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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.

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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).

Playback stimuli consisted of the grunts of five consorting males, three nonconsorting males and four consorting females. Calls used as playback stimuli were recorded opportunistically from known individuals using Sennheisser ME88 microphones and NOMAD digital recorders. Digital sound files were saved in Wave format and used within 6 months from the time of the recording. After transferring the calls from the NOMAD digital recorder to a computer, we used CoolEdit software (Syntrillium, Phoenix, Arizona, U.S.A.) to ensure that the natural call sequences used as playback stimuli were high quality, without vocalizations from other baboons or masking background noise. For each vocalization type, playback sequences were similar in call length, bout length and call rate. They were equated for amplitude and played at an amplitude matching that of naturally occurring calls. Calls were broadcast from two Bose Roommate II loudspeakers.

Copulation calls vary considerably in rate, length and number of syllables. In Semple et al.'s (2002) study of yellow baboons, copulation calls increased in duration and number of units with increasing swelling size and rank of the consort male. Given that consortships with high-ranking males usually occur during the final week of swelling, we used copulation calls recorded during the final swelling stage as playback stimuli. Thus the copulation call playback stimuli were consistent with both the swelling phase and the rank of the consort male.

To avoid the possibility that some calls might have been more salient than others, each subject heard the same copulation call in all three conditions. Different subjects heard different copulation calls. Likewise, the same male grunt sequence was played to each subject but was not repeated for different subjects.

Experimental Protocol

The experiment followed a within-subject design, with each subject appearing in three separate trials: two while a dominant male (individual A) was engaged in a sexual consortship, and the third as soon as possible after the consortship had ended. In each case, the subject heard a series of male grunts played from one loudspeaker, followed several seconds later ($\overline{X} \pm SE = 4.7 \pm 0.5$ s) by a female's copulation call played from another, widely separated loudspeaker. From the subject's perspective, the side from which each type of call was played alternated across trials.

Call sequences were played to a previously designated subject who was sitting and either resting or eating a food item (e.g. palm nut or sausage fruit) that required extensive processing. As soon as the subject was sitting, we placed one loudspeaker 20−25 m to his left and another 20−25 m to his right at a roughly 90° orientation. Playback experiments were only initiated after establishing that the consort pair was not only out of sight but also out of earshot (i.e. >100 m away).

In the test trial, conducted during the consortship, the subject first heard the consorting male's (A's) grunts played from one speaker (speaker 1) and then his consort's copulation call played from the other (speaker 2). This sequence suggested that the male and his consort had temporarily separated, and that the female was mating with another male while her consort was engaged in a friendly interaction with another individual some distance away.

In the first control trial, also conducted during the consortship, subjects first heard the grunts of another, nonconsorting, high-ranking male (individual B) played from speaker 1 and then the same female's copulation call played from speaker 2. This sequence suggested that another male was in the general vicinity of the consort pair, a very common occurrence that is entirely consistent with an ongoing consortship. The order of playback of the test and first control trial was alternated, so that half the subjects heard the test trial first and half heard the control trial first.

The second control trial was conducted as soon as possible after the consortship had ended. In this trial, the subject again heard the recent consort's (A's) grunts from speaker 1 and the female's copulation call from speaker 2. As in the first trial, this sequence suggested that the consort male had separated from his female and that she was mating with another male. After consortships have ended, this is not an unusual occurrence. Trials in the second control condition were conducted within 24 h of the consortship's end. In four cases they were conducted within 4 h after its end. The playback design is summarized in Table 1.

