

Indications for female mate choice in grey-cheeked mangabeys *Lophocebus albigena johnstoni* in Kibale National Park, Uganda

Malgorzata E. Arlet · Freerk Molleman · Colin Chapman

Received: 4 January 2007 / Revised: 3 March 2007 / Accepted: 16 July 2007 / Published online: 4 September 2007
© Springer-Verlag and ISPA 2007

Abstract Female sexual strategies affect male strategies and can play an important role in shaping mating systems. We investigated female sexual behaviour within five groups of grey-cheeked mangabeys in Kibale National Park, Uganda, and tested the hypothesis that females exhibit mate choice using as indications the prevalence of (1) females soliciting matings by presenting to males and (2) females refusing to mate with approaching males. In addition, we describe how these behaviours as well as grooming and copulation calls are distributed over high-ranking, low-ranking and migrating males and discuss these patterns with regard to trade-offs that could play a role in female mate choice in multi-male groups. Females were promiscuous and initiated almost half of the matings, with both resident and

migrating males. More than half of male mating approaches were refused by peak females. Female mate choice in this species may depend on individual female preferences, oestrus phase and male tactic.

Keywords Female reproductive tactic · Sexual presentation · Sexual refusal · Copulatory calls · Sexual swelling · Male migrations

Introduction

Female mate choice is one of the main processes of sexual selection (Darwin 1859). Despite the fact that for humans (Buss 1994) and a wide variety of animals (Andersson 1994) the importance of female mate preferences and mate choice has been widely accepted, for non-human primates, evidence for female mate preferences remains largely anecdotal (Paul 2002). Gowaty (1997) postulated that this is a consequence of highly variable and often antagonistic sexual tactics, and therefore, in non-human primates, female mate choice can be constrained by female–female competition, male–male contests, reproductive suppression, male choice and male coercion. Thus, female preferences will remain speculative, but behavioural studies can produce data on female choice (Manson 1992).

There is evidence for female mate choice in non-human primates (Keddy-Hector 1992; Paul 2002; Pusey and Wolf 1996; Small 1989; Smuts 1987). However, in species where females stay in multi-male groups and females can mate with several males (as in grey-cheeked mangabeys), female choice can be especially important, but also cryptic (Smuts and Smuts 1993), due to male behaviour or female–female competition (Bercovitch 1991; Manson 1992; Soltis et al.

Communicated by R.F. Oliveira

M. E. Arlet (✉) · F. Molleman
Department of Entomology, University of California, Davis,
1 Shields Avenue,
Davis, CA 95616, USA
e-mail: maarlet@yahoo.com

F. Molleman
e-mail: fmolleman@ucdavis.edu

M. E. Arlet
Department of Anthropology, University of California,
Davis, 1 Shields Avenue,
Davis, CA 95616, USA

C. Chapman
Anthropology Department, McGill University,
Montreal, Quebec H3A 2T7, Canada
e-mail: Colin.Chapman@McGill.ca

C. Chapman
McGill School of Environment, McGill University,
Montreal, Quebec H3A 2T7, Canada

2001). In Papionines, there are several examples of active involvement of females in the mating process such as following, presentation and grooming between non-consort females and males, participation in ‘sneak’ matings with subordinate males (Nunn 1999; Smuts 1983) and female competition for mating partners (Bercovitch 1995).

