



**The functional significance of grooming behaviour in higher primates:
the case of free-living chimpanzees**

by

Kerry Slater

Submitted in partial fulfilment of the requirements for the degree of

Doctor of Philosophy (Zoology)

in the Faculty of Natural & Agricultural Sciences

University of Pretoria

Pretoria

April 2009



“Out of clutter, find simplicity, from discord, find harmony. In the middle of difficulty
lies opportunity”

Albert Einstein

**The functional significance of grooming behaviour in higher primates:
the case of free-living chimpanzees**

Kerry Slater^{1,2}

Supervisors: Prof Johan du Toit ^{1,4}, Elissa Cameron¹, Trudy Turner^{1, 3} & Prof Vernon Reynolds⁵

Departments:

¹ Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, South Africa

² Department of Environmental Sciences, University of South Africa (UNISA)

³ Department of Anthropology, University of Wisconsin-Milwaukee

⁴ Department of Wildland Resources, Utah State University, Logan, UT 84322-5230, USA

⁵ Biological Anthropology, School of Anthropology, 51 Banbury Road, Oxford OX2 6PE, UK

Submitted for the degree of Doctor of Philosophy (Zoology) in the Faculty of Natural & Agricultural Sciences

Summary

As a contribution to the existing knowledge of grooming in primates five and a half years of grooming data were examined from a group of free-living chimpanzees (*Pan troglodytes*) in the Budongo Forest, Uganda, to investigate various functional significances of grooming behaviour within the context of social reinforcement. The fission–fusion social structure of chimpanzees results in group members not moving around as a single unit, but forming temporary units as the need arises. This reduces

opportunities for individuals to groom others and therefore, based on time and association constraints alone, grooming was as expected found to be unevenly distributed among group members. Grooming patterns found among this group of chimpanzees were comparable to those observed in other free-living populations with variations possibly being attributed to resource base, population numbers and differences in age-sex class composition.

One of the suggested social benefits of grooming is that it is used to enhance reproductive success, either by allowing males to enhance their proximity to oestrous females, or by influencing female choice through the development of affiliative relationships with males. Grooming was found to increase between males and females, whilst females displayed sexual receptivity through the presence of anogenital swellings and grooming may be a strategy used by males to increase their access to copulation opportunities, whereas females may use grooming to increase protection from harassment by less preferred males during swollen periods and also increase the likelihood of copulation with preferred partners.

Based on the availability of oestrous females, copulations between males and adult females occurred significantly less frequently than expected, whereas copulations between males and subadult females occurred significantly more frequently than expected. Overall a positive correlation was found between grooming of females by males and frequency of copulations.

Due to concerns regarding the validity of different sampling methods, scan-focal and *ad libitum* sampling methods were compared to establish if results from different sampling methods were similar. Results from the scan-focal and *ad libitum* sampling methods had

very few discrepancies, and it is suggested that *ad libitum* sampling methods which record behaviour types whenever they occur, may be more beneficial for species which don't move around as a single unit and live in environments where visibility is reduced, therefore increasing the possibility of recording individuals or behaviours that are observed infrequently. Scan-focal sampling may be more beneficial in studying species which move around together in habitats which are conducive to greater visibility, therefore allowing all or most group members to be observed simultaneously.

Keywords: Chimpanzees, *Pan troglodytes*, grooming, oestrous, copulations, scan sampling, focal sampling, *ad libitum* sampling

Acknowledgements

I would like to thank all those who in some way, big or small contributed to the success of this dissertation. A special thanks to my mom and dad for all their support through the years of growing up and during my studying. Thanks to my sister Jenny for all the articles and support provided over the years. To all my friends and colleagues I would like to express my appreciation for their support and friendship during my studies especially Lindie and Magdel (who had a continuous flow of coffee going), Liesl (for physically removing me from my computer to eat), Lydia, Marietjie, Marie and Marna for moral support. To Prof. Johan du Toit, a very special thanks for supervising me through yet another very challenging qualification. Your endless support and enthusiasm has been a great inspiration. To my other supervisors, Prof. Trudy Turner and Prof. Elissa Cameron, thank you for your guidance and support with this thesis, I really appreciate it. I would also like to thank Prof Vernon Reynolds for making the data from the Budongo Forest Project available for use. Elmarie Cronje, thank you for all the logistical assistance in the department, always ready to lend a helping hand. The University of Pretoria provided financial support which enabled me to travel to the Budongo Forest in Uganda. All the field assistants and staff at the Budongo Forest site, thank-you for your dedication to the chimpanzees and the Budongo Forest project. A big thank-you to Mr Andre Swanepoel of STATOMET for all your statistical advice. Charlotte Hemelrijk made valuable comments on some of the chapters that made use of her MATRIXTESTER. I would like to extend a very special thank-you to my husband Gary, for all his support and tolerance through the duration of yet another qualification and to my daughter Caitlin, for being such a wonderful, loving child even when you were chased out the room in the interest of chimpanzees. To everyone else who in some way or another contributed to the success of this dissertation, whether logistically or emotionally, you are all very much appreciated.

