

# The influence of oestrous swellings on the grooming behaviour of chimpanzees of the Budongo Forest, Uganda

Kerry Slater<sup>1,2,5)</sup>, Elissa Cameron<sup>1)</sup>, Trudy Turner<sup>1,3)</sup> & Johan T. du Toit<sup>1,4)</sup>

<sup>1)</sup> Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, South Africa; <sup>2)</sup> Department of Environmental Sciences, University of South Africa (UNISA); <sup>3)</sup> Department of Anthropology, University of Wisconsin–Milwaukee; <sup>4)</sup> Department of Wildland Resources, Utah State University, Logan, UT 84322-5230, USA)

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## Summary

Allogrooming among primates has been suggested as a strategy for enhancing reproductive success, by allowing males to enhance their proximity to oestrous females, or by influencing female choice through the development of affiliative relationships with males. Female chimpanzees have swollen anogenital regions signalling receptivity and by adapting their grooming investment accordingly, males could increase their copulatory success whilst females may increase chances of copulations with preferred males. Five and a half years of data from chimpanzees in the Budongo Forest, Uganda, were examined to investigate how sexual swellings influence grooming behaviour between males and females of different age classes. Based on the availability of oestrous females, significantly less grooming than expected occurred between anoestrous females and adult males, as well as between adult (anoestrous and oestrous) females and subadult males, but significantly more grooming than expected occurred between oestrous females and adult males or subadult males. Both oestrous adult and subadult females devoted more time to grooming interactions with adult males than did anoestrous females. Grooming interactions between adult males and oestrous adult females were initiated and terminated significantly more often by males, but those between anoestrous subadult females and adult males were initiated significantly more frequently by females.

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<sup>5)</sup> Corresponding author's e-mail address: slatek@unisa.ac.za

## **Introduction**

One of the most frequently observed social behaviours in primates is allogrooming, indicating willingness to invest time and effort in relationships with other group members (Hemelrijk & Luteijn, 1998). Using grooming to strengthen social bonds may increase an individual's chances of copulation (Tutin, 1979). It may consequently be in a male's best interest to invest time and effort in grooming potentially reproductive females rather than non-reproductive ones; whereas females may benefit more by developing grooming relationships with strong, healthy adult males rather than with subadult males who are generally smaller, weaker and subordinate (Anderson & Bielert, 1994).

Females of between 26 and 35 species of old world primates experience swollen anogenital regions caused by changes in oestrogen and progesterone levels as they progress through the reproductive cycle (Hrdy & Whitten, 1987; Anderson & Bielert, 1994). Suggestions as to why sexual swellings have evolved in only some species include: the use of oestrous swellings as a 'passport' by young female chimpanzees, allowing them to join new groups safely (Wallis & Goodall, 1993; Boesch & Boesch-Achermann, 2000); their use as a means of initiating competition between males (Reynolds, 2005) and between females to help determine male quality (Clutton-Brock & Harvey, 1976); their function in the context of the many-male hypothesis (Hrdy & Whitten, 1987), in which females mate with a number of males, resulting in positive interactions between males and offspring, creating an illusion of paternity and decreasing the chances of infanticide (Goodall et al., 1979; Harcourt, 1981); and their use as an indicator of ovulation (Wallis, 1982).

If grooming is one of the strategies used by males to increase their chances of copulation, grooming with females would be expected to increase during female oestrous periods as has been found in captive chimpanzees (Wallis, 1992). Observations suggest that this may also occur in free-living chimpanzees, but this has not been empirically investigated (Goodall, 1986). Swollen females may also increase grooming interactions with specific males to keep preferred males close by during a period sometimes characterised by considerable harassment from other males. Females, thus, obtain protection as well as increase the likelihood of impregnation by a preferred partner (Smuts & Smuts, 1993; Stumpf & Boesch, 2005). Assuming that both males and females benefit from increased grooming during female

receptive periods, the effort put into initiating and maintaining grooming bouts by the different sexes may also change. Furthermore, if grooming is used as a strategy to increase reproductive success, the age class of an individual would be expected to have an impact on these grooming relationships.

Chimpanzees exhibit both extensive social grooming and obvious sexual swellings. Females may also experience these swellings during the early stages of pregnancy and it is suggested (Wallis, 1982) that any benefits gained by oestrous females will also apply to swollen pregnant females and that because females tend to transfer to new communities whilst displaying anogenital swellings, being swollen whilst pregnant will create an illusion of sexual receptivity and facilitate the increase of genetic diversity between communities.