Although mate preference criteria of females are usually unknown, skewed female mate choice has been demonstrated in some non-human primate species living in multi-male groups. Females may choose to mate with high-ranking males (Dixon et al. 1993); *Macaca mulatta*: (Bercovitch and Nurnberg 1997); *Papio cynocephalus*: (Altmann et al. 1996); *Cercocebus torquatus atys*: (Gust et al. 1998) or mid-ranking males [*Macaca mulatta*: (Manson 1992, 1994); *Macaca fuscata*: (Huffman 1991; Soltis et al. 2001)]. In baboons, females mate with multiple males but may try to develop a special relationship with at least one male (Smuts 1985), who also forms an affiliative bond with her offspring (Bercovitch 1991; Palombit et al. 1997). However, that relationship rarely has a positive influence on male mating success (Bercovitch 1991; Huffman 1991; Manson 1994). In contrast to these affiliative bonds, females may show preferences towards newcomer males (Bercovitch 1997; Small 1989). Several paternity studies provided evidence that such female behaviour towards newcomers can have a positive impact on the reproductive success of migrating males (Berard et al. 1994; Fietz et al. 2000; Gagneux et al. 1997; Launhardt et al. 2001).

One means whereby females can manipulate male sexual behaviour is signalling fertility. Sexual swellings are common signals among female primates that live in multi-male groups (Clutton-Brock and Harvey 1976). The function of exaggerated swelling is controversial and may vary among species; it may be a reliable indicator of timing of ovulation (Nunn 1999), or female quality (Pagel 1994), or it may be a within-female indicator of conception across cycles (Emery and Whitten 2003; Zinner et al. 2002). The timing of exaggerated sexual swellings in females is not always synchronised with ovulation (Dixon 1998; Nunn 1999), and therefore, females may have a large time window to exhibit sexual behaviour that does not lead to fertilisation, increasing the opportunity for female manipulation of male behaviours (Pagel 1994; van Schaik et al. 2000). The presence of sexual swellings can promote male competition which often concentrates paternity in one, dominant male (the best male hypothesis; Clutton-Brock and Harvey 1976). On the other hand, sexual swellings can confuse paternity among males to reduce aggression towards infants, when females mate with many males during the periods with sexual swellings (the many males hypothesis; Hrdy and Whitten 1987). During their ovarian cycle, females can also employ both strategies, depending on fertility (the graded signal hypothesis; Nunn 1999).

Post-copulation calls can be indicators of female choice although their ultimate function remains often a matter of speculation (O’Connell and Cowlshaw 1994). At least 15 different hypotheses have been proposed to explain the function of female copulation calls in primates (Maestripieri and Roney 2005). For example, (a) female copulation calls may be associated with orgasm [Japanese macaques: (Troisi and Carosi 1998)], (b) females call to synchronise orgasm with the male (Hamilton and Arrowood 1978) and therefore promote the sperm transfer to aid conception (Fox and Fox 1971), (c) female copulation calls can incite male sperm competition to ensure that sons will inherit the best sperm [‘sexy sons’ hypothesis; (O’Connell and Cowlshaw 1994)] and (d) female copulation calls may also have a function of announcing paternity certainty to promote paternal investment (Henzi 1996).

Grey-cheeked mangabeys live in multi-male groups, and males often migrate between groups, while females tend to stay in their natal groups. Females exhibit sexual swellings that cover a relatively small area ventral to the base of the tail (Chalmers and Rowell 1971; Danjou 1972; Rowell and Chalmers 1970; Wallis 1983). Females with sexual swellings are present throughout the year, and matings are recorded only during the oestrus period (Wallis 1983). Females usually copulate with more than one male (Chalmers 1968; Wallis 1979). High-ranking males were about five times more aggressive towards females than migrating males, and low-ranking males behave almost three times more aggressively towards females than migrating males. However, high-ranking males are seven times less aggressive towards juveniles than migrating males, and in comparison to migrating males, low-ranking males are 14 times less aggressive towards juveniles (Arlet et al., in preparation). Dr. William Olupot (personal communication) observed two females carrying dead infants shortly after new males entered the group, which suggests that migrating male aggression towards infants can be lethal. Males can also care for offspring (Arlet et al., in preparation; Struhsaker and Leyland 1979; Wallis 1979).

