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Baboons eavesdrop to deduce mating opportunities

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Many animals appear to monitor changes in other individuals' dominance ranks and social relationships and to track changes in them. However, it is not known whether they also track changes in very transient relationships. Rapid recognition of a temporary separation between a dominant male and a sexually receptive female, for example, should be adaptive in species where subordinate males use opportunistic strategies to achieve mating success. Dominant male baboons (*Papio hamadryas ursinus*) form sexual consortships with oestrous females that are characterized by mate guarding and close proximity. To assess whether subordinate males track temporary changes in the status of other males' consortships, we conducted playback experiments using a two-speaker paradigm. In the test condition, subjects heard the consort male's grunts played from one speaker and his consort female's copulation call played from a speaker approximately 40 m away. This sequence suggested that the male and female had temporarily separated and that the female was mating with another male. In a control trial, subjects heard another dominant male's grunts played from one speaker and the female's copulation call played from the other. In a second control trial, conducted within 24 h after the consortship had ended, subjects again heard the consort male's grunt and the female's copulation call played from separate speakers. As predicted, subjects responded strongly only in the test condition. Eavesdropping upon the temporal and spatial juxtaposition of other individuals' vocalizations may be one strategy by which male baboons achieve sneaky matings.

Keywords: baboon; cognition; eavesdropping; extrapair copulation; mate guarding; *Papio hamadryas ursinus*; primate; social intelligence; third-party relationships; transient relationships

Males living in multimale social groups often form linear dominance hierarchies characterized by strong reproductive skew. Although dominant males typically monopolize matings, subordinate males can achieve mating success by copulating surreptitiously, or 'sneakily', undetected by higher-ranking males (Parker 1990; reviewed in: Gross 1996; Kappeler & van Schaik 2004). To take advantage of the brief occasions for 'sneaky' matings, however, subordinate males must monitor the status of dominant males' proximity to females and note precisely whether and when they become temporarily separated.

Like males in other primate species that live in multimale groups, male baboons form linear dominance hierarchies in which the highest-ranking, or alpha, male usually accounts for most copulations (Hausfater 1975; Bulger 1993; Alberts et al. 2003). When a female comes into oestrus, she often forms a 'consortship' with the highest-ranking male, who follows her closely and guards her against the approaches of other males. Such consortships can last from a few hours to as long as a week. If two or more females are in oestrus simultaneously, other males may also be able to form consortships, according to their relative ranks (Alberts et al. 2003). Otherwise, lower-ranking males achieve mating success only if they can form a new consortship with the female soon after the dominant male has abandoned her or by mating sneakily with the female if the pair temporarily separates.

Consortships are transient in both time and occurrence. Whereas male and female baboons always occupy a specific, if variable, position in a dominance hierarchy, their consort status may change from one hour to the next. In addition, males and oestrous females do not always form consortships, and the same individual may form several, sequential consortships with different partners in the same week. To maximize their mating success, it behoves subordinate males to monitor the consort status of others, because the existence (or lack) of a consortship determines access to receptive females (Bulger 1993; Alberts et al. 2003). Given what is already

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known about baboons' ability to recognize other individuals' long-term social relationships (reviewed by Cheney & Seyfarth 2007), it seems likely that males also recognize the status of other males' transient consortships.

Observational data suggest that subordinate males monitor the status of consortships on an almost minute-by-minute basis. Lower-ranking males often take over an oestrous female within minutes after a higher-ranking male has ceased consorting with her, suggesting that they are quick to observe changes in consort status. Similarly, when a consorting pair temporarily separates, subordinate males often attempt to mate sneakily with the female, again suggesting that the subordinates keep assiduous track of consort pairs. In the absence of experimental evidence, however, it is impossible to determine how precisely males track changes in consort relationships.

