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Animal behaviour

Odour-based kin discrimination in the cooperatively breeding meerkat

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Kin recognition is a useful ability for animals, facilitating cooperation among relatives and avoidance of excessive kin competition or inbreeding. In meerkats, *Suricata suricatta*, encounters between unfamiliar kin are relatively frequent, and kin recognition by phenotype matching is expected to avoid inbreeding with close relatives. Here, we investigate whether female meerkats are able to discriminate the scent of unfamiliar kin from unfamiliar non-kin. Dominant females were presented with anal gland secretion from unfamiliar individuals that varied in their relatedness. Our result indicates that females spent more time investigating the scent of related than unrelated unfamiliar individuals, suggesting that females may use a phenotype matching mechanism (or recognition alleles) to discriminate the odour of their kin from the odour of their non-kin. Our study provides a key starting point for further investigations into the use of kin recognition for inbreeding avoidance in the widely studied meerkat.

1. Introduction

Inbreeding is usually costly, and inbreeding avoidance by females has evolved in many species [1,2]. To avoid inbreeding, females may delay maturation or disperse when kin are available as mates [2–4], or they may avoid mating with kin. Kin may be identified by several mechanisms, including spatial distribution, recognition alleles, familiarity or phenotype matching [5–7], the last two mechanisms being the most common. In the familiarity mechanism, animals learn the phenotypes of relatives through social interactions and later discriminate these familiar relatives from unfamiliar animals. In phenotype matching, individuals learn their own phenotype or that of their familiar kin and later compare it with the phenotypes of unfamiliar individuals [7–9]. Therefore, while familiarity leads only to the recognition of previously encountered familiar individuals [8], phenotype matching provides a way of identifying unfamiliar kin. Phenotype matching has been shown in several taxa (birds [10,11]; fish [12,13]; primates [14,15]; rodents [16,17] and insects [18]) but firm evidence that it occurs in non-rodent or non-primate mammals is limited.

In this study, we investigate whether wild meerkats (*Suricata suricatta*) are capable of discriminating kin from non-kin on the basis of phenotype matching. Meerkats are obligate cooperatively breeding herpestids, which typically live in groups consisting of a dominant breeding pair and their offspring [19]. Given high levels of dominant-biased reproductive skew, long dominance tenure and common short-distance extraterritorial forays [20] and dispersal by both

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sexes [21], unfamiliar siblings from different litters can encounter each other relatively frequently outside the natal territory. Inbreeding depression is evident for several early-life traits [22] and kin discrimination by phenotype matching may, therefore, be a useful ability for females to avoid close inbreeding with unfamiliar kin.

Here, we determined whether dominant female meerkats use a phenotype-matching mechanism to discriminate between their kin and their non-kin by presenting scent cues from anal gland secretions of unfamiliar males of variable relatedness. We focused our experiment on anal gland secretion, because meerkats frequently scent-mark their territory with these secretions and an encounter between two meerkats is generally associated with mutual scent investigation of the anal area.

2. Material and methods

(a) Study site

This study was conducted in November 2011 on a wild population of meerkats at the Kuruman River Reserve (latitude 26°59′ S and longitude 21°50′ E), and surrounding ranch land in the southern Kalahari Desert, South Africa. All animals in the population could be individually identified by the use of unique dye mark combinations and most individuals were habituated to close observation (less than 2 m).

(b) Pedigree relatedness

Full details of the genetic and pedigree methods can be found in Nielsen *et al*. [22]. Based on the pedigree relationships, a matrix of pair-wise coefficients of relatedness (R) was calculated for the whole population.