We predicted that, if males monitor the status of other males' consortships, they should respond most strongly to the test trial, since sneaky matings that occur outside an ongoing consortship are rare events and therefore likely to be unexpected. Specifically, we predicted that subjects would look more often to the speaker that had played the female's copulation call in the test trial than in either of the two control trials. (It is well established that humans and other animals look longer towards stimuli that are unexpected; Cheney & Seyfarth 1990; Wang et al. 2004). On the assumption that subordinate males take advantage

Table 1. Design of the playback experiment

			Playback to subject	
Condition	Status of consortship	Simulation	Speaker 1	Speaker 2
Test	Current	Nonconsort ('sneaky') mating	Consort male's grunt	Consort female's copulation call
Control 1	Current	Consort pair copulation	Other male's grunt	Consort female's copulation call
Control 2	Ended	Nonconsort mating	Consort male's grunt	Consort female's copulation call

of the temporary separation between a male and his consort to attempt a sneaky mating, we also predicted that subjects would be more likely to approach speaker 2 in the test trial than in either of the two control trials. We expected that subjects would respond weakly to the first control trial, because it suggested that the consortship was still intact: a consort female mating with the consort male is a very predictable, regular occurrence. We also predicted that they would respond weakly to the second control trial: if subordinate male baboons monitor other males' consort status, confirmation that a male has abandoned his consort should not be unexpected.

Finally, we predicted that subjects would look for equal durations towards the loudspeaker broadcasting the males' grunts in all three conditions, because all suggested the proximity of a more dominant male (Bergman et al. 2006). Specifically, we predicted that they would look towards the speaker but not approach it. This prediction assumes that the male's grunts were only relevant because they lent significance and context to the female's copulation calls.

To minimize the possibility that the baboons might habituate to the playback stimuli, we conducted a maximum of two playback experiments daily. Playback experiments were never conducted within 2 h of each other, and the same subject never appeared in more than one playback experiment per day. All of the vocalizations used in experiments occurred naturally at high rates, and we ensured that trials using a particular call type were conducted at a rate that was less than one-tenth its naturally occurring rate. This was not the case for the test condition, which mimicked a rare sneaky mating. However, these nine test trials were conducted at a very low rate, over a 10-month period.

We used a SONY DCR-TRV25 digital video camera to record any changes in the subject's head position relative to the speaker in the 10 s before and 1 min after the playback trial. Subjects were then followed for an additional 10 min, during which time we recorded all social interactions and any approaches to either speaker.

Data Analysis

Video films were analysed using Adobe Premier software. When coding films, we measured two different responses for each speaker: number of looks towards the speaker in the first minute after playback and whether or not the subject approached the speaker. Although the number of looks has not been used as measure of response in previous experiments using a single speaker, it is a logical choice when using a two-speaker design because subjects presented with stimuli from two different directions are expected to look back and forth in both directions for as long as their interest is aroused. A 'look' was defined as a change in head orientation directly towards the speaker. Movement was only recorded as an 'approach' when it was directly towards the speaker and when it was the first move in any direction after the playback.

To determine the validity of using two behavioural responses (number of looks and approach to each speaker) as dependent measures, we conducted a bivariate correlation test between the two variables. In the correlation for each speaker, r was less than 0.7, indicating minimal likelihood of multicollinearity; thus, there was no need to exclude any variables (Tabachnick & Fidell 2001). In our analysis, we used a matched-pairs design, testing all three conditions simultaneously using a Friedman test (and a Cochran test for categorical data). If the Friedman test was significant, we conducted exact Wilcoxon matched-pairs signed-ranks tests (Mundry & Fischer 1998) and a sign test for categorical data to compare subjects' behaviour between trials (Siegel & Castellan 1988). Because our hypotheses generated clear directional predictions, we planned two comparisons, or two Wilcoxon tests, per variable: the test condition compared with each control. Since this did not exceed the number of degrees of freedom for effects, we did not need to use a post hoc correction, such as Bonferroni (Tabachnick & Fidell 2001). All tests were one tailed ($\alpha = 0.05$).

