

Mechanisms of sexual selection: Sexual swellings and estrogen concentrations as fertility indicators and cues for male consort decisions in wild baboons

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Abstract

Male mate-guarding episodes ('consortships'), are taxonomically widespread, yet costly to individual males. Consequently, males should bias consortships toward females with whom the probability of conception is high. We combined data on consortships with visual scoring of sexual swellings and assays of fecal estrogen concentrations (fE) in a wild population of baboons (*Papio cynocephalus*) to test the hypotheses that sexual swellings are reliable indicators of (1) within-cycle timing of ovulation, (2) differences in conception probability among females that differ in maturational stage, and (3) conceptive versus non-conceptive cycles of parous females. We also evaluated whether adult males might rely on swellings or other estrogen-dependent signals (e.g., fE) for mate-guarding decisions. We found that sexual swellings reflected conception probability within and among cycles. Adult males limited their consortships to the turgescent phase of cycles, and consorted more with adult females than with newly cycling adolescents. The highest ranking (alpha) males discriminated more than did males of other ranks; they (1) limited their consortships to the 5-day peri-ovulatory period, (2) consorted more with adult than with adolescent females, and (3) consorted more with adult females on conceptive cycles than on non-conceptive cycles, all to a greater extent than did males of other ranks. Male mate choice based on sexual swellings and other estrogenic cues of fertility may result in sexual selection on these female traits and enhance dominance-based reproductive skew in males. Alpha males are the least constrained in their mating behavior and can best take advantage of these cues to mate selectively.

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Introduction

Both pre- and post-copulatory mate guarding are widespread across animal taxa, conferring mating and paternity advantage, but often imposing costs in terms of energetic expenditure, time, feeding opportunities, or direct survival risks (Alberts et al., 1996; Alcock, 1994; Bercovitch, 1983; Clutton-Brock et al., 1982; Ellis, 1995; Low, 2006; Packer, 1979). Among many primate species, including baboons, *Papio cynocephalus*, mate

guarding takes the form of "sexual consortships", extended periods of guarding that last from several hours to several days or even weeks. During consortships males follow, groom and maintain close proximity to an estrous female, threatening other males who approach her and monopolizing mating (e.g., Bercovitch, 1987; Hausfater, 1975; van Noordwijk, 1985; Packer, 1979; Saayman, 1970; Setchell et al., 2005; Tutin, 1979). By so doing, males experience an increased chance of fathering offspring (Alberts et al., in press; Altmann et al., 1996; Buchan et al., 2003; Setchell et al., 2005).

Because mate guarding imposes costs on male primates (Alberts et al., 1996; Packer, 1979; Rasmussen, 1985), males

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may not have the energy to engage in mate guarding continuously without rests. This is particularly true if cycling females are continuously available for extended periods, as they are in species such as baboons, chimpanzees, and humans that are not seasonal in their mating (Bercovitch, 1988). When faced with such constraints, adult males are predicted to be discriminating in mate guarding decisions. In particular, males are predicted to discriminate among females based on fertility differences (1) within female reproductive cycles (based on the timing of the mating opportunity relative to ovulation), (2) between females in their fertility (if fertility changes with age, for instance), and (3) between cycles of a given female (if differences in fertility are a function of how old her current infant is, for instance) (Bercovitch, 2001; Domb and Pagel, 2001; Pagel, 1994; Zinner et al., 2002). However, not all males are predicted to discriminate to the same extent. In particular, in a number of primates, including baboons, male mating success is dominance rank-based, so that high ranking males achieve the highest mating success (Altmann, 1962; Bulger, 1993; Cowlishaw and Dunbar, 1991; Pope, 1990; de Ruiter and van Hooff, 1993; de Ruiter et al., 1994; Weingrill et al., 2000). When this occurs, the highest ranking male in a group (the alpha male) is predicted to be the least constrained by male–male competition, and hence the one most likely to exhibit fertility-based mate choice.

Data are available to evaluate some of these predictions in a number of primate species. First, in several species adult males were most likely to consort on days when conception was most probable (Aujard et al., 1998; Bercovitch, 1986, 1987; Bulger, 1993; Deschner et al., 2004; Engelhardt et al., 2004; Hausfater, 1975; Packer, 1979; de Ruiter et al., 1994; Setchell et al., 2005). Second, males of several primate species exhibited discrimination among females of different age classes by ignoring newly cycling adolescent females (who are unlikely to conceive in the first few cycles after menarche) even though these females solicited matings at high levels (reviewed in Anderson, 1986; see also Perry and Manson, 1995; Thierry et al., 1996). Finally, alpha males discriminated between the conceptive and non-conceptive cycles of fully adult females at least under some conditions (Alberts et al., in press; Bulger, 1993; Deschner et al., 2004; Setchell et al., 2005; Weingrill et al., 2003).

