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Male Guinea baboon tracking of female whereabouts

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Abstract

In group-living species, evolution puts a premium on the ability of individuals to track the state, whereabouts, and interactions of others. The value of social information might vary with the degree of competition within and between groups, however. We investigated male monitoring of female location in wild Guinea baboons (*Papio papio*). Guinea baboons live in socially tolerant multi-level societies with one-male-units comprising 1-6 females and young at the core. Using field playback experiments, we tested whether males (N=22 males, N=62 trials) keep track of the whereabouts of associated females by playing back unit females' calls from locations that were either consistent or inconsistent with the actual position of the female. Contrary to predictions, males responded equally strongly in both conditions. In a preparatory experiment, males (N=14) responded more strongly to playbacks of unit vs. non-unit females. While males seem to recognize their females by voice, they were not able or not motivated to track their females' movements. These results reinforce the view that the value of social information may vary substantially with the distribution of power in a society. While highly competitive regimes necessitate high attention to deviations from expected patterns, egalitarian societies allow for a certain degree of obliviousness.

Introduction

Knowledge about conspecifics and their relationships guides social decision-making in many group-living animals. The use of such social knowledge is documented for a large number of species, ranging from simple and more complex forms of individual recognition [1] to the assessment and monitoring of stable or transient social attributes of group members, like kinship, rank, or bond strengths. Such knowledge extends not only to an individual's direct associations but also to third-party relationships [2]. When navigating the social environment, knowledge about previous interactions with group members, the capabilities of potential partners or competitors, and the nature and quality of relationships between others, aids in

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predicting the outcomes of future interactions and allows to act strategically. For example, spotted hyenas (*Crocuta crocuta*) joining into dyadic fights mainly support the dominant individual and are subsequently also more likely to attack relatives of the subordinate [3]. Pinyon jays (*Gymnorhinus cyanocephalus*) assess their relative rank difference to strangers by observing them in encounters with known individuals [4]. Tonkean macaques (*Macaca tonkeana*) respond more strongly to conflicts between strongly bonded individuals ('friends') compared to non-friends [5].

Besides kin and allies, mating partners are of particular value to an individual. Males compete not only for access to females [6,7]; they are also under selection to monitor the state and behaviour of females. Males may increase their reproductive success by assessing suited mating partners [8] or mating opportunities [9,10]. In many species, females become the centre of male attention when they approach the fertile phase of their reproductive cycle. In contrast, in species where males and females form long-lasting bonds as in monogamous [11] or polygynandrous species (e.g., plains zebras (*Equus burchellii*) [12], hamadryas baboons (*Papio hamadryas*) [13]), males are permanently incentivised to monitor and control associated females' whereabouts and interactions with other group members.

We tested male knowledge of female whereabouts in wild Guinea baboons (*Papio papio*). The species lives in multi-level societies. At the core are one-male units consisting of one primary male, one to six associated females, and their offspring. Bachelor males may be associated with several such units [14]. Several units form a party, which in turn aggregate into gangs [15]. Females associate with one primary male and show mate fidelity [16], but in contrast to hamadryas baboons, they also enjoy spatial freedom, i.e., they may spend considerable time away from their male [16].

We hypothesized that males keep track of the movement patterns of associated females. To test this hypothesis, we conducted a playback experiment [17], in which we presented female grunts from a location that was either consistent or inconsistent with the actual position of the female. We made use of the violation-of-expectation paradigm and

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presented the animals with a physically impossible scenario, similar to Townsend et al. (2012). We tested a male immediately after the female had left him and assumed that he would have noticed the direction in which she disappeared. We predicted that males would show ‘signs of surprise’, meaning a stronger response, when they were confronted with information that the female was in an unexpected - indeed physically impossible – location compared to their response when the female’s vocalisation came from the direction into which she had recently disappeared. In a preparatory experiment, we tested the prerequisite that males can recognise their associated females by voice. We tested if males respond more strongly to the vocalizations of females from their unit compared to the vocalizations from females of another unit, but the same party. We predicted that males would show stronger responses when presented with vocalisation from unit-females.