RESULTS

Responses Towards the Speaker Playing Male Grunts (Speaker 1)

Subjects' responses towards the speaker broadcasting male grunts were similar across all three conditions. Subjects did not look towards the speaker more times in the test compared with either of the control conditions (Friedman two-way ANOVA: $X_2^2 = 7.8$, $P < 0.69$; $\overline{X} \pm SE$: test: 1.9 ± 2; control 1: 1.6 ± 1.2; control 2: 1.6 ± 2.5). Furthermore, subjects rarely approached the speaker in the 10 min following playback (Cochran's Q test: $Q_2 = 1.33$, $P < 0.51$). No subjects approached the speaker in the test condition. In each of the two control conditions, only one subject did so.

Responses Towards the Speaker Playing Female Copulation Calls (Speaker 2)

Subjects responded significantly more strongly to the copulation call in the test condition than in either of the two control conditions. During the first minute following playback of the copulation call, they looked towards speaker 2 more often in the test than in the control conditions (Friedman two-way ANOVA: $X_2^2 = 14.35$, $P < 0.000$; one-tailed Wilcoxon matched-pairs signed-ranks test: test versus control 1: $T^+ = 45$, $N = 9$, 0 ties, $P < 0.002$; test versus control 2: $T^+ = 45$, $N = 9$, 0 ties, $P < 0.002$; Fig. 1).

Subjects were also significantly more likely to approach speaker 2 in the test condition than in either control condition (Cochran's Q test: $Q_2 = 8.86$, $P < 0.012$). Whereas six of nine subjects approached speaker 2 in the test condition, none did so in the first control condition (one-tailed sign test: $k = 0$, $N = 9$, 3 ties, $P < 0.016$; Fig. 2). Similarly, only one subject approached speaker 2 in the second control condition, conducted after the consortship had ended ($k = 1$, $N = 9$, 2 ties, $P < 0.062$; Fig. 2). All six subjects who approached speaker 2 in the test condition showed considerable vigilance and searching behaviour, scanning the area
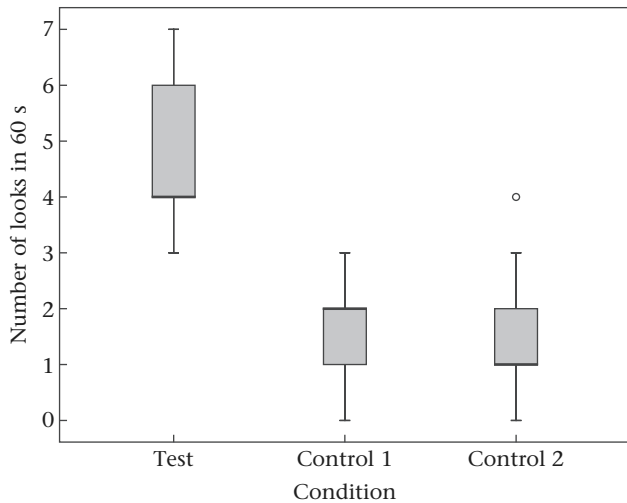
Figure 1. Number of looks given by subjects towards the speaker playing the female copulation call in the first minute after playback for each of the three conditions. $N = 9$ in each condition. Test = consort male and female during consortship; control 1 = other male and female during consortship; control 2 = consort male and female after end of consort. Each box encompasses the 25th through 75th percentiles, with the median represented by an interior line. Whiskers denote 10th and 90th percentiles.

around the speaker for a prolonged time ($\overline{X} \pm SE = 70.6 \pm 64.8$ s; range $21-166$ s).

Although all nine subjects were tested within 24 h of the end of the consort, at least four were tested less than 4 h after its end (45 min, 1 h, 2 h and 3.5 h). These four subjects' responses were similar to those of the other subjects.