We investigated female sexual behaviour within five groups of grey-cheeked mangabeys in Kibale National Park, Uganda, and tested the hypothesis that females exhibit mate choice using as indications the prevalence of (1) females soliciting matings by presenting to males and (2) females refusing to mate with approaching males. In addition, we describe how these behaviours as well as grooming and copulation calls are distributed over high-ranking, low-ranking and migrating males and discuss these patterns with regard to trade-offs that can be expected to play a role in female mate choice in multi-female–multi-male groups. While much is known about female sexual behaviour in the closely related baboons, arboreal mangabeys can provide an interesting comparison because habitat can be an important factor in mating systems.

Materials and methods

Study site and subjects

After a pilot study in 1999, data were collected for 6 months in 2001 (January–June) and supplemented with observations in 2002 (April–June) in Kibale National Park (0°13′–0°41′N and 30°19′–30°32′E). Kibale (795 km²) is a moist, evergreen medium altitude forest with a mosaic of swamp, grassland, thicket and colonizing forest (Chapman and Lambert 2000). Mangabeys in Kibale live in multi-male groups of on average 14 individuals (Olupot 1999; Wallis 1979; Waser 1977). In total, we observed 26 sub-adult and adult males and 35 females.

Fourteen males were recognised by the unique colour combination of their collars or attached radios placed on them in an earlier study (Olupot 1999). Males without a collar were classified as adult male (AM, $N=7$) or sub-adult male (SAM, $N=5$) and were recognisable on the basis of their relative sizes and other distinguishing features. In each of the groups, there were at least two individual males present in the same group between January–June 2001. These males were regarded as resident males ($N=16$). Males that emigrated at least once from a group or that immigrated into a group and then dispersed during these 6 months were called migrating males ($N=10$). This excluded visiting males that were sighted only briefly (<2 days) in groups.

Females with sexual swellings were present throughout the year. The swelling increases in size and colour gradually, deepening to pink (oestrous adult female inflating: OAFi) until the maximum stage of swelling is reached (oestrous adult female peak: OAFp). As oestrus passes, the swelling becomes less turgid and the colour changes to dark purple (oestrous adult female deflating: OAFd; Danjou 1972; Deputte 1991; Wallis 1983). The duration of sexual swellings average 17–31 days, with the phase from quiescence to peak swelling being 4–14 days long, the peak size of sexual swelling lasting 2–4 days and the deflating stage lasting 7–14 days (Danjou 1972; Deputte 1991; Rowell and Chalmers 1970; Wallis 1983).

Observation methods

From January 2001 to June 2001, two observers collected behavioural observations for 8–9 h/day, for 6 consecutive days per week, for a total of 2,036 h. To measure the rate of movement of males between groups, we censused the focal group every day during each observation period. Dominance interactions among males were recorded on the basis of approach–retreat interactions following de Waal (1987), which were scored for all nearby males during focal follows of oestrus females (Olupot and Waser 2001). Dominance relationships are ordinal within a group, and therefore, we

simplified this classification to compare males across groups; the highest-ranking male was classified as high ranking and others as low ranking. In two groups, the ranks of the two highest-ranking males could not be distinguished and both males were classified as high ranking. Mating was defined as a mount involving intromission (Wallis 1983), and mating success of a male was measured as the number of observed matings.

We predominantly followed females with sexual swellings. Focal females were classified as ‘adult female’—without sexual swelling (AF), or female with sexual swelling—‘inflating female’ (OAFi), ‘peak female’ (OAFp) and ‘deflating female’ (OAFd). The behaviours of focal females were recorded all day, divided into 30-min sampling blocks with no more than 5 min between blocks. During these all-day follows we recorded female behaviour. During focal sampling of females with sexual swellings, we recorded all occurrences of interactions with males and other group members within 10 m of the focal female. We focussed on the following behaviours which have been used to study female mate choice in the socially similar baboons (Bercovitch 1995): (1) the direction and frequency of grooming during the oestrous period, (2) the direction of sexual presentation by females, (3) sexual refusals, (4) subsequent successful matings and (5) the presence of female copulation calls.

