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Male chimpanzees' grooming rates vary by female age, parity and fertility status

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Abstract

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 appears to have evolved to effectively distribute costly social resources in a pattern which may increase their overall reproductive success.

Keywords

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 while 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 [Williams 1975; Parker 1983; Ridley 1983].

In chimpanzees (*Pan troglodytes*) there is variation in female reproductive success [Pusey, Williams and Goodall 1997], predicting some degree of male selectivity. While 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; Tutin 1979; Mueller & Mitani 2005; Stumpf & Boesch 2005]. Moreover, male behavior indicates choosiness; there are anecdotal reports of male chimpanzees refusing a female solicitation [Allen 1981; Yerkes 1939; Small 1993; Goodall 1986; Keddy-Hector 1992]. This all 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 *et al.* 1994; 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 with, or attempt to copulate with, mature females who have had multiple offspring (multiparous females) [Muller *et al.* 2006; Mueller & Mitani 2005; 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 and Boesch-Ackerman 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; Korlandt 1972; Nishida *et al.* 1992; Nishida & Hosaka 1996; Mitani & Watts 2001; Moore 1984]. 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 of farms with fertile females, which the authors posit may reflect both showing off and provisioning of valuable resources by the males [Hockings *et al.* 2006]. 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 1992; Wallis 1992] estrous females. Males may also utilize consortships [Tutin 1979] although these result in only a 10-20% increase in reproductive success [Constable *et al.* 2001; Boesch & Boesch-Achermann 2000]. 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 [McGinnis 1979; de Waal 1982; Boesch & Boesch-Ackerman 2000; Hemelrijk, van Laere, & van Hooff 1992], 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 chances 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 Thompson and Whitten 2003], despite not being a perfectly reliable cue [Descher *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 year of age to have the highest reproductive potential. Finally, we included female parity, which is known to influence male copulation decisions [Muller *et al.* 2006; Mueller & Mitani 2005; Stumpf & Boesch 2005] and reflects past reproductive success. To assess this, we examined male chimpanzee grooming patterns of females in six stable, multi-male, 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 per 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 10 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 1 for a summary of female demographic characteristics. Each group was observed for 16 to 21 hours (mean of 19 hours per group, total of 108 hours) over 11 months from 2004-2005. Observations consisted of one hour instantaneous scan samples of the group to record state behaviors [e.g. grooming, proximity, etc; Altmann 1974]. Every three minutes, 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 inter-rater 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 colony. This study was conducted as a post-hoc analysis from this database.

For the current 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, while 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 data base 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) to a 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 non-linear dominance hierarchy, making rank difficult to assess [Pusey, Williams and Goodall 1997]. Pusey and colleagues suggest that the most reliable indicators of female rank relationships are pant-grunts. However, there were not a sufficient number 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 SPL, 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 intra-uterine devices (IUDs) 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: 6).

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 2-tailed and significance is considered $p < 0.05$.

Results

Among female chimpanzees, age and rank tend to be correlated [Nishida 1990; Pusey, Williams and Goodall 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 ($R = .477$, $P = 0.002$). 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 2 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 (Figure 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 (Figure 2).

There were no significant effects of any of the factors among females with medium swellings. This is likely due 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% of grooming bouts observed included females aged 20-27 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 non-cycling 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; Figure 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 (Figure 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, *et al.* 2006; Mueller & Mitani 2005; 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, Williams and Goodall 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 [Mueller, Emery Thompson and Wrangham 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 the current study. First, while we had a range of ages represented in our sample, the sample is skewed toward older chimpanzees due 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, while age and rank were strongly correlated in our experiment, they contributed different amounts of variance to our regression models. While 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 [Williams 1975; Parker 1983; Ridley 1983], as well as copulation patterns which have been observed in chimpanzees [Muller *et al.* 2006; Mueller & Mitani 2005; 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. Since 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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References