Disclaimer

The present study forms part of a larger long term study on the dynamics and management of the Budongo Forest, Uganda. This study focuses on one of the groups of free-living chimpanzees within the forest (known as the Sonso group) and its main objective is to increase the knowledge base of the chimpanzees as a component of the management plan for the forest as well as towards the understanding of this species. This dissertation consists of a series of chapters that have been prepared as “stand alone” manuscripts for subsequent submission to specific scientific journals for publication purposes. Consequently, unavoidable overlaps and inconsistencies with regards to format and layout may occur between chapters.

Although throughout this dissertation the study site is referred to as the Budongo Forest Project (BFP), it has recently been changed to the Budongo Conservation Field station.

I declare that although I did not collect the data used in this study myself, all the ideas, extraction of data from the database, analysis and write-up thereof is my own work.

Constraints to this dissertation:

The influence of rank on grooming interactions was not included in this study, but has been investigated for this group of chimpanzees in other studies referred to in the text.

At the time that this dissertation was written up, the paternity of the chimpanzees in the group was not certain and although maternal kin were controlled for where necessary, paternal kin were not.

Investigation into the difference of age effects is limited due to classification of different age classes being subjective. It is acknowledged that although the distinction between age classes is not clear cut, the method of age classification is appropriate in the context of this study.

It is further acknowledged that the different stages of female ovulation cycles as well as early stages of pregnancy may influence grooming interactions and female choice of copulation partners. The data for these variables were not available and therefore not included in this study.

Statistical power is always dependant on sample size. With chimpanzees, it is difficult to achieve samples as large as could be achieved with smaller animals which have shorter generation times, such as mice or insects. This presents the problem that statistical tests will have a limited power in detecting relatively weak effects, especially when data is broken into subcategories. If a test is not significant, it must not be excluded that the sample size was too small to detect a real but weak effect. Therefore, some results may show a tendency only and not a statistical significance (p -value <0.05).



Contents

Summary.....	iii
Acknowledgments	vi
Disclaimer and constraints to this dissertation.....	vii
Contents.....	ix
List of Tables.....	xii
List of Figures.....	xv
Chapter 1: General Introduction	1
1.1 Relevance of study.....	7
1.2 Key questions and dissertation outline.....	8
1.3 References.....	10
Chapter 2: Grooming distributions across age-sex classes.....	16
2.1 Introduction.....	17
2.2 Study area and methods.....	21
2.2.1 Study area.....	21
2.2.2 Study group.....	22
2.2.3 Data Collection.....	25
2.2.4 Analysis.....	25
2.3 Results.....	29
2.3.1 General grooming distributions between age-sex classes.....	29
2.3.2 Mutual versus unidirectional grooming bouts.....	29
2.3.3 Grooming distributions of different age-sex classes.....	32
2.3.4 Number of grooming partners.....	45



2.3.5 Grooming reciprocity between age-sex classes.....	46
2.4 Discussion.....	48
2.5 References.....	55
Chapter 3: Grooming distributions between anoestrous and oestrous females.....	62
3.1 Introduction.....	64
3.2 Study area and methods.....	69
3.2.1 Study area.....	69
3.2.2 Study group.....	69
3.2.3 Data Collection.....	72
3.2.4 Analysis.....	72
3.3 Results.....	74
3.3.1 Frequency of grooming given by anoestrous and oestrous females to males....	74
3.3.2 Frequency of grooming received by anoestrous and oestrous females from males.....	75
3.3.3 Duration of grooming bouts between anoestrous and oestrous females.....	78
3.3.4 Initiation of grooming interactions between males and females.....	83
3.3.5 Termination of grooming interactions between males and females.....	83
3.4 Discussion.....	86
3.5 References.....	89
Chapter 4: Grooming distributions and copulations.....	96
4.1 Introduction.....	97
4.2 Study area and methods.....	102
4.2.1 Study area.....	102
4.2.2 Study group.....	102