Data analysis

To compare the behaviour of different classes of females with sexual swellings and males, the observations were divided by the number of days the interaction could have occurred during the 6-month period (when a particular male and female were observed together in a group). For the grooming data, we excluded males that were guarding females. In our analysis, each day represented one data point for females and for males. These standardised values were then used for statistical comparisons and graphical representations. To simultaneously explore multiple factors and their interactions we used an Analysis of Multi-Factor Regression (GLM) approach on the number of events (such as sexual presentations, matings, copulation calls, mating refusals and grooming) per the number of days an interaction could have occurred, thus using a single data point for each male. The analyses were performed using Statgraphics 5.0. (two-tailed probability with alpha at 0.05).

Results

Sexual presentations

Grey-checked mangabey females mated only when they had a sexual swelling. Forty-eight percent of sexual presenta-

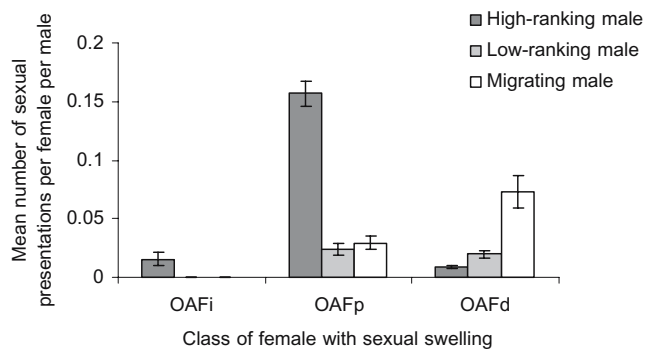


Fig. 1 Mean number of sexual presentations of oestrous females towards high-ranking, low-ranking and migrating males. The error bars show the interval mean \pm 2 SE

tions by females led to matings ($N=63$ sexual presentations of 26 females). Most of the sexual presentations that resulted in mating were performed by females with peak swellings (66%), then inflating females (18%) and deflating (16%; GLM analysis: $p=0.01$, $df=2$, $F=4.84$, $R^2=32.67\%$).

There was no difference between male categories in receiving sexual presentations, but peak females presented mainly to high-ranking males, and deflating females to migrating males (GLM analysis: $R^2=32.67\%$, male category $p=0.1$ $df=2$ $F=2.29$, male category \times female category $p=0.002$, $df=4$, $F=4.85$; Fig. 1)

Mating

Fifty-three percent of matings were initiated by females ($N=56$ matings). Females mated with between one and three different partners ($N=28$ oestrus females) during one cycle. Usually, one of the partners was a high-ranking male who also followed the females during this period, and in addition, she mated with one of the low-ranking or migrating males. During days with maximum swelling, females mated with two to three males, but during the deflating stage, females mated with one to two males only. Some matings with migrating males occurred outside the group (sneaky copulations). Most matings were recorded with high-ranking males (GLM analysis: $p=0.0002$, $df=8$, $F=9.67$, $R^2=60.5\%$). Peak females mated mainly with high-ranking males but also migrating males and low-ranking males (GLM analysis: $p=0.00001$, $df=4$, $F=7.86$, $R^2=60.5\%$; Fig. 2).

Copulation calls

We recorded 25 matings that were accompanied by a female call (grunt), which represents 46% of all recorded matings. The presence of female copulation calls depended on male rank (GLM: $F=8.72$, $df=25$, $R^2=0.66$, $p=0.0003$); most female copulation calls occurred during matings with

high-ranking males, except for matings with one migrating male, who elicited many copulation calls.

Mating refusals

One third of all mating approaches by males were refused ($N=87$ approaches), and 59% was refused by peak females. High-ranking males approached more and received more refusals than other males (Poisson Regression, $p=0.0005$), hence there was no difference between the male categories in proportion of approaches refused.