- Allen M. Individual copulatory preference and the “strange female effect” in a captive group-living male chimpanzee (*Pan troglodytes*). *Primates*. 1981; 22:221–236.
- Altmann J. Observational study of behavior: Sampling methods. *Behaviour*. 1974; 49(3):227–267. [PubMed: 4597405]
- Anderson CM. Female age: Male preference and reproductive success in primates. *International Journal of Primatology*. 1986; 7(3):305–326.
- Andersson, M. Sexual selection. Princeton: Princeton University Press; 1994.
- Bateman AJ. Intrasexual selection in *Drosophila*. *Heredity*. 1948; 2:349–368. [PubMed: 18103134]
- Boesch, C.; Boesch-Achermann, H. The chimpanzees of the Tai Forest. Oxford: Oxford University Press; 2000.
- Boggs, CL. Male nuptial gifts: Phenotypic consequences and evolutionary implications. In: Leather, SR.; Hardie, J., editors. *Insect Reproduction*. New York: CRC Press; 1995. p. 215–242.
- Buskirk RE, Frolid C, Ross KG. The natural selection of sexual cannibalism. *American Naturalist*. 1984; 133:454–457.
- Clutton-Brock TH, Vincent ACJ. Sexual selection and the potential reproductive rates of males and females. *Nature*. 1991; 351:58–60. [PubMed: 2027382]
- Cohen, J.; Cohen, P.; West, SG.; Aiken, LS. Applied multiple regression/correlation analysis for the behavioral sciences. Mahwah, NJ: Lawrence Erlbaum Associates; 2003.
- Constable JL, Ashley MV, Goodall J, Pusey AE. Noninvasive paternity assignment in Gombe chimpanzees. *Molecular Ecology*. 2001; 10:1279–1300. [PubMed: 11380884]
- Darwin, C. *The Descent of Man and Selection in Relation to Sex*. London: John Murray; 1871.
- Deschner T, Heistermann M, Hodges K, Boesch C. Timing and probability of ovulation in relation to sex skin swelling in wild West African chimpanzees, *Pan troglodytes* *versus*. *Animal Behaviour*. 2003; 66:551–560.
- Deschner T, Heistermann M, Hodges K, Boesch C. Female sexual swelling size, timing of ovulation, and male behavior in wild West African chimpanzees. *Hormones and Behavior*. 2004; 46(2):204–215. [PubMed: 15256310]
- de Waal, FBM. *Chimpanzee Politics: Power and Sex among Apes*. Baltimore: Johns Hopkins University Press; 1982.
- Emery MA, Whitten PL. Size of sexual swellings reflects ovarian function in chimpanzees (*Pan troglodytes*). *Behavioral Ecology and Sociobiology*. 2003; 54(4):340–351.
- Emery Thompson M. Reproductive endocrinology of wild female chimpanzees (*Pan troglodytes schweinfurthii*): Methodological considerations and the role of hormones in sex and conception. *American Journal of Primatology*. 2005; 67:137–158. [PubMed: 16163723]
- Emery Thompson M, Jones JH, Pusey AE, Brewer-Marsden S, Goodall J, Marsden D, Matsuzawa T, Nishida T, Reynolds V, Sugiyama Y, et al. Aging and Fertility Patterns in Wild Chimpanzees Provide Insights into the Evolution of Menopause. *Current Biology*. 2007; 17(24):2150–2156. [PubMed: 18083515]
- Goodall, J. *The Chimpanzees of Gombe: Patterns of Behavior*. Cambridge, MA: Belknap; 1986.
- Goosen, C. Social grooming in primates. In: Mitchell, G.; Erwin, J., editors. *Comparative Primate Biology*, Vol 2B: Behavior, Cognition and Motivation. New York: Alan R. Liss; 1987.
- Hemelrijk CK, van Laere GJ, van Hooft JARAM. Sexual exchange relationships in captive chimpanzees. *Behavioral Ecology and Sociobiology*. 1992; 30:269–275.
- Hockings KJ, Humle T, Anderson J, Biro D, Sousa C, Ohashi G, Matsuzawa T. Chimpanzees share forbidden fruit. *PLoS ONE*. 2007; 2(9):e886. [PubMed: 17849015]
- Keddy-Hector AC. Mate choice in non-human primates. *American Zoologist*. 1992; 32:62–70.
- Kortlandt A. *New perspectives on ape and human evolution*. Amsterdam: Stichting voor Psychobiologie. 1972