(c) Scent presentation

Eleven dominant females were presented with the scent of unfamiliar subordinate males who varied in their relatedness. Secretion samples were obtained by rubbing cotton-buds on the anal area of subordinate males when they were resting near their burrow. Ten dominant females were tested twice (i.e. once with a moderately related unfamiliar male ($R > 0.10$; range: 0.11–0.31, mean: 0.20 ± 0.03) and once with a lowly related unfamiliar male ($R < 0.10$; range: 0–0.06, mean: 0.05 ± 0.01)) with an interval of more than one week between the two tests, and with randomized presentation order. The remaining female was tested only once, i.e. with a moderately related unfamiliar male.

During presentation, the tip of the cotton-bud was placed at 2–5 cm from the nose of the target female until the female moved away. The investigation time of each individual was recorded with a digital video camera. Number of recruitment calls, which are typically emitted when encountering the smell of conspecifics or other animals [23], was measured directly during presentation. As soon as the recipient finished investigating the cotton-bud, we conducted 8 min focal to record vigilance behaviour of the recipient.

Further details on the protocol can be found in the electronic supplementary material, S1.

(d) Statistical analyses

We used generalized linear mixed models (GLMM) to determine whether the behaviour of dominant females varied according to their relatedness to scent donors. Investigation time, vigilance behaviour, probability of emitting calls or number of calls when emitting calls was the dependent variable and relatedness between recipients and donors was the fixed effect. In meerkats, dominant females can be paired with two distinct classes of dominant males. Most commonly, they are paired with a male originating from another group, who are usually distantly related to the female and sire most of the pups within the group [24]. Less commonly, dominant females are paired with their son or brother who inherited the dominant position within the group. As the dominant male and female are closely related to each other, they never breed with each other, and the female occasionally breeds with extra-group roving males. Dominant females may, therefore, respond to intruder males according to the status of their mate (natal or immigrant male). The status of the dominant male in the recipient group was thus included as a fixed effect. Quantity of secretion and number of the test (first or second) were entered as covariates. Donor and recipient identity were entered as random factors.

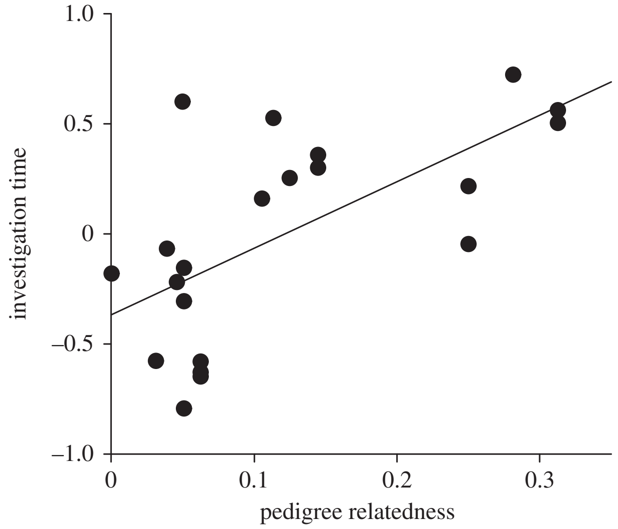

Figure 1. Investigation time of dominant females to the scent of unfamiliar subordinate males with varying degrees of pedigree relatedness. Investigation time is expressed by the residuals of a GLMM with investigation time as the dependant variable, quantity of secretion and number of tests as fixed effects, and recipient and donor identity as random factors.

All statistical tests were conducted within the SAS system v. 9.1 and used the Satterthwaite correction for the calculation of fixed effects degrees of freedom. We used two-tailed type-3 tests for fixed effects with a significance level set to $\alpha = 0.05$. Values are expressed as mean ± s.e. throughout.

3. Results

Dominant females biased their behaviour according to their relatedness to unfamiliar subordinate males. Dominant females investigated for longer ($F_{1,7.42} = 22.26$, $p = 0.0019$; mean: 1.93 ± 0.22 s, range: 0.4–4.6 s; figure 1 and electronic supplementary material, S3) and were less vigilant ($F_{1,12} = 7.23$, $p = 0.020$; mean: 19.6 ± 5.6 s, range: 0–75 s, figure 2 and electronic supplementary material, S4) when presented with the scent of more related males.