DISCUSSION

When male baboons heard a sequence of calls suggesting that a consorting male and his female had temporarily separated, they responded significantly more strongly than they did in control trials. They looked towards the speaker broadcasting the female's copulation calls significantly more times and also approached it. Their behaviour suggested that they inferred that the consort pair had temporarily separated, that the female was engaged in a sneaky mating, and that further mating opportunities might be possible.
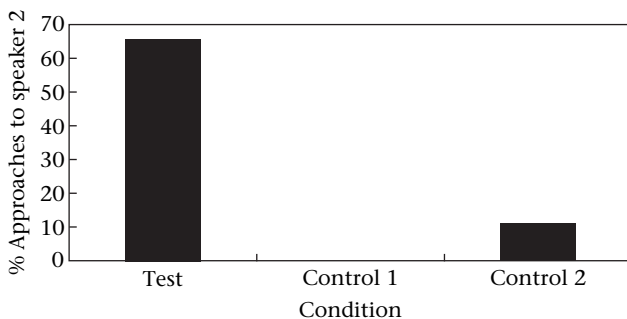

Figure 2. The percentage of approaches made by subjects towards the speaker playing the female copulation call. $N = 9$. Legend as in Fig. 1.

In contrast, subjects responded more weakly when they heard a nonconsorting male's grunts and the female's copulation call played from different speakers. Their relative lack of response suggests that they interpreted this call sequence as indicating that the consortship was still active, and that a nonconsorting male was simply nearby. This information did not violate their expectations or signal a mating opportunity.

Subjects also responded weakly when they heard the consort male's grunts and the female's copulation call played from separate speakers after the consortship had ended, even when it had ended only a few hours ago. Their weak responses could not be explained by a decrease in the attractiveness of the female, because eight of nine females were still fully swollen and all continued to mate with lower-ranking adult and adolescent males for at least a day after the playback. Instead, subjects appeared to respond weakly to the playback stimulus because it provided redundant information: they already knew that the consortship had ended.

In summary, the same sequence of calls that elicited a strong response from subjects when a sexual consortship was in progress elicited a much weaker response from the same subjects soon after the consortship had ended. Results are best explained by assuming that, in the test condition, call sequences violated subjects' expectations about the status of the consortship. In the control conditions, however, they did not. Apparently, male baboons monitor consortships so assiduously that they rapidly recognize both when an unexpected mating opportunity arises and when a consortship has ended.

Rapid assessment of extrapair mating opportunities has previously been demonstrated in playback experiments on several bird species. Male whitethroats, *Sylvia communis*, for example, are likely to intrude onto a neighbour's territory if they hear the neighbour courting a female (Balsby & Dabelsteen 2005), and female chickadees, *Poecile atricapillus*, seek extrapair matings from neighbouring males who appear to dominate their mates in singing contests (Mennill et al. 2002). These assessments, however, do not demand deductions about temporary changes in the status of a transient relationship. In contrast, in the present experiments, male baboons responded significantly more strongly to the same call sequence when it was played during the consortship than when it was played shortly after the consortship had ended. Subjects appeared to monitor not only the identities of the signallers and their consort status but also momentary changes in the pair's proximity. As a result, the same information was unexpected and relevant in one context but not in another. Eavesdropping on the temporal and spatial juxtaposition of other individuals' vocalizations, therefore, may be one strategy by which male baboons achieve sneaky matings.

The results from these playback experiments support the hypothesis that baboons and other monkeys classify social relationships according to a number of different behavioural metrics and rules (Seyfarth & Cheney 2003). Although they doubtless use high association rates as one criterion for identifying a close social bond, they seem to recognize that different types of relationships are characterized by different patterns of spatial proximity. As a result, they

do not respond strongly when a playback experiment suggests, for example, that a female is not in close proximity to her adult or juvenile daughter. They do, however, respond strongly to playbacks suggesting even a temporary separation between a male and his consort female. Baboons apparently understand that some close social relationships are characterized by continuous spatial proximity, while others are not. Moreover, they appear to recognize that some very close relationships are extremely transient. To recognize that some relationships are defined by close spatial proximity and others are not, and that some relationships are enduring and others are not, a baboon must take note of a variety of different patterns of grooming, proximity and vocalizations. There is no threshold or simple defining criterion for a 'close' social bond.

Acknowledgments

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