Methods

The experiments took place between January 2019 and August 2021 at the Centre de Recherche de Primatologie Simenti in the Niokolo-Koba National Park in Senegal, a field station maintained by the German Primate Center (see Fischer et al., 2017 for details). The study population comprised ~ 200 individually identified Guinea baboons that belonged to three parties, with a varying number of reproductive units (between 15 and 25 per year across three parties) suitable for the experiments. For the experimental stimuli, we recorded ‘grunt’ vocalisations of sub-adult and adult females during their non-receptive phase (electronic supplementary material, appendix S1, S2). Grunts are the most frequently occurring vocalisation in Guinea baboons and are mainly produced in affiliative contexts [20].

In Experiment 1 (individual recognition), we presented males with calls from a female from their unit (*unit-female* condition) and a female from another unit (*non-unit-female* condition). Trials were separated by at least five days and conducted only when females were non-receptive. Once the female whose call was to be played back was not visible to the subject, a loudspeaker was positioned at a 90° angle to the left or right of the male depending

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on the actual position of the female, and the stimulus presented. Male responses were video recorded for three minutes after the onset of the stimulus. We conducted 28 playback trials testing 14 primary males.

In Experiment 2 (spatial monitoring), we tested males in a within-subject design and presented grunts from a unit-female on two occasions separated by at least seven days. As above, trials were conducted only when females were non-receptive. In the *consistent* condition, the speaker was hidden in a location matching the actual direction of the departed female, whereas in the *inconsistent* condition in the opposite direction, presenting an impossible scenario (figure 1). A male was tested after he had been near a unit-female, she had then walked away and was no longer in sight (median time out-of-sight: 70s, range 8 s – 273 s). A loudspeaker was then hidden in vegetation, at a 90° angle to the left or right of the male and a distance of approximately 10 m. Male responses were video recorded for 10 min. after the onset of the stimulus. We conducted 62 playback trials with 22 primary males. Nine of these males were tested twice with the call of a different female (average time between first and second run: 43 weeks (min: 3, max: 100)) (electronic supplementary material, appendix S3).

Video recordings were coded using Solomon coder beta (András Péter, solomoncoder.com) on a frame-by-frame basis (25 frames/s). We examined male responses by coding changes in their head orientation; i.e., changes between the neutral position: male faces camera, and subsequent looks exceeding an angle of 45° towards the direction of the speaker or away from it. We measured the duration of the first look and the latency to respond. Trials where the latency exceeded the cut-off were coded as “no response”. As the first look in the inconsistent condition could be truncated because the male may turn his attention to look into the direction where the female was last seen, we additionally measured the total time vigilant (all looks toward the speaker or actual position of the female) within 30 s after stimulus onset in the social monitoring experiment, (electronic supplementary material, appendix S4 (observer reliability); appendix S5, figure S1, S2 (classification of responses)).

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Analyses were carried out in R (version 4.1.1; R Core Team, 2021). GLMMs, LMMs, and Cox proportional hazard model were fitted using the R package *lme4*, *survival* and *coxme* (electronic supplementary material, appendix S6, S7). We used a Linear Mixed model [22] for first look duration (experiment 1) and vigilance time, a Generalized Linear Mixed Model with gamma error structure and log link function [22] for the duration of the first look (experiment 2), and a survival analysis [23] for latencies. In addition to the main predictor 'experimental condition', we included unit size as a fixed effect to control for the influence of the number of unit-females and male identity as random intercept. As in experiment 1, the same call could be used in the unit-female and non-unit-female conditions for different males, and some calls (stimuli) stemmed from the same female, we included female ID and stimulus ID as additional random intercept effects. To investigate the effect of the main predictor we compared the full model to a null model lacking experimental condition using a likelihood ratio test (Dobson & Barnett, 2008). Confidence intervals of estimates and fitted values were determined using a parametric (LMM & GLMM) and non-parametric (survival analysis) bootstrap (N=1000 bootstraps).