Grooming

For this analysis we used data of males that were not guarding females. Receptive females groomed males more than non-oestrus females (GLM: $F=8.09$, $df=1$, $R^2=57\%$, $p=0.007$). Most of the grooming by oestrus females was observed with high-ranking males (GLM: $F=8.19$, $df=1$, $R^2=57\%$, $p=0.0001$).

Discussion

This study revealed that females actively participate in mate choice; females are not just accepting mating with eager males but refuse as well as actively approach and solicit copulations by males. The observed behaviour can be seen as the range of solutions for the female's dilemma—on one hand, she could choose to mate the best male, capable to protect her and her offspring, but she may also mate with many males to avoid inbreeding or reduce aggression or risk of infanticide (van Schaik et al. 2000). The evolution of prolonged follicular phases and unpredictable ovulations (van Schaik et al. 2000) as well as sexual swelling that advertises female reproductive state (Domb and Pagel 2001; Nunn 1999) and also copulation calls (Semple and McComb 2000) may give females opportunity to express their preferences within the social context.

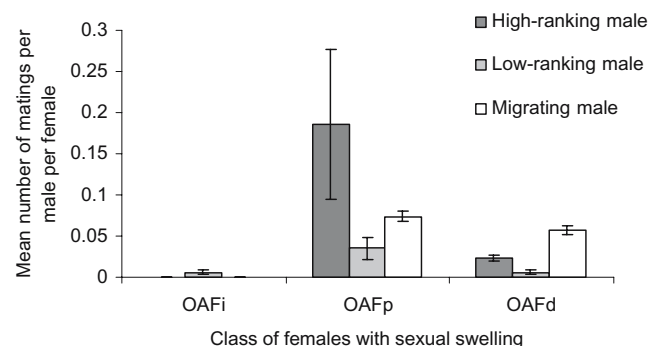


Fig. 2 Mean number of matings with inflating females, peak females and deflating females. The error bars show the interval mean \pm 2 SE

In grey-cheeked mangabeys, 48% of the observed sexual presentations initiated by females resulted in matings. On average, resident and migrating males received similar presentation rates from females but females at the peak of sexual swelling presented mainly to high-ranking males and deflating females to migrating males. Oestrus females were also more active in grooming males than non-oestrus females, with preferences toward high-ranking males and then towards migrating males. Females tended to mate with more males during the peak of sexual swelling than during the deflating stage.

Mangabey females at the peak of sexual swelling refuse almost 60% of male mating approaches. High-ranking males are the ones who approach the most and receive more refusals than other males. That the proportion of mating refusals received by the male categories did not differ significantly conceals that particular females did refuse to mate more or less with particular males or male classes. The high incidence of refusals and variation among females indicates that they are not mating with any approaching male but are choosy. Moreover, mangabey females initiated more than half of the observed copulations and mated with more than one partner. This result corroborates the findings of Wallis (1983), where 42% of copulations were initiated by females. In many social species, females show physiological and behavioural adaptations that lead to copulation with more males and over a longer period than is necessary to ensure fertilisation (Smuts 1985). It seems that, similar to rhesus macaques (Manson 1992, 1994), mangabey females can mate with males of various ranks, but in some groups, they can be monopolised by high-ranking males which are able to prevent them from mating with other males as high-ranking males often attacked females that mated with other males.

That females mainly gave copulation calls when mating high-ranking males can be explained in two different ways. Firstly, it is possible that females of mangabeys give copulation calls to promote paternity of these males by advertising their interest in mating with high-ranking males or to synchronise orgasm with the preferred male (Hamilton and Arrowood 1978) and, therefore, promote the sperm transfer up the reproductive track which aids conception (Fox and Fox 1971). Secondly, when a high-ranking male was in the proximity of a female mating with a migrating male or low-ranking male, he would attack them, and this risk may, therefore, explain why females only rarely gave copulation calls when mating these males.