Adolescent or subadult females also display sexual swellings, but may go through approximately 19 menstrual cycles before becoming fertile (Tutin, 1980; Boesch & Boesch-Achermann, 2000). It has been suggested that this is a strategy allowing individuals to practise sexual behaviour as a means of ensuring immediate insemination once females become fertile (Turke, 1984). Adult males of many species show an aversion to mating with subadult females (Anderson, 1986), so it would be expected that if grooming is used as a strategy to increase copulations, adult males would show a similar aversion to grooming subadult females. Subadult males, on the other hand, may be physiologically capable of inseminating females, but are generally smaller and weaker, have shorter canines and are subordinate to adult males and are, therefore, less effective in protecting females and infants (Anderson & Bielert, 1994). Subadult males should, therefore, be the grooming age group less preferred by sexually receptive adult females.

Our study, based on a large and long-term data set, aimed to investigate how sexual swellings influence grooming behaviour between males and females of different age classes within a group of free-living chimpanzees. It is hypothesised that if males are the instigators of grooming, they will give more grooming to oestrous rather than anoestrous females and, therefore, use this as a strategy to increase their opportunities for successful copulations. If females are the instigators, they are expected to give more grooming to selected adult males when displaying oestrous swellings as a strategy to protect themselves from harassment by lower-ranking males.

## Materials and methods

### *Study area and subjects*

The Budongo Forest Reserve consists of 793 km<sup>2</sup> of moist, semi-deciduous forest and grassland, and is situated at a mean altitude of 1100 m on the edge of the western Rift Valley in western Uganda (Eggeling, 1947; Plumptre, 1996). The average annual rainfall in the region is approximately 1400 mm, with a dry season between December and February. Daily mean temperatures range between 14 and 28°C (Eggeling, 1947).

The study site was established in 1990 and is maintained by the Budongo Forest Project which, has recently been renamed the Budongo Conservation Field Station. A system of trails covering an area of approximately 31 km<sup>2</sup> aids travel through the study area, allowing researchers relatively easy access to the forest. During the period over which the data were collected, the Sonso group consisted of between 26 and 54 individuals, all of which were individually recognisable and named. The group consisted of 10 to 12 adult males, 10 to 15 adult females, 1 to 4 subadult males, 2 to 5 subadult females, 1 to 4 juvenile males, 0 to 7 juvenile females, 0 to 5 infant males, and 1 to 5 infant females.

### *Data collection*

Data were collected continuously between September 1995 and April 2001 as part of a long-term study on the behaviour and ecology of the Sonso chimpanzees. Eleven field assistants (a mean of four at any given time) employed by the Budongo Forest Project conducted sampling daily (weather permitting) between 07:30 and 13:00 and then again between 14:00 and 16:30 on an ad libitum basis (Altmann, 1974) whilst following the chimpanzees. Grooming interactions recorded included the identities of individuals involved, the initiator (the individual who starts grooming another individual) and terminator of the grooming bout, the duration of the bout (recorded to the nearest minute) and female anogenital swellings, if present. Individuals involved in mutual grooming interactions (individuals grooming each other simultaneously) were recorded as both giving and receiving grooming. The following abbreviations will be used throughout the remainder of the article to refer to different age–sex classes: AM, adult males; AF, adult females; SM, subadult males; and SF, subadult females.

*Analysis*

A total of 1445 grooming bouts involving either SF or AF and males were analysed. For the purpose of analysis the presence of anogenital swellings were categorized for SF and AF with scores of 0, no swelling (anoestrous), or 1, swelling (oestrous). We acknowledge that different stages of swellings may influence access to copulations as well as the fact that females may display swellings during early stages of pregnancy. These data were however, not available so were not included in the study reported here. All grooming interactions involving infants, juveniles, maternal siblings and between mother and offspring were removed so as to eliminate the influence of these classes on grooming interactions.

Grooming bouts were then separated into the following combinations: AF0 and AM; AF0 and SM; AF1 and AM; AF1 and SM; SF0 and AM; SF1 and AM; SF0 and SM; SF1 and SM. Within these combinations, grooming bouts involving the same two individuals were converted into dyads, which then formed the basis for further analysis. Thus, 380 grooming interactions made up of 35 dyads (or partnerships) were recorded for AF0. Using these dyads, the following were calculated: The number (frequency) of grooming bouts that occurred between each of the above age–sex class groups; the percentage of each female's grooming time (minutes) that she gave to, and received from males and the number of initiations and terminations by either males or females that resulted in grooming interactions. The influence of male rank on grooming relationships was not investigated during this study, but has been investigated for this group of chimpanzees by Arnold & Whiten (2003). Whether or not females were pregnant during the data collection was not recorded and could, therefore, not be included in the analysis.