- Lorek G. Copulation behavior, mixed reproductive strategy, and mate guarding in the great grey shrike. *Proceedings of the Western Foundation of Vertebrate Zoology*. 1995; 6:218–227.
- McGinnis, PR. Sexual behavior in free-living chimpanzees: Consort relationships. In: Hamburg, DA.; McCown, ER., editors. *The Great Apes*. Menlo Park, CA: Benjamin/Cummings; 1979.
- Mitani JC, Watts DP. Why do chimpanzees hunt and share meat? *Animal Behaviour*. 2001; 61(5):915–924.
- Moore J. The evolution of reciprocal sharing. *Ethology and Sociobiology*. 1984; 5:5–14.
- Muller MN, Thompson ME, Wrangham RW. Male chimpanzees prefer mating with old females. *Current Biology*. 2006; 16:2234–2238. [PubMed: 17113387]
- Muller MN, Mitani JC. Conflict and cooperation in wild chimpanzees. *Advances in the Study of Behavior*. 2005; 35(275-331)
- Newton-Fisher NE, Emery Thompson M, Reynolds V, Boesch C, Vigilant L. Paternity and social rank in wild chimpanzees (*Pan troglodytes*) from the Budongo Forest, Uganda. *American Journal of Physical Anthropology*. 2010; 142(3):417–428. [PubMed: 20033921]
- Nishida, T. *Understanding Chimpanzees*. Heltne, PG.; Marquardt, LA., editors. Cambridge, MA: Harvard University Press; 1990.
- Nishida, T.; Hasegawa, T.; Hayaki, H.; Takahata, N.; Uehara, S. Meat-sharing as a coalitional strategy by an alpha male chimpanzee?. In: Nishida, T.; McGrew, WC.; Marler, P.; Pickford, M.; de Waal, FBM., editors. *Topics in Primatology, Vol 1 Human Origins*. Tokyo: Tokyo University Press; 1992.
- Nishida, T.; Hosaka, K. Coalition strategies among adult male chimpanzees of the Mahale Mountains, Tanzania. In: McGrew, WC.; Marchant, LF.; Nishida, T., editors. *Great Ape Societies*. Cambridge: Cambridge University Press; 1996.
- Parga J. Male mate choice in *Lemur catta*. *International Journal of Primatology*. 2006; 27(1):107–131.
- Parker, GA. Mate quality and mating decisions. In: Bateson, P., editor. *Mate Choice*. Cambridge: Cambridge University Press; 1983.
- Pusey AE, Williams J, Goodall J. The influence of dominance rank on the reproductive success of female chimpanzees. *Science*. 1997; 277:828–831. [PubMed: 9242614]
- Ridley, M. *The Explanation of Organic Diversity*. Oxford: Oxford University Press; 1983.
- Seyfarth R. A model of social grooming among adult female monkeys. *Journal of Theoretical Biology*. 1977; 28:798–813.
- Silk JB. Feeding, foraging and food sharing behavior of immature chimpanzees. *Folia Primatologica*. 1979; 31:123–142.
- Slocombe KE, Newton-Fisher NE. Fruit sharing between wild adult chimpanzees (*Pan troglodytes schweinfurthii*): A socially significant event? *American Journal of Primatology*. 2005; 65:385–391. [PubMed: 15834886]
- Small, M. *Female choices: Sexual behavior of female primates*. New York: Cornell University Press; 1993.
- Smuts, B. *Sex and Friendship in Baboons*. Edison: Transaction Publishers; 1985.
- SPSS for Windows, Rel. 16.0.1. Chicago. SPSS Inc; 2007.
- Stumpf R, Boesch C. Does promiscuous mating preclude female choice? Female sexual strategies in chimpanzees (*Pan troglodytes* versus) of the Tai National Park, Cote d'Ivoire. *Behavioral Ecology and Sociobiology*. 2005; 57:511–524.
- Stumpf R, Emery Thompson M, Knott CD. A comparison of female mating strategies in *Pan troglodytes* and *Pongo* spp. *International Journal of Primatology*. 2008; 29:865–884.
- Takasaki H. Female life history and mating patterns among the M group chimpanzees of the Mahale national park, Tanzania. *Primates*. 1985; 26(2):121–129.
- Thornhill R. Sexual selection and paternal investment in insects. *American Naturalist*. 1976; 110:153.
- Thornhill, R.; Alcock, J. *The evolution of insect mating systems*. Cambridge: Harvard University Press; 1983.
- Trivers, RL. Parental investment and sexual selection. In: Campbell, B., editor. *Sexual Selection and the Descent of Man*. Chicago: Aldine; 1972.

