzees with fewer high-ranking females. Additional data from field sites or longitudinal studies will further clarify this issue.

We also found that using the number of offspring the female had currently living with them in the group had more explanatory power in our model than did the females' total number of offspring. Some of these females' offspring had been moved to other social groups for colony management purposes, which mirrors offspring mortality and emigration in the wild. Both in the wild and in captivity, the number of offspring currently present in the group may be a sufficient proxy for parity and avoids issues related to long-term memory or imperfect knowledge about females' previous offspring. This, too, mirrors previous work on copulations, which found that males' interactions with females were based, in part,

on the offspring who were currently part of the group [Muller et al., 2006]. However, as noted previously, the chimpanzees at this facility had been on birth control for some years. Further research should be done to see if this pattern of grooming interactions holds true in a group of chimpanzees without this restriction.

There are additional limitations to this study. First, although we had a range of ages represented in our sample, the sample is skewed toward older chimpanzees owing to the use of birth control in captivity. It is possible that, in this older population of chimpanzees, there are more grooming opportunities with older individuals than is typical or that the absence of younger individuals affected males' grooming patterns. Additionally, although age and rank were strongly correlated in our experiment, they contributed different amounts of variance to our regression models. Although this may suggest that biological factors play a larger role than social factors in male decision making, it could also be that there is an unknown confound or that our system of ranking was not sufficiently detailed. Of course, it is also possible that as rank in female chimpanzees is neither linear nor stable, age may be a more informative indication for males of a female's quality.

Our data support those theories that suggest that males prefer females with the highest reproductive success when females vary in reproductive quality [Parker, 1983; Ridley, 1983; Williams, 1975], as well as copulation patterns which have been observed in chimpanzees [Muller & Mitani, 2005; Muller et al., 2006; Stumpf & Boesch, 2005] and other primate species [Anderson, 1986]. However, copulations are limited by other social pressures in chimpanzees and less restricted behaviors, such as grooming and food sharing, may also serve as measures of male preference. Additionally, lower ranking males may have an increased need for selectivity, as not all females are worth the risk of aggression from higher ranking males. Because grooming requires a significant time investment, male selectivity may have evolved to most effectively distribute this costly social resource to high-quality females, a phenomenon that may be observed among other species as well. Future work will help to further clarify the myriad ways in which males may make investments to increase their long-term fitness.

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