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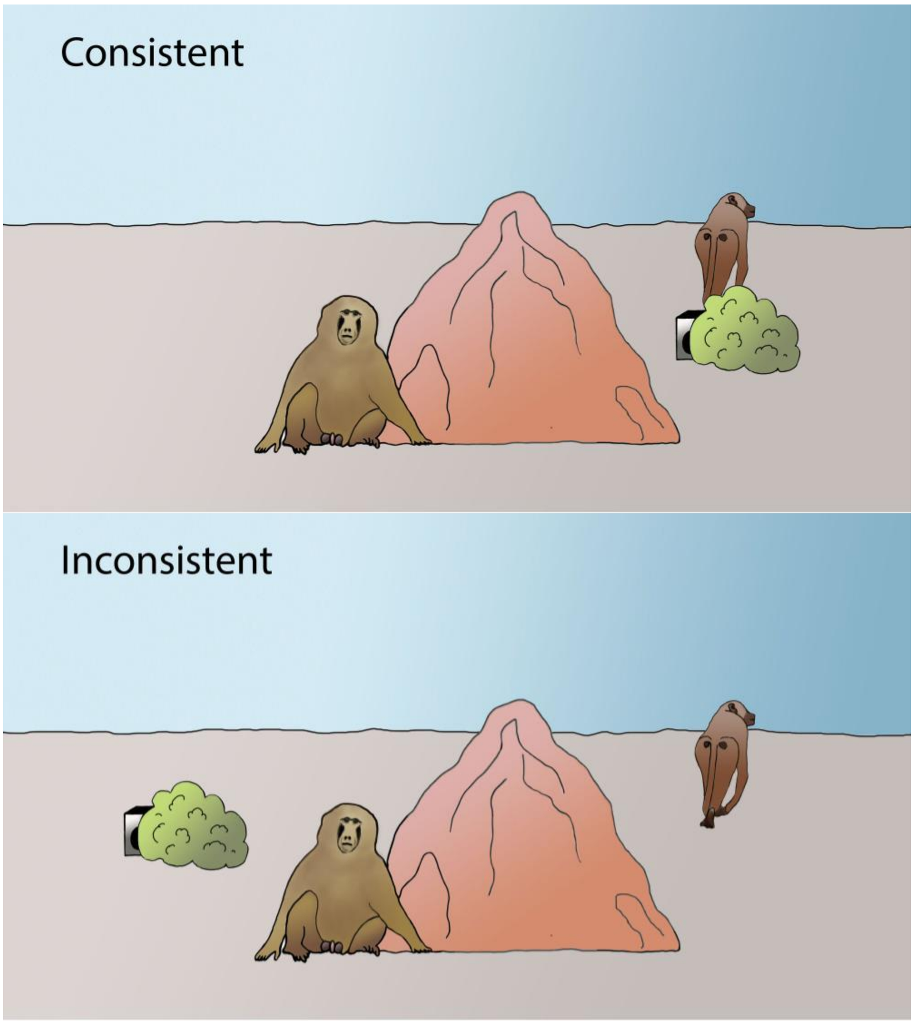

Figure 1. Set-up experiment 2 (spatial monitoring). In the consistent condition, a speaker is positioned close to the actual position of the female, in the inconsistent condition, the speaker is placed in the opposite direction.

Results

In experiment 1 (individual recognition), males responded to the playback of calls in 24 out of 28 trials. The average duration of the first response was 3.18 s ± 2.53 s (median ± IQR). Males looked longer when presented with calls from unit-females (3.38 s ± 4.60 s) compared to non-unit females (2.32 s ± 3.80 s) (full-null model comparison: χ^2_1=8110, p=0.004, table S1a). The average latency of responses was 0.96 s ± 0.86 s for the unit-female and 1.26 s ± 3.21 s for

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non-unit-females (median ± IQR). Unit size had no obvious effect on response duration or latency (Duration: p=0.48; Latency: p=0.37, table S1a, S2).