Female baboons develop sexual swellings that reach their maximum size around the time of ovulation (Dixson 1998), and they utter loud, distinctive 'copulation calls' when mating that vary acoustically according to swelling size (Semple et al. 2002). It is not difficult, therefore, to determine when a female is sexually receptive. However, not all sexually receptive females form consortships, and no single behavioural measure defines a consort relationship. Consorting males and females maintain close proximity to each other and engage in frequent grooming interactions, but consortships are not the only relationships between males and females that are defined by close proximity. Male baboons also form close 'friendships' with lactating females as an apparent response against the threat of infanticide (Palombit et al. 1997). These friendships, too, are characterized by close spatial proximity and grooming. Furthermore, a large proportion of mating occurs outside consortships, when oestrous females are not consistently in close proximity to any particular male. As a result, baboons must take note of a suite of behaviours to track a sexual consortship.

We conducted a playback experiment designed to test whether free-ranging male baboons track changes in the status of highly transient sexual consortships, and how rapidly they might recognize the chance for a sneaky mating. Subordinate male subjects were played a dominant male's grunts from one loudspeaker and his consort female's copulation call from another, spatially separated speaker. Trials were conducted both during the dominant male's consortship and as soon as possible after the consortship had ended. Based on the hypothesis that males keep track of the consort status of other males in order to take advantage of mating opportunities, we predicted that subjects would respond most strongly to call sequences suggesting that the female had temporarily separated from her consort and was mating with another male.

METHODS

Study Area and Subjects

The study was conducted on a troop of free-ranging chacma baboons, *Papio hamadryas ursinus*, in the Moremi Game Reserve in the Okavango Delta of Botswana. The study group's habitat consists of seasonal flood plains interspersed with small 'islands' (Bulger & Hamilton 1987; Cheney et al. 2004). The group has been observed since 1978 and all animals are fully habituated to human observers on foot. At the time of these experiments (January–October 2005), the group contained approximately 70 individuals, including 21–26 adult females, 5–10 adult males, 4–5 adolescent males, 2–9 adolescent females and 21–40 juveniles and infants. Experimental subjects were five adult males (>9 years) and four adolescent males (>7 years). Dominance ranks were determined by the outcome of aggressive and approach–retreat interactions (supplants) (Bulger 1993; Kitchen et al. 2003). All subjects were relatively subordinate individuals who might be expected to attempt to take over a consortship after a dominant male had abandoned it, or to mate sneakily with a female during an ongoing consortship.

Sexual consortships involve male mate-guarding of a female whose sexual swelling is maximally tumescent. We defined a male as being in consort with a particular female when he: mated, or attempted to mate, at least once an hour with her; looked repeatedly towards her; followed her if she moved away; demonstrated urgent searching behaviour if she moved out of sight (including standing bipedally and running in the direction where she was last seen); and threatened or chased other males who approached or were approached by the female (Hausfater 1975). In this population, consortships lasted from several hours to several days, with the male aggressively excluding the mating attempts, and even approaches, of other males. For the purposes of these experiments, we excluded consortships that lasted less than 24 h. Subjects were tested during and after consortships that lasted 2–8 days ($\overline{X} \pm \mathrm{SE} = 6 \pm 0.75$ days).

We determined that a consortship had ended as soon as we saw the female either being followed by or mating with another male without any intervention by the consort male, or feeding or moving out of sight of her recent consort for more than 1 min.

Playback Stimuli

Playback sequences consisted of male grunts followed by a female copulation call. Male grunts are low-amplitude, tonal vocalizations with a rich formant structure (Owren et al. 1997) that are given by males in friendly interactions with other males or females (Palombit et al. 1999). Males often grunt to females before or soon after mating with them. Playback experiments have shown that grunts are individually distinctive (Cheney & Seyfarth 1997; Rendall et al. 1999). Female copulation calls are loud, highly distinctive, and almost always produced in the context of copulating. They are tonal, rhythmic, multisyllabic vocalizations, usually starting with long units produced at a slow rate and speeding up towards the end of the call. Like grunts, copulation calls contain sufficient acoustic information to enable individual identification of signallers (Hamilton & Arrowood 1978; Todt et al. 1995; Semple 2001).