



Male mating behaviour in relation to female sexual swellings, socio-sexual behaviour and hormonal changes in wild Barbary macaques

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ABSTRACT

In many cercopithecine primates females display probabilistic cues of fertility to indicate the periovulatory period to males. These cues may include female behaviour, acoustic signals, and morphological signs such as the anogenital swelling. However, the extent to which males can utilise this information varies between species. We describe male sexual behaviour in relation to changes in anogenital swelling size, timing of ovulation and female socio-sexual behaviour in wild Barbary macaques (*Macaca sylvanus*). We further compare male sexual behaviour during conception and post-conception cycles to evaluate if males differentiate between these qualitatively different cycle types. Our results show that during conception cycles male mating behaviour was concentrated around the fertile phase implying that males inferred information from more than swelling size alone. Male mating frequency increased in line with female socio-sexual behaviour, namely female presenting and the frequency of copulations with copulation calls. Most strikingly our results show that males invested equally in mating during fertile and non-fertile, i.e. post-conception, maximum swelling phases. Whether post-conception swellings were merely a result of changes in hormone concentrations during pregnancy or part of a female reproductive strategy remains elusive. In sum, this study adds to the body of research on the evolution of female sexual signals and how males may infer information from these cues.

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Introduction

In most mammalian species females are only sexually receptive around the time of ovulation, the period when conception is possible (McCarthy and Becker, 2002). Females may indicate this period by behavioural, visual, olfactory, vocal or tactile cues to males (Lisk et al., 1983; Rasmussen and Schulte, 1998; Sherman, 1989; Swaisgood et al., 2002; Westlin, 1996). Many female primates differ from this general mammalian trend by having a prolonged period of receptivity which extends beyond the fertile phase (Aujard et al., 1998; Bielert and Anderson, 1985; Carnegie et al., 2005; Deschner et al., 2004; Engelhardt et al., 2004; for review see Hrdy and Whitten, 1987) and even into gestation (Engelhardt et al., 2007; Fürtbauer et al., 2011; Lu et al., 2012; Ostner et al., 2006). It has been proposed that females use this extended receptivity to both confuse and concentrate mating activity in order to reduce the future risk of infanticide by males (van Schaik et al., 2000). In this study, we investigate male sexual behaviour in relation to changes in female anogenital swelling size, timing

of ovulation and female socio-sexual behaviour in Barbary macaques (*Macaca sylvanus*), a species with prominent sexual swellings.

Anogenital sexual swellings may function as part of a female strategy to balance paternity confusion and concentration in primates living in multi-male multi-female groups (van Schaik et al., 2000). Sexual swellings may act as probabilistic visual cues to males of the timing of ovulation, reaching maximum size around ovulation (Brauch et al., 2007; Deschner et al., 2003; Higham et al., 2008b; Reichert et al., 2002; for review see Dixon, 1998; Nunn, 1999; Nunn and Altizer, 2004). By signalling to males the most likely time of ovulation, females enable dominant males to concentrate their efforts around this most important period, while still confusing paternity and mating with multiple males at smaller swelling stages when ovulation is less likely but still possible (Nunn et al., 2001). Across several anthropoid taxa such as baboons (Higham et al., 2009), mandrills (Setchell et al., 2005), macaques (Engelhardt et al., 2004; Higham et al., 2012; O'Neill et al., 2004), and apes (Barelli et al., 2008; Deschner et al., 2003; Emery and Whitten, 2003) ovulation occurs during maximum swelling (but see Shelmidine et al., 2007). However, whether males hone further information from more subtle changes in swelling size (Deschner et al., 2004; Higham et al., 2009), olfactory cues around ovulation (Cerdeña-Molina et al., 2006) or female

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proceptive behaviour (Aujard et al., 1998; Engelhardt et al., 2005; Wallen et al., 1984; Zehr et al., 1998, 2000) to infer when to concentrate mating varies between species.

In macaques, female proceptive behaviour has been shown to vary during the reproductive cycle and may thus be used by males as a cue to discern the fertile phase. Several studies have shown that the expression of female proceptive behaviours, such as approaching, soliciting and presenting to males is strongly related to changes in oestrogen levels and increase in frequency around the fertile phase (Aujard et al., 1998; Wallen et al., 1984; Zehr et al., 1998, 2000). Further research has shown that female sexual behaviour and motivation may be influenced by the social environment; in rhesus macaques, *M. mulatta*, for example, social group composition (differing male and female composition) influenced how closely related copulation rates were to female reproductive state (Wallen, 2001). The social and environmental conditions of primates can therefore influence sexual behaviour so research under natural conditions can build on previous studies under a more controlled environment.

Mating activity in numerous primate species continues into gestation and a few species even exhibit additional sexual swellings during this post-conception, i.e. non-fertile, period, which may serve as an additional mechanism of females to further confuse paternity and decrease the risk of infanticide (van Schaik et al., 2000, 2004). One of these species is the Barbary macaque, where females show exaggerated swellings both during fertile as well as post-conception phases (Brauch et al., 2007; Küster and Paul, 1984; Möhle et al., 2005). Both swelling types follow similar underlying endocrine changes, particularly an increase in the oestrogen to progesterone ratio (E/P ratio) coinciding with the occurrence of the maximum swelling (Möhle et al., 2005). To date few studies have looked into the function of post-conception swellings and male sexual behaviour in relation to these additional swelling phases in this or other species (Engelhardt et al., 2007; Gordon et al., 1991; Gust, 1994).