- Tutin CEG. Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). Behavioral Ecology and Sociobiology. 1979; 6:29–38.
- Yerkes RM. Sexual behavior in the chimpanzee. Human Biology. 1939; 11:78–111.
- Yosef R, Pinshow B. Cache size in shrikes influences female mate choice and reproductive success. The Auk. 1989; 106:418–421.
- Vahed K. The function of nuptial feeding in insects: a review of empirical studies. Biology Reviews. 1998; 73:43–78.
- Williams, GC. Sex and Evolution. Princeton: Princeton University Press; 1975.
- Wroblewski EE, Murray CM, Keele BF, Schumacher-Stankey JC, Hahn BH, Pusey AE. Male dominance rank and reproductive success in chimpanzees, *Pan troglodytes schweinfurthii*. Animal Behaviour. 2009; 77(4):873–885. [PubMed: 19498952]

Figure 1. Grooming bouts by age among minimally swollen females

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

Figure 2. Grooming bouts by age among maximally swollen females

During 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 1

Female Chimpanzee Demographic Features

Chimpanzee	Days at Swelling Size				Group	Observation Days	Age	Parity	Rank
	Maximum	Medium	Minimum						
Abbey ^b	0	0	18		c4	17	43	2	medium
April	0	1	6		c2	21	29	2	medium
Bashful ^b	4	0	14		c3	16	43	2	high
Bernie ^b	9	0	10		c5	16	42	2	low
Betsy ^b	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
Derna ^b	0	0	15		c8	19	42	0	medium
Emily	5	3	10		c4	17	25	0	high
Gertrude ^b	1	0	20		c6	19	41	2	medium
Glenda ^b	0	0	15		c4	17	42	2	medium
Hannah	1	1	20		c2	21	19	0	medium
Helga ^b	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 ^b	6	4	11		c6	19	38	2	low
Jessie	6	2	10		c3	16	16	0	low
Judy ^b	2	0	16		c3	16	41	2	high
Junie	4	1	17		c2	21	43	0	medium
Karin ^b	0	0	0		c5	16	47	0	medium
Kelley ^b	0	2	19		c8	19	41	2	low
Lulu	10	1	7		c4	17	27	2	medium
Mae ^b	5	3	14		c2	21	44	2	medium

Chimpanzee	Days at Swelling Size				Group	Observation Days	Age	Parity	Rank
	Maximum	Medium	Minimum						
Martha ^b	3	2	16		c8	19	43	0	medium
Mary ^b	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 ^b	8	0	13		c6	19	42	2	medium
Rhoda ^b	3	2	17		c2	21	46	2	high
Sandy ^b	8	2	8		c4	17	37	0	medium
Sindee ^a	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 ^a	0	0	0		c3	16	10	0	low
Zoe ^a	0	0	0		c8	19	7	0	low

^a denotes non-cycling juvenile female

^b denotes females whose ages are estimated

Table 2

Parameter Estimates of the Regression Model

Dependent Variable	Parameter	B	Std. Error	t	Sig.
Grooming Bouts when minimally swollen	Intercept	2.663	1.942	1.371	0.179
	Age	-.058	.130	-.446	0.659
	Offspring	3.282	1.194	2.749	0.009*
	Age Squared	-.008	.010	-.849	0.402
	Age*Offspring	-.053	.124	-.431	0.669
Grooming Bouts when medium swollen	Intercept	1.105	.969	1.140	0.262
	Age	-.054	.065	-.832	0.411
	Offspring	.920	.596	1.543	0.132
	Age Squared	-.006	.005	-1.217	0.232
	Age*Offspring	-.043	.062	-.705	0.486
Grooming bouts when fully swollen	Intercept	1.778	1.349	1.318	0.196
	Age	-.074	.090	-.813	0.422
	Offspring	3.107	.829	3.746	0.001
	Age Squared	-.006	.007	-.927	0.360
	Age*Offspring	-.266	.086	-3.103	0.004*

* denotes significant result at $P < 0.05$