4.2.3 Data Collection.....	105
4.2.4 Analysis.....	105
4.3 Results.....	107
4.4 Discussion.....	111
4.5 References.....	115
Chapter 5: A comparative analysis of using scan-focal versus <i>ad libitum</i> sampling methods in the investigation of grooming behaviour	122
5.1 Introduction.....	123
5.2 Study area and methods.....	125
5.2.1 Study area.....	125
5.2.2 Study group.....	126
5.2.3 Data Collection.....	127
5.2.4 Analysis.....	127
5.3 Results.....	128
5.4 Discussion.....	135
5.5 References.....	137
Chapter 6: Synopsis and conclusion	139
6.1 References.....	146
APPENDIX A.....	150
GLOSSARY	151



List of Tables

Table 2.1 The number of individuals within each age-sex class from which grooming interactions were recorded during the five and a half year study period..... 24

Table 2.2 Comparison between the percentages of mutual and unidirectional grooming bouts between age-sex class combinations using Wilcoxon signed rank test. Mean values (\pm SE) are given. (N=4819 bouts). A-adult, S-subadult, J-juvenile, I-infant, M-male, F-female 31

Table 2.3 Results of Kr, R and Z tests (Hemelrijk 1990a) for grooming reciprocity between different age-sex classes. All results are based on 2000 permutations. N=17 adult males (AM), 17 adult females (AF), 6 subadult males (SM), 7 subadult females (SF), 11 juvenile males (JM), 7 juvenile females (JF), 7 infant males (IM) and 9 infant females (IF)..... 47

Table 3.1 The number of individuals within each age-sex class from which grooming interactions were recorded during the five and a half year study period..... 71

Table 3.2 Bonferroni confidence intervals for the number of grooming bouts that anoestrous and oestrous females gave to males. AF0 – anoestrous adult females, AF1 – oestrous adult females, SF0-anoestrous subadult females, SF1 – oestrous subadult females, AM-adult males, SM-subadult males. * = All results significant at $p < 0.05$ 76

Table 3.3 Bonferroni confidence intervals for the number of grooming bouts that anoestrous and oestrous females received from males. AF0 – anoestrous adult females, AF1 – oestrous adult females, SF0 - anoestrous subadult females, SF1 – oestrous subadult females, AM - adult males, SM – subadult males. * = All results significant at $p < 0.05$ 77

Table 3.4 Binomial test comparison of the number of initiations by either males or females that resulted in grooming interactions. * indicates where chi-square significance lies. A-adult, S-subadult, M-male, F-female, 0- anoestrous, 1- oestrous..... 84

Table 3.5 Binomial test comparison of the number of terminations from grooming interactions made by either males or females. * indicates where chi-square significance lies. A-adult, S-subadult, F-female, M-male, 0- anoestrous, 1- oestrous..... 85

Table 4.1 The number of individuals within each age-sex class from which grooming interactions were recorded during the five and a half year study period..... 104

Table 4.2 Bonferroni confidence intervals for the number of copulations between oestrus females and males. AF1 – oestrous adult females, SF1 – oestrous subadult females, AM-adult males, SM-subadult males. * = All results significant at $p < 0.05$ 109

Table 4.3 Results of Kr, R and Z tests (Hemelrijk 1990a) for correlations between grooming and copulations between males and females of different age classes. All results are based on 2000 permutations. N=16 AM, 13 AF, 6 SM, 5 SF..... 110

Table 5.1 Comparison of scan-focal and *ad libitum* sampling methods with regard to the mean number of grooming partners of different age-sex classes. AM – adult males, AF – adult females, SM – subadult males, SF – subadult females..... 131

Table 5.2 Comparison of scan-focal and *ad libitum* sampling methods with regards to the overall percentage of grooming time that adult males (AM) gave and received to and from different age - sex classes. AM – adult males, AF – adult females, SM – subadult males, SF – subadult females..... 132

Table 5.3 Comparison of scan-focal and *ad libitum* sampling methods with regards to the overall percentage of grooming time that adult males (AM) gave to and received from different age - sex classes, taking into account the number of members of each age-sex class. AM – adult males, AF – adult females, SM – subadult males, SF – subadult females 133

Table 5.4 Results of Wilcoxon signed rank tests for both scan-focal and *ad libitum* methods with regards to the amount of grooming given and received by adult males (AM) to and from other AM compared to other age-sex classes. AM – adult males, AF – adult females, SM – subadult males, SF – subadult females..... 134