Resident males are more aggressive to females than migrating males who, at the other hand, attack juveniles more often, which could probably lead to infanticide (Dr. W. Olupot, personal communication). Therefore, sexual interaction with more than one male may reduce aggression from migrating males to her juveniles, as a result of confused

paternity (van Noordwijk and van Schaik 2000), but may increase aggression from high-ranking males.

It is also interesting that mainly high-ranking males provided infant care, and those males were most successful at obtaining matings. Similarly, female baboons may preferentially mate with males who invest most in parental care (Bercovitch 1991). It is possible that caretakers are more likely to be fathers based on their general mating success (as high-ranking males) and, although females mate with many partners, males may even recognise their own infants (Buchan et al. 2003), and thus this care could be regarded as paternal investment in offspring rather than a tactic to obtain more matings.

In mangabeys in Kibale, mate choice was mainly indicated by more than half of the matings being initiated by females and almost 60% of male approaches being refused by peak females. Female sexual behaviour depended on oestrus phase (number of partners, proportion of male categories presented to and mated with) and male tactic in the group.

Females mated mainly with high-ranking males, and that can be explained by monopolisation by these males (mate guarding), their aggression towards females, female preference based on 'the best male' or infant care. However, females also mated with migrating males and lower ranking males despite efforts of the high-ranking male to monopolise matings. This can be explained by attractiveness towards novel males (possibly to avoid inbreeding) or as a tactic to avoid their aggression towards juveniles. Female sexual behaviour in grey-cheeked mangabeys changes with oestrus phase and may therefore serve different functions at different times of the female reproductive cycle. These results indicate that female choice has an important role in shaping mating systems in multi-male and multi-female groups.

Acknowledgements We thank Prof Lynne Isbell and Dr Mark Grote for their valuable comments on the manuscript and statistical advices. We are grateful to William Olupot for allowing us to build on his work and use his telemetry system. We thank the Uganda National Council of Science and Technology, Uganda Wildlife Authority and Makerere University Biological Field Station for permission to conduct the research. Many thanks to John Rusoke, Richard Kaserengenyu, Clovis Kaganzi and Michał Ścinski for their invaluable help in the field. The research was made possible by financial support from the Polish Committee of Science, KBN Grant 6 PO4C 014 19 PB1125/PO4/2000/19 to Prof. K. Kaczanowski. The research complies with the current laws of Uganda.

References

- Altmann J, Alberts SC, Haines SA, Dubach J, Muruthi P, Coote T, Geffen E, Cheesman DJ, Mututua RS, Saiyalel SN, Wayne RK, Lacy RC, Bruford MW (1996) Behavior predicts genetic structure in a wild primate group. *Proc Natl Acad Sci U S A* 93:5797–5801