A chi-square goodness of fit test (Zar, 1999) was used to determine whether the observed frequencies of grooming bouts between anoestrous or oestrous females and males differed significantly from expected frequencies (calculated by dividing the proportion of available oestrous females at any one time during the study period by the total number of grooming bouts). Bonferroni confidence intervals (Neu et al., 1974) were performed for those chi-square tests that revealed significant differences to determine preference for or avoidance of different age–oestrous classes. Wilcoxon rank sum tests were used to determine whether anoestrous and oestrous females distributed their grooming time between different age–sex classes differently. Binomial

hypothesis post hoc tests were used to determine whether sexual swellings influenced which sex initiated or terminated heterosexual grooming bouts.

## Results

### *Frequency of grooming between anoestrous and oestrous females and males*

Bonferroni confidence intervals indicated that AF0 and SF0 gave and received significantly less grooming to and from AM than would be expected if grooming dyads occurred at random (Table 1). Conversely, AF1 and SF1 gave and received significantly more grooming to and from AM than would be expected. Both AF0 and AF1 gave and received significantly less grooming to and from SM, whereas SF0 and SF1 gave and received significantly more grooming to and from SM than would be expected.

### *Difference in the duration of grooming bouts involving anoestrous and oestrous females*

Oestrous females allocate their grooming time differently from anoestrous females in terms of the different age–sex classes available to them for grooming. Although the difference was not significant, AF1 allocated more of their grooming time to AM than did AF0 whilst receiving significantly more grooming time from AM than did AF0 ( $p = 0.0001$ ). Although AF1 gave and received slightly more grooming to and from SM than AF0, the differences were not significant. Oestrous subadult females gave both AM and SM more grooming than did SF0, although only AM were given significantly more ( $p = 0.02$ ). Oestrous subadult females received more grooming from AM than did SF0, although the difference was not significant. Both SF0 and SF1 received more or less equivalent amounts of grooming time from SM.

### *Initiation and termination of grooming interactions between males and females*

Results from the binomial test (Table 2) show that grooming interactions between AM and AF1 were initiated significantly more frequently by the males than by the females ( $z = -4.087$ ), whereas grooming interactions between SF0 and AM were initiated significantly more frequently by the females ( $z = 3.283$ ). Although no other significant differences were found,

**Table 1.** Bonferroni confidence intervals for the number of grooming bouts between anoestrous and oestrous females and males.

Grooming partnership	Availability of females at any one time	Grooming bouts		Confidence interval (95%) on observed proportion of occurrence	More/Less than expected
		Number observed	Proportion observed		
Grooming given by females to males					
AF0 and AM	13	209	0.441	0.438 ≤ <i>p</i> ≤ 0.444	Less*
AF1 and AM	4	95	0.200	0.198 ≤ <i>p</i> ≤ 0.203	More*
SF0 and AM	5	67	0.141	0.140 ≤ <i>p</i> ≤ 0.143	Less*
SF1 and AM	2	103	0.217	0.215 ≤ <i>p</i> ≤ 0.219	More*
AF0 and SM	13	45	0.249	0.243 ≤ <i>p</i> ≤ 0.255	Less*
AF1 and SM	4	26	0.144	0.139 ≤ <i>p</i> ≤ 0.148	Less*
SF0 and SM	5	47	0.260	0.254 ≤ <i>p</i> ≤ 0.266	More*
SF1 and SM	2	63	0.348	0.341 ≤ <i>p</i> ≤ 0.355	More*
Grooming received by females from males					
AF0 and AM	13	206	0.334	0.332 ≤ <i>p</i> ≤ 0.336	Less*
AF1 and AM	4	162	0.263	0.261 ≤ <i>p</i> ≤ 0.264	More*
SF0 and AM	5	97	0.157	0.156 ≤ <i>p</i> ≤ 0.159	Less*
SF1 and AM	2	152	0.246	0.245 ≤ <i>p</i> ≤ 0.248	More*
AF0 and SM	13	47	0.2701	0.264 ≤ <i>p</i> ≤ 0.277	Less*
AF1 and SM	4	23	0.1322	0.127 ≤ <i>p</i> ≤ 0.137	Less*
SF0 and SM	5	40	0.2299	0.224 ≤ <i>p</i> ≤ 0.234	More*
SF1 and SM	2	64	0.3676	0.361 ≤ <i>p</i> ≤ 0.375	More*

AF0, anoestrous adult females; AF1, oestrous adult females; SF0, anoestrous subadult females; SF1, oestrous subadult females; AM, adult males; SM, subadult males.

\* All results are significant at *p* < 0.05.

**Table 2.** Binomial test comparison of the number of initiations and terminations by either males or females of grooming interactions.