List of Figures

- Figure 2.1** The percentage of the study group’s total grooming time (1301.4 hours) that different age-sex class combinations contributed. A-adult, S-subadult, J-juvenile, I-infant, M-male, F-female, other = sum of percentages of grooming between age-sex classes that were < 1%. N=17 AM, 17 AF, 6 SM, 7 SF, 11 JM, 7 JF, 7 IM and 9 IF..... 30
- Figure 2.2** The percentage of adult male’s total grooming time distributed to different age-sex classes. A-adult, S-subadult, J-juvenile, I-infant, M-male, F-female, nk-nonkin. Column height gives mean across all adult males (N=17); bars give std error. Mutual = mutual grooming bouts, Gave = grooming given by adult males to different age-sex classes (unidirectional bouts) and received = grooming received by adult males from different age-sex classes (unidirectional bouts)..... 34
- Figure 2.3** The percentage of adult female’s total grooming time distributed to different age-sex classes. A-adult, S-subadult, J-juvenile, I-infant, M-male, F-female, k-kin, nk-nonkin. Column height gives mean across all adult females (N=17); bars give std error. Mutual = mutual grooming bouts, Gave = grooming given by adult females to different age-sex classes (unidirectional bouts) and received = grooming received by adult females from different age-sex classes (unidirectional bouts)..... 35

Figure 2.4 The percentage of subadult male’s total grooming time distributed to different age-sex classes. A-adult, S-subadult, J-juvenile, I-infant, M-male, F-female, k-kin, nk-nonkin. Column height gives mean across all subadult males (N=6); bars give std error. Mutual = mutual grooming bouts, Gave = grooming given by subadult males to different age-sex classes (unidirectional bouts) and received = grooming received by subadult males from different age-sex classes (unidirectional bouts)..... 37

Figure 2.5 The percentage of subadult female’s total grooming time distributed to different age-sex classes. A-adult, S-subadult, J-juvenile, I-infant, M-male, F-female, k-kin, nk-nonkin. Column height gives mean across all subadult females (N=7); bars give std error. Mutual = mutual grooming bouts, Gave = grooming given by subadult females to different age-sex classes (unidirectional bouts) and received = grooming received by subadult females from different age-sex classes (unidirectional bouts)..... 38

Figure 2.6 The percentage of juvenile male’s total grooming time distributed to different age-sex classes. A-adult, S-subadult, J-juvenile, I-infant, M-male, F-female, k-kin, nk-nonkin. Column height gives mean across all juvenile males (N=11); bars give std error. Mutual = mutual grooming bouts, Gave = grooming given by juvenile males to different age-sex classes (unidirectional bouts) and received = grooming received by juvenile males from different age-sex classes (unidirectional bouts)..... 40

Figure 2.7 The percentage of juvenile female’s total grooming time distributed to different age-sex classes A-adult, S-subadult, J-juvenile, I-infant, M-male, F-female, k-kin, nk-nonkin. Column height gives mean across all juveniles females (N=7); bars give std error. Mutual = mutual grooming bouts, Gave = grooming given by juvenile females to different age-sex classes (unidirectional bouts) and received = grooming received by juveniles females from different age-sex classes (unidirectional bouts)..... 41

Figure 2.8 The percentage of infant male’s total grooming time distributed to different age-sex classes. A-adult, S-subadult, J-juvenile, M-male, F-female, k-kin, nk-nonkin. Column height gives mean across all infant males (N=7); bars give std error. Mutual = mutual grooming bouts, Gaive = grooming given by infant males to different age-sex classes (unidirectional bouts) and received = grooming received by infant males from different age-sex classes (unidirectional bouts)..... 43

Figure 2.9 The percentage of infant female’s total grooming time distributed to different age-sex classes. A-adult, S-subadult, J-juvenile, M-male, F-female, k-kin, nk-nonkin. Column height gives mean across all infant females (N=9); bars give std error. Mutual = mutual grooming bouts, Gave = grooming given by infant females to different age-sex classes (unidirectional bouts) and received = grooming received by infant females from different age-sex classes (unidirectional bouts)..... 44

Figure 3.1 The proportion of grooming time (minutes) that adult females gave to different age-sex classes. A-adult, S-subadult, F-female, M-male, 0-anoestrous, 1- oestrous..... 79

Figure 3.2 The proportion of grooming time (minutes) that adult females received from different age-sex classes. A-adult, S-subadult, F-female, M-male, 0-anoestrous, 1-oestrous..... 80

Figure 3.3 The proportion of grooming time (minutes) that subadult females gave to different age-sex classes. A-adult, S-subadult, F-female, M-male, 0-anoestrous, 1-oestrous..... 81

Figure 3.4 The proportion of grooming time (minutes) that subadult females received from different age-sex classes. A-adult, S-subadult, F-female, M-male, 0-anoestrous, 1-oestrous..... 82

Figure 4.1 The percentage of copulations that each age-sex class combination contributed during the study period. A-adult, S-subadult, M-male, F-female. N= 888 copulations..... 108

Figure 5.1 Comparison between scan-focal and *ad libitum* sampling methods for the percentage of dyads in each age-sex class that had grooming interactions. A-adult, S-subadult, M-male, F-female..... 130