- Andersson M (1994) Sexual selection. Princeton University Press, Princeton, NJ
- Berard JD, Nurnberg P, Epplen JT, Schmidtke J (1994) Alternative reproductive tactics and reproductive success in male rhesus macaques. *Behaviour* 129:177–201
- Bercovitch FB (1991) Mate selection, consortship formation and reproductive tactics in adult savanna baboons. *Primates* 32:437–452
- Bercovitch FB (1995) Female cooperation, consortship maintenance, and male mating success in savanna baboons. *anim behav* 50:137–149
- Bercovitch FB (1997) Reproductive strategies of rhesus macaques. *Primates* 38:247–263
- Bercovitch FB, Nurnberg P (1997) Genetic determination of paternity and variation in male reproductive success in two populations of rhesus macaques. *Electrophoresis* 18:1701–1705
- Buchan JC, Alberts SC, Silk JB, Altman J (2003) True paternal care in a multi-male primate society. *Nature* 425:179–181
- Buss D (1994) The evolution of desire. Strategies of human mating. Basic Books, New York
- Chalmers NR (1968) The social behavior of free living mangabeys in Uganda. *Folia Primatol* 8:263–281
- Chalmers NR, Rowell TE (1971) Behavior and female reproductive cycles in a captive group of mangabeys. *Folia Primatol* 14:1–14
- Chapman CA, Lambert JE (2000) Habitat alteration and the conservation of African primates: a case study of Kibale National Park, Uganda. *Am J Primatol* 50:169–186
- Clutton-Brock TH, Harvey PH (1976) Evolutionary rules and primate societies. In: Bateson PPG, Hinde RA (eds) *Growing points in ethology*. Cambridge University Press, Cambridge, pp 195–237
- Danjou MC (1972) Contribution à l'Etude du Comportement Sexuel de *Cercocebus albigena*. Unpublished thesis, Université de Rennes, France
- Darwin C (1859) On the origin of species by means of natural selection. Murray, London
- De Waal FBM (1987) Dynamics of social relationships. In: Hinde RA (ed) *Primate social relationships*. Blackwell, Oxford, pp 112–116
- Deputte B (1991) Reproductive parameters of captive grey-cheeked mangabeys. *Folia Primatol* 57:57–69
- Dixon AF (1998) Primate sexuality. Comparative studies of the prosimians, monkeys, apes and human beings. Oxford University Press, Oxford
- Dixon AF, Bossi T, Wickings EJ (1993) Male dominance and genetically determined reproductive success in the mandrill. *Primates* 34:525–532
- Domb LG, Pagel M (2001) Sexual swellings advertise female quality in baboons. *Nature* 410:204–206
- Emery MA, Whitten PL (2003) Size of sexual swellings reflects ovarian function in chimpanzees (*Pan troglodytes*). *Behav Ecol Sociobiol* 54:340–351
- Fietz J, Zischler H, Schwegk C, Tomiuk J, Dausmann KH, Ganzhorn JU (2000) High rates of extra-pair young in the pair-living fat-tailed dwarf lemur, *Cheirogaleus medius*. *Behav Ecol Sociobiol* 49:8–17
- Fox CA, Fox B (1971) A comparative study of coital physiology with special reference to the sexual climax. *J Reprod Fertil* 24:319–336
- Gagneux P, Woodruff DS, Boesch C (1997) Furtive mating in female chimpanzees. *Nature* 387:358–359
- Gowaty PA (1997) Sexual dialectics, sexual selection and variation in mating behavior. In: Gowaty PA (ed) *Feminism and evolutionary biology: boundaries, intersections, and frontiers*. Chapman and Hall, New York, pp 351–384
- Gust DA, McCaster T, Gordon TP, Gergits W, Casna N, McLure HM (1998) Paternity in sooty mangabeys. *Int J Primatol* 19:83–94
- Hamilton WJ III, Arrowood PC (1978) Copulation vocalisations of chacma baboons (*Papio ursinus*), gibbons (*Hylobates hoolock*) and humans. *Science* 200:1405–1409
- Henzi SP (1996) Copulation calls and paternity in chacma baboons. *Anim Behav* 51:233–234
- Hrdy SB, Whitten PL (1987) Patterning of sexual activity. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, (eds). *Primate societies*. Chicago University Press, Chicago, pp 370–384
- Huffman MA (1991) Mate selection and partner preferences in female Japanese macaques. In: Fedigan LM, Asquith PJ (eds) *The monkeys of Arashiyama. thirty-five years of research in Japan and in the West*. SUNY, New York, pp 101–116
- Keddy-Hector AC (1992) Mate choice in non-human primates. *Am Zool* 32:62–70
- Launhardt K, Borries C, Hardt C, Epplen JT, Winkler P (2001) Paternity analysis of alternative male reproductive routes among the langurs (*Semnopithecus entellus*) of Ramnagar. *Anim Behav* 61:53–64
- Maestripieri D, Roney JR (2005) Primate copulation calls and postcopulatory female choice. *Behav Ecol* 16:106–113
- Manson JH (1992) Measuring female mate choice in Cajo Santiago rhesus macaques. *Anim Behav* 44:405–416
- Manson JH (1994) Male aggression: a cost of female mate choice in Cajo Santiago rhesus macaques. *Anim Behav* 48:473–475
- Nunn CL (1999) The evolution of exaggerated sexual swellings in primates and the graded-signal hypothesis. *Anim Behav* 58:229–246
- O'Connell SM, Cowlshaw G (1994) Infanticide avoidance, sperm competition and mate choice: the function of copulation calls in female baboons. *Anim Behav* 48:687–694
- Olupot W (1999) Mangabey dispersal and conservation in Kibale Forest National Park, Uganda. Ph.D. thesis, Purdue University, USA
- Olupot W, Waser, PM (2001) Correlates of intra-group transfer in male grey-cheeked mangabeys. *Int J Primatol* 22:169–187
- Pagel M (1994) The evolution of conspicuous oestrus advertisement in Old World monkeys. *Anim Behav* 47:1333–1341
- Palombit RA, Seyfarth RM, Cheney DL (1997) The adaptive value of 'friendships' to female baboons: experimental and observational evidence. *Anim Behav* 54:599–614
- Paul A (2002) Sexual selection and mate choice. *Int J Primatol* 23:877–904
- Pusey A, Wolf M (1996) Inbreeding avoidance in animals. *TREE* 11:201–206
- Rowell TE, Chalmers NR (1970) Reproductive cycles of the mangabey *Cercocebus albigena*. *Folia Primatol* 12:264–272
- Semple S, McComb K (2000) Perception of female reproductive state from vocal cues in a mammal species. *Proc R Soc Lond Ser Biol Scie* 267(1444):707–712
- Small MF (1989) Female choice in nonhuman primates. *Yearb Phys Anthropol* 32:103–127
- Smuts BB (1983) Dynamics of 'special relationships' between adult male and female olive baboons. In: Hinde RA (ed) *Primate social relationships*. Blackwell, Oxford, pp 112–116
- Smuts BB (1985) Sex and friendship in baboons. Aldine, New York
- Smuts BB (1987) Sexual competition and mate choice. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) *Primate societies*. University of Chicago Press, Chicago, pp 385–399
- Smuts BB, Smuts R (1993) Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. *Adv Study Behav* 22:1–63
- Soltis J, Thomsen R, Takenaka O (2001) The interaction of male and female reproductive strategies and paternity in wild Japanese macaques, *Macaca fuscata*. *Anim Behav* 62:485–494