The aim of this study was two-fold. We firstly aimed to investigate how male Barbary macaques change their sexual behaviours in relation to females' timing of ovulation, changes in swelling size and socio-sexual behaviour. Secondly, we examined whether males differentiate between qualitatively different swelling types by comparing the frequency of male behaviour during conception and post-conception swelling phases. In order to provide the context for these analyses we describe how female sexual swelling size is related to her hormonally assessed fertile phase.

Methods

Study site and subjects

Data were collected from two wild, unprovisioned groups ("Green" (Gn) and "Scarlet" (Sc)) of Barbary macaques living in a deciduous cedar and oak forest in the Middle-Atlas Mountains of Morocco (33°24'9N–005°12'9W). The groups consisted of 7–9 adult males and 8 adult females (Gn) and 6 males and 8 females (Sc), respectively. Data were collected on the Green group from Oct. 2009–Apr. 2011, data here represent the mating seasons Oct.–Dec. 2009 (Gn09) and Sept.–Dec. 2010 (Gn10). Data on the Scarlet group were collected from Jul. 2010–Apr. 2011, data here represent the mating season Sept.–Dec. 2010 (Sc10). The mating season was defined as the first to last observed ejaculatory copulation during either focal or ad libitum data collection. This study adhered to the legal requirements of Morocco, Germany and Great Britain.

Behavioural data collection and construction of the hierarchy

Behavioural data were collected by CY and 5 field assistants from 0700 to 1900 h. All adult males in both groups were subject to continuous focal animal observation of social and sexual behaviour (Altmann,

1974), yielding a total of 820 focal hours during the mating seasons (341 h Gn09, 304 h Gn10 and 175 h Sc10). Data were collected using handheld HP iPAQ 114 series pocket PCs loaded with Pendragon Forms Version 5.1 (© Pendragon Software Cooperation, U.S.A.). Focal sampling was randomised within groups and one 40-min focal session per male was recorded per observation day so as to give an even number of focal sessions per individual.

Ejaculatory copulations were recorded and indicated by the occurrence of an ejaculatory pause in pelvic thrusts (Küster and Paul, 1984) and/or the presence of fresh ejaculate around the female's genital area after the copulation. Male inspection (tactile, olfactory or visual) of female's anogenital region as well as female "presenting" behaviour (female presents anogenital region to male; "presenting", Brauch et al., 2007), was also recorded. During ejaculatory copulations the following female socio-sexual behaviours were recorded: the female reaches back to the male during copulation ("reach back", Deag, 1974), female looks back at the male during copulation ("look back"), and female vocalizations during copulation ("copulation call", Semple, 1998).

Agonistic interactions or conflicts were defined by the occurrence of aggressive (bite, chase, slap, grab, stare, open-mouth, head-bob and charge) and/or submissive behaviours (give-ground, make-room, flee, crouch submission). In total 1238 (Gn) and 195 (Sc) male–male dyadic conflicts were observed where a clear winner and loser of a conflict could be determined with no counter-aggression. Based on this, a winner–loser matrix was constructed and a male's dominance rank was assessed using corrected Normalized David's Scores (de Vries et al., 2006) to give a continuous measure of dominance. We used the "Steepness" package (Leiva and de Vries, 2011) in R 2.14.0 (R Development Core Team, 2011) based on a matrix of proportions of wins calculated for each dyad.

Faecal sample collection, hormone analysis and definition of the fertile phase

Faecal samples of all adult females of the study groups were collected within 15 min of defecation to assess timing of ovulation (N = 1066 samples). Samples were collected for each female when the anogenital swelling began to increase in size towards maximum swelling, throughout the maximum swelling period and 10 days after detumescence. Samples were homogenized and a 3–5 g piece was placed in a polypropylene vial, which was in-turn placed in an ice bag and kept cold until samples were transferred to a freezer at –20 °C at the end of the day. Samples were transferred in a frozen state to the German Primate Centre for hormonal analysis. Samples were freeze-dried, pulverized and an aliquot of 0.05–0.08 g was extracted with 3 ml 80% methanol in water according to the method reported by Heistermann et al. (1995). Extracts were analysed for concentrations of immunoreactive progesterone metabolites (5 α -reduced-20-oxo pregnanes, 5-P-3OH) using a previously validated enzyme immunoassay (EIA) (Brauch et al., 2007; Heistermann et al., 2008; Möhle et al., 2005) and according to procedures previously described by Hodges et al. (1997). Intra- and inter-assay coefficients of variation, calculated from replicate determinations of high- and low-value quality controls, were 5.8% and 11.5% (high) and 8.8% and 13.9% (low), respectively.

For the two groups and three mating seasons we were able to analyse 23 cycles. However, analysis of behavioural data was restricted to those cycles in which the frequency of faecal sample collection was sufficiently high (sample gap of no greater than 3 days before post-ovulatory progesterone rise) to allow the estimation of the day of ovulation to an acceptable level of precision (see Dubuc et al., 2011; Heistermann et al., 2008). This gave a total 155 samples from 12 cycles from 10 different females for analysis. The fertile period was determined for each cycle, as previously described by Heistermann et al. (2008). Specifically, a defined rise in faecal 5-P-3OH levels above a threshold value (2 SDs above the preceding mean baseline level) was

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