Dominant females also biased their vigilance behaviour according to whether they were paired with a natal or immigrant dominant male. Females paired with a natal male were more vigilant than females paired with an immigrant male (38 ± 19 versus 14 ± 4 s; $F_{1,12} = 12.56$, $p = 0.004$).

Only two females emitted calls when presented with the scent of subordinate males. One dominant female emitted 11 calls to a distantly related male ($R = 0.05$) and one

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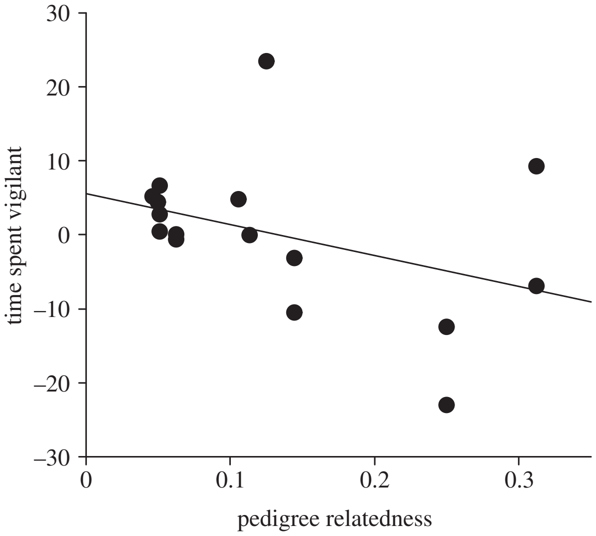

Figure 2. Time spent vigilant by dominant females in response to the scent of unfamiliar subordinate males with varying degrees of pedigree relatedness. Time spent vigilant is expressed by the residuals of a GLMM with investigation time as the dependant variable, quantity of secretion and number of tests as fixed effects, and recipient and donor identity as random factors.

dominant female emitted two calls to a more closely related male ($R = 0.31$). The probability of emitting calls and the number of emitted calls did not depend on relatedness between recipient and donor.

4. Discussion

We found that dominant females investigated for longer and were less vigilant to the scent of unfamiliar closer related males. This suggests that meerkats can rely on a phenotype-matching mechanism, either through self-referent or known-kin matching, to discriminate between their kin and their non-kin. Our results bring thus new support on kin discrimination by phenotype matching in non-rodent and non-primate mammals in which evidence has remained limited. Our results, however, do not preclude the use of recognition alleles that cause expression of a phenotypic cue and allow intrinsic recognition without learning [5,6]. This mechanism, which is very difficult to separate experimentally from self-referent phenotype matching, currently lacks direct evidence, and has been downplayed as a high-priority kin recognition mechanism [5].

Although kin discrimination by phenotype matching is a useful ability for inbreeding avoidance or nepotism, the ability is not necessarily associated with its use [25]. In our study population of meerkats, moderate inbreeding is not avoided albeit costly [22], and individuals do not direct vigilance, grooming, baby-sitting or pup feeding effort towards close kin [26–29]. Therefore, kin recognition by phenotype matching may have evolved in meerkats, but the action component involving mate choice or nepotistic behaviour has not been elaborated. Lack of nepotism and inbreeding avoidance with unfamiliar kin in meerkats has been explained by the importance of direct benefits to cooperative behaviour and lack of opportunity for reproduction with non-kin [21,29]. However, our results show that dominant females were more vigilant when they were paired with a closely related male. In meerkats, subordinate males conduct extraterritorial prospecting forays [20] during which they seek and sometimes achieve breeding opportunities with dominant and subordinate females from outside groups [24]. Females paired with a closely related male may thus benefit by being more attentive to an unrelated intruder that may be a better breeding partner than a related intruder. Our study provides a key starting point for further investigations into the use of phenotype matching for inbreeding avoidance in the widely studied meerkat.

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