In experiment 2 (spatial monitoring), males responded to the playback in 49 out of 62 trials (consistent condition: N=22, inconsistent: N=27). There was no obvious difference in the duration of first look in the consistent (2.80 s ± 4.36 s, median ± IQR) compared to the inconsistent (2.92 s ± 2.62 s) condition (full-null model comparison: χ^2_1=0.0002, p=0.99, table S3) (figure 2b). There were no obvious differences in response latencies between the two conditions (consistent: 0.72 s ± 0.48 s; inconsistent: 0.80 ± 0.64 (median ± IQR); full-null model comparison: χ^2_1 =1.10, p=0.29, table S4). There were also no obvious differences in the overall time vigilant (consistent: 7.84 s ± 7.19 s (median ± IQR); inconsistent: 8.08 s ± 6.39 s; full-null model comparison: χ^2_1 =0.04, p =0.84, table S5). We found no evidence that unit size influenced any of the response variables (Duration: p=0.38; Latency: p=0.63, Vigilance: p=0.15, table S3, S4, S5).

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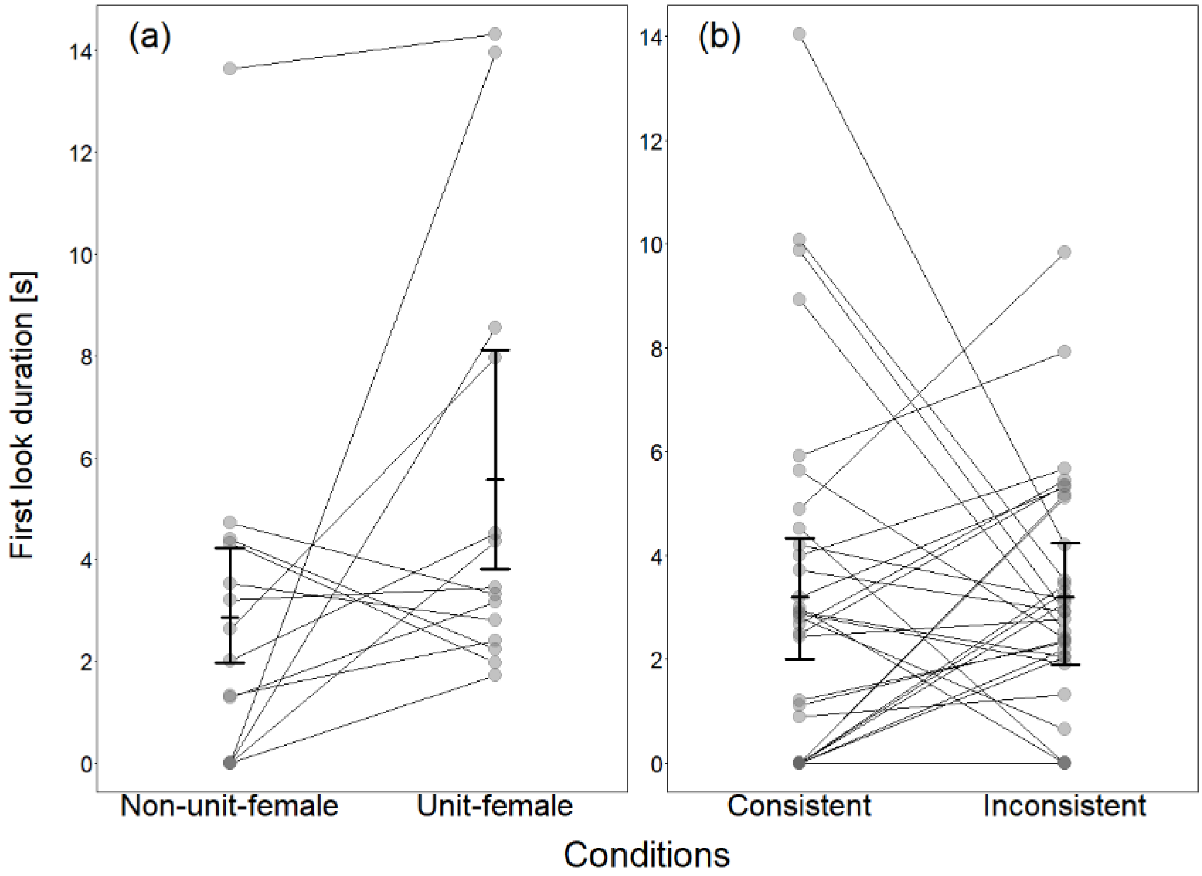

Figure 2. First look duration for males in the a) individual recognition experiment and b) spatial monitoring experiment. Connected points represent data from the same individual (a: N=14; b: N=22). Thick black lines depict bootstrapped mean and 95% confidence intervals for males with average unit size.