Age–sex class grooming partnership	No grooming bouts	Female initiations (N)	Male initiations (N)	Binomial test initiations (z value)	Female terminations (N)	Male terminations (N)	Binomial test terminations (z value)
AF0 and AM	415	316	272	1.815	301	337	–1.425
AF1 and AM	257	123	196	–4.087*	131	194	–3.495*
SF0 and AM	164	126	79	3.283*	118	109	0.597
SF1 and AM	255	208	182	1.317	178	181	–0.158
AF0 and SM	92	54	60	–0.680	72	58	1.228
AF1 and SM	49	31	34	–0.493	30	34	–0.500
SF0 and SM	87	50	47	0.280	63	68	–0.437
SF1 and SM	127	101	89	0.509	98	94	0.289

\* Chi-square significance. A, adult; S, subadult; M, male; F, female; 0, anoestrous; 1, oestrous.

both AF0 and SF1 were more likely to initiate grooming interactions with AM. Both AF0 and AF1 were less likely to initiate grooming interactions with SM than were the males. However both SF0 and SF1 initiated more grooming interactions with SM than did males. Although the trend seems to be that when involved in grooming bouts with oestrous females, males are more likely to terminate grooming interactions than are females, the only significant difference found was that AM were significantly more likely than AF1 to terminate grooming interactions ( $z = -3.495$ ).

## Discussion

The results of this study confirm earlier suggestions that sexual swellings influence grooming interactions between chimpanzees (Goodall, 1986; Hemelrijk et al., 1992). Similar influences have also been found in baboons (Seyfarth, 1978), suggesting that associations of males with females may be a pre-mating component of male reproductive effort. By investing time and effort in grooming interactions with potentially reproductive females, males increase their own chances of siring offspring in the future. Females, on the other hand, may prefer to form strong social bonds with AM so that when they do display sexual swellings, they minimise the likelihood of being harassed (Anderson & Bielert, 1994).



Grooming patterns between AM and females were found, as predicted, to increase during oestrous periods, whereas grooming patterns involving AF and SM and involving AM and SF support other primate studies which found that grooming between these age–sex classes is either generally avoided or occurs between low-ranking or older AF and SM (Anderson, 1986). Both SF0 and SF1 initiated grooming with SM more frequently than SM initiated with SF, suggesting that SF could be using grooming as a means of gaining protection and/or reinforcing relationships.

Oestrous females showed a clear preference for grooming interactions with AM, which is in accordance with observations by Goodall (1986) as well as studies on captive chimpanzees (Hemelrijk et al., 1992), Barbary macaques (*Macaca sylvanus*) (Wallner et al., 1999) and savanna baboons (Rowell, 1968). Although subadults may prefer to associate with adults, they find it easier to develop and reinforce social bonds with each other for future benefits than risk injury by competing with older and stronger adults, thereby explaining the preference of subadult females but avoidance by adult females for subadult males as grooming partners. It must also be remembered that there is no clear-cut point at which an individual changes from being a subadult to an adult and, therefore, individuals that were classified as subadults by human observers may have been viewed as young adults by other chimpanzees, which may explain grooming interactions occurring between adults and subadults that coincidentally became adults during the study period.

Due to the preference of AM for grooming interactions with AF, it is not surprising that grooming interactions between SF and AM are more likely to be initiated by the SF. These AM may be low-ranking, older males, or they may simply recognise the future reproductive potential of these females. Females are subject to more aggression from males whilst displaying sexual swellings (Matsumoto-Oda & Oda, 1998), and SF respond to SM aggression by engaging in grooming interactions with them. Adult females are less likely to initiate grooming interactions with SM despite their reproductive maturity, possibly in response to aggression by AM.

As hypothesised, males tend to initiate grooming bouts with oestrous females, whereas when anoestrous, females are more likely to initiate grooming bouts, which supports findings by Wallis (1992). As previously discussed, other benefits of allogrooming may govern grooming interactions

during anoestrous periods, and as a result social bonds are reinforced, making the occurrence of reproductive opportunities more likely. The willingness of males to invest increased grooming in females when they come into oestrous may be the final deciding factor for females. Adult females will try and keep preferred males close by as long as possible, which would explain the increased likelihood of AM terminating grooming with AF1. Grooming could also be terminated as a result of the arrival of another higher-ranking or older male, which would explain why SM are more likely than AF1 to terminate grooming (Smuts & Smuts, 1993).

We conclude that, first both male age and female oestrous status influence grooming interactions between chimpanzees. Second, the use of grooming by each sex is consistent with strategies for males to increase copulation opportunities and for females to increase protection from harassment when displaying anogenital swellings. Adult females might also use grooming to increase their opportunities for mate choice. These findings serve to demonstrate that although oestrus in chimpanzees is openly advertised to all group members by the visual stimulus of the anogenital swelling, there is a complex overlay of social interactions that influence the identities of mating individuals. Grooming behaviour is a central component of those social interactions.

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