- Struhsaker TT, Leyland L (1979) Socioecology of five sympatric monkey species in the Kibale Forest, Uganda. *Adv Study Behav* 9:159–228
- Troisi A, Carosi M (1998) Female orgasm rate increases with male dominance in Japanese macaques. *Anim Behav* 56:1261–1266
- Van Noordwijk MA, van Schaik CP (2000) Reproductive patterns in eutherian mammals: Adaptations against infanticide? In: Van Schaik CP, Janson CH (eds) *Infanticide by males and its consequences*. Cambridge University Press, Cambridge, pp 332–360
- Van Schaik CP, Hodges JK, Nunn CL (2000) Paternity confusion and the ovarian cycles of female primates. In: Van Schaik CP, Janson CH (eds) *Infanticide by males and its consequences*. Cambridge University Press, Cambridge, pp 361–387
- Wallis SJ (1979) The sociology of *Cercocebus albigena johnstonii* (Lydekker). An arboreal, rain forest monkey. Ph.D. thesis, University of London, London
- Wallis SJ (1983) Sexual behavior and reproduction of *Cercocebus albigena johnstoni* in Kibale Forest, western Uganda. *Int J Primatol* 4:153–166
- Waser PM (1977) Feeding, ranging and group size in the mangabey *Cercocebus albigena johnstoni* in Kibale Forest, Western Uganda. *Int J Primatol* 4:153–166
- Zinner D, Alberts SC, Nunn CL, Altmann J (2002) Significance of primate sexual swelling. *Nature* 420:142