Discussion

Male Guinea baboons showed no signs of surprise when calls from associated females were played back from an impossible location. Instead, they responded equally strongly to playbacks of calls from an impossible or a possible location. Further, males responded more strongly to the playback of vocalizations from unit-females compared to non-unit-females. While males seemed to be able to recognise their unit's females by voice, they lacked either the ability or the motivation to track their females' positions.

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These findings were not in line with our initial prediction that primary males monitor the whereabouts of their females. Guinea baboons form one-male units similar to hamadryas baboons or mountain gorillas (*Gorilla b. beringei*). In both of these species, sexual coercion [25] is used by leader males to control female movement and interactions and to prevent transfers to other males [26,27]. In Guinea baboons, we did not observe such overt aggression towards females, except for some occasional chasing of females. Indeed, female Guinea baboons can roam relatively unimpeded and interact socially with other group members, including other adult males [16].

The lack of differentiated response fits with the relatively laid-back stance of Guinea baboon males. Males form strong bonds with other males [14,15,28]. They also show low levels of overt aggression, preventing us from discerning a clear dominance hierarchy [14]. At the same time, female Guinea baboons have considerable leverage in mate choice and intersexual bond maintenance [16]. Male strategies mainly seem to consist of investing their social time into female grooming and support. Interestingly, males appear to face a trade-off in the allocation of social time, as male investment into socio-positive interactions with other male declines with increasing unit size [28]. Social investment into females thus might be important for intersexual bond maintenance and potentially female mate choice in the first place.

Since we tested males when the female whose calls were played was not receptive, we do not know whether males would be more attentive if the female would be able to conceive. We conducted the trials only while females were non-receptive because, during females' oestrus, primary males and females are less likely to separate [29], leaving very few opportunities for conducting the experimental trials. Thus, we cannot exclude the possibility that males would respond differentially in conditions where they should be more motivated to track their female's whereabouts.

Our study adds to the accumulating evidence that the need to monitor the social environment varies between species with the degree of competition among individuals. For

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instance, the highly competitive chacma baboons (*Papio ursinus*), which live in female philopatric groups show strong responses to the playback of vocalisation from unfamiliar males [30,31], while Guinea baboons showed greater attention to vocalisations from familiar males compared to neighbours or strangers [20]. In geladas (*Theropithecus gelada*), which live in a multi-level society in aggregations of up to several hundred individuals, vocal recognition seems to be limited to individuals with a high degree of social overlap [32]. Additionally, when presenting individuals with information about changes in association patterns, chacma baboons responded strongly to simulated separations of consortships [10], while Guinea baboons paid more attention to information consistent with current male-female association patterns [33]. Similarly, Geladas did not differentiate between consistent or inconsistent information about male-female relationships at all [34].

While the link between group-living and sophisticated social knowledge is well documented [2], it is still unclear whether life in a socially complex environment per se [35] or rather the degree of competition within and between groups selects for advanced socio-cognitive skills (“Machiavellian intelligence”) [36]. Bergman (2010, p. 2050) argued that “missing social knowledge” might be a consequence of the absence of a competitive environment that offers no benefits for the ability to assess and use of specific social information of conspecifics. Our results as well as results of previous from the same population [20,33] suggest that a reduced competitive environment affects the value of social information, and as a consequence, the motivation or ability of an individual to attend to them. At the same time, both Guinea baboons and geladas live in highly structured multi-level groups, suggesting that a complex social organisation does not per se select for a high motivation to monitor the social environment. We contend that a skewed distribution of power influences the value of social information and therefore the motivation to attend to events in the social environment.

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