What information is available to males to make these mating decisions and how reliable is this information? Three potentially important proximate cues – behavioral, visual (specifically sexual skin swellings) and olfactory – have been proposed. In this study, we focus on fecal estrogen concentrations, which may be involved in producing such cues, and on swelling size as one potential specific cue. Estrogens not only are implicated in the development of sexual swellings (Gillman, 1937, 1942), they also have an important role in the production of olfactory cues (Goldfoot, 1981; Michael et al., 1971, 1974; Singh and Bronstad, 2001) and in female sexual behavior (Aujard et al., 1998; Engelhardt et al., 2005; O'Neill et al., 2004; Saayman, 1970; reviewed in Dixson, 1998, Chapter 12). In particular, we seek to clarify whether sexual swellings and fecal estrogen concentrations provide reliable indicators of fertility in female baboons, and to evaluate the extent to which adult males seem

to rely on swelling size or on other estrogen-dependant cues to make decisions as to whether to consort with a female.

Turgescence of the primate sexual skin is induced by increasing estrogen concentrations, whereas deturgescence is stimulated by declining estrogen and increasing progesterone concentrations (Carlisle et al., 1981; Gillman, 1937, 1940, 1942; Gillman and Gilbert, 1946; Gillman and Stein, 1941; Onouchi and Kato, 1983; Ozasa and Gould, 1982, 1984; West et al., 1990). Based on laboratory experiments, the prominent swellings of baboons are considered to be a relatively good indicator of the timing of ovulation within cycles (Shaikh et al., 1982; Wildt et al., 1977). Furthermore, male baboons become sexually aroused in response to the sight of sexual swellings (Bielert and Girolami, 1986; Bielert et al., 1989; Girolami and Bielert, 1987; reviewed in Snowdon, 2004). Males may, therefore, attend closely to swelling size and use it to choose the best time of the cycle to consort (Bercovitch, 1987, 1999; Bulger, 1993; Hausfater, 1975; Hendrickx and Kraemer, 1969; Packer, 1979). Less clear is whether differences in swelling size among cycles can indicate differences in conception probability and thereby provide a cue that males could use to make individual or cycle-to-cycle mating decisions (Bercovitch, 1987, 1999; Domb and Pagel, 2001; Emery and Whitten, 2003; Nunn et al., 2001; Scott, 1984; Setchell and Wickings, 2004; Zinner et al., 2002).

In the present investigation, we measured the frequency of male mate guarding (i.e., male consortship activity) as a function of fecal estrogen (fE) concentrations and of swelling turgescence and size in a population of wild baboons, *P. cynocephalus*. We sought to identify differences across the menstrual cycle, between cycles of adolescent and adult females, and between conceptive and non-conceptive cycles of adult females. That is, we tested both for increasingly fine differences in swelling size and estrogen concentrations and for increasingly challenging mate choice by males. In testing male mate choice, we analyzed data on mate guarding by the alpha male separately from that by other males, because of the prediction that alpha males are the least constrained in their mating decisions (see above; see also Alberts et al., in press; Bulger, 1993; Deschner et al., 2004; Setchell et al., 2005; Weingrill et al., 2003).

Methods

Field site and subjects

Subjects were the individually identified members of five social groups in the Amboseli baboon population that has been monitored for reproductive, demographic, and behavioral events on a near-daily basis over three decades (e.g., Alberts and Altmann, 1995a,b; Altmann and Alberts, 2003; Altmann et al., 1988; Hausfater, 1975; Noë and Sluiter, 1990; Shopland, 1987). Since December 1999, physiological data have been obtained through non-invasive collection of freshly deposited feces from known individuals and subsequent analysis of steroid hormones extracted from the feces.

For this study we used all data for cycling females from late 1999 through 2004. The records included swelling size and consortships for a total of 1139 ovarian cycles, corresponding to 104 females. For a subset of those females and cycles we also had fecal samples, from which we determined fE concentrations (422 cycles, 88 females). We excluded data from one sterile adult female and one very old female (26–27 years old), both of whom had abnormally small

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