Odour-based social recognition in Damaraland mole-rats *Fukomys damarensis*

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Highlights

•Damaraland mole-rats recognize conspecifics using substrate-borne odour cues.

•Both sexes dig the most in sand from the tunnels of unfamiliar, opposite-sex mole-rats.

•Digging effort is reduced in sand taken from the tunnels of other breeding groups.

•A primary role for olfaction in social recognition is supported in this species.

ABSTRACT

The ability to discriminate between conspecifics functions in mate choice, kin-selected cooperation and territory defence. In mammals, olfaction plays a key role in such social interactions. Olfactory cues may be particularly important for subterranean mammals, for which visual and acoustic cues are less effective. Damaraland mole-rats *Fukomys damarensis* live in groups comprising a breeding pair and their non-breeding offspring. They are xenophobic, obligate outbreeders and independent dispersal represents the usual route to reproduction for both sexes. As yet, little is known about how dispersing individuals locate mates. Using a series of behavioural experiments, we reveal that mole-rats can discriminate between unfamiliar breeding groups and solitary, non-breeders of the opposite sex using odour cues. Our experiments showed that subjects spent more time investigating sand taken from other mole-rat groups than control sand, indicating an ability to recognize substrate-borne conspecific odours. Mole-rats also spent more time digging and sweeping in sand taken from the tunnels of unfamiliar, solitary animals of the opposite sex than sand taken from unfamiliar breeding groups, and removed a higher volume of this sand during the experiments. Together, these results suggest an olfactory preference in both sexes for solitary, opposite-sex animals over breeding groups. Our results are supported by observations from the field that immigration into breeding groups is rare, with dispersing females typically establishing new groups, where they are subsequently joined by unfamiliar males. This study supports olfaction as a potential recognition cue which may facilitate adaptive dispersal.

Keywords: Cooperative breeding, dispersal, mammals, olfaction, recognition, subterranean.

INTRODUCTION

Adaptive social decision making depends on an ability to discriminate between conspecifics that offer alternative fitness outcomes upon interaction (Reeve 1989). Conspecifics might differ in their quality (Buchanan et al. 2003), competitive ability (Wyman et al. 2008), or relatedness (Sharp et al. 2005), and mechanisms that allow discriminating individuals, or actors, to distinguish between conspecifics in which these characteristics vary are likely to be under strong selection in many species. There is now both theoretical and empirical evidence that kin discrimination, the differential treatment of conspecifics on the basis of relatedness (Sherman et al. 1997), facilitates the evolution of both cooperative behaviour (Hamilton 1971; Wright et al. 2010) and inbreeding avoidance (Lehmann and Perrin 2003; Leedale et al. 2020). Discrimination between individuals based on fitness outcomes is usually termed social recognition (Insley et al. 2003). In order to evolve, recognition requires that different categories of conspecifics produce alternative cues or signals that convey information about themselves to actors. It also demands an ability in actors to perceive these cues and perform appropriate discriminatory behaviour (Reeve 1989). When certain categories of conspecifics, such as kin, are predictably distributed in space, location can act as a reliable recognition cue (Komdeur and Hatchwell 1999), but when spatial information is unreliable, phenotypic cues are often used to discriminate conspecifics, relaying sensory information via visual, acoustic or olfactory stimuli (Halpin 1991). Any cue or combination of cues that reliably correlate with the characteristic affecting fitness may be used for recognition (Beecher 1982).

In many mammals, olfaction serves as the primary sensory modality for social behaviour (Brown and MacDonald 1985; Gosling and Roberts 2001). The sensory capacities of the olfactory system have been particularly well studied in rodents, stimulated by the long tradition of work with laboratory mice and rats (Ferguson et al. 2002; Johnston 2003), and there is evidence from several rodent taxa that olfaction is used in a variety of social contexts. Odour cues can denote sex, reproductive status (Brennan and Kendrick 2006) and group membership (Heth et al. 2002a), mediating a suite of social behaviours involved in mate choice, maternal care, competition and cooperation (Willis and Poulin 2000; Stockley et al. 2013; Rymer 2020). For example, in communally nesting house mice *Mus musculus domesticus*, females often form nursing partnerships to rear offspring, and prefer nest partners with their own major urinary protein genotype (Green et al. 2015), assessed using unique odour 'signatures' (Roberts et al. 2018). In Belding's ground squirrels *Urocitellus beldingi*, odour-based kin discrimination also facilitates the formation of social relationships (Mateo 2003), promoting kin preferences in nest burrow establishment and territorial defence (Sherman 1981). There is also some evidence for disassortative mating in rodents using the highly polymorphic major histocompatibility complex (MHC), which is thought to be mediated through odour (Radwan et al. 2008), though the extent to which MHC functions in mate choice in both captive and wild rodent populations remains controversial, and there are many cases where no such association is found (e.g. Sommer 2005; Meléndez-Rosa et al. 2018).

The use of olfactory signals for social recognition is predicted to be especially important among subterranean rodents because odour cues deposited in substrate can remain active for long periods and near-permanent life underground may render visual and acoustic signals less effective (Francescoli 2000). In numerous subterranean rodents, such as the blind mole-rats of eastern Europe and the Middle East (family: Spalacidae) the eyes have been covered by a layer of skin and are no longer able to detect light (Sanyal et al. 1990). In others, such as the African mole-rats (family: Bathyergidae), the eyes have degenerated to rudimentary organs that retain only a basic ability to differentiate light from dark (Hetling et al. 2005). By contrast, African mole-rats display high functional genetic variability at olfactory receptor loci, suggesting that an ability to recognize a broad range of olfactory cues is under strong selection in this family (Stathopoulos et al. 2014). There is also a sizeable body of experimental evidence supporting olfactory recognition in subterranean rodents (Heth et al. 2002b; Heth et al. 2004; Hagemayer et al. 2006; Heth and Todrank 2007; Toor et al. 2015). A review of the topic by Heth and Todrank (2007) concluded that numerous species respond differentially to the odours of conspecifics that differ in their genetic relatedness or degree of familiarity. Empirical evidence from Ansell's mole-rats *Cryptomys anselli*, suggests phenotype matching, whereby a reliable association between genetic and odour similarity allows individuals to assess relatedness, is the most likely mechanism of kin recognition in this species (Heth and Todrank 2004). In laboratory experiments, highly social naked mole-rats *Heterocephalus glaber* exhibit strong preferences for their own colony odour (Toor et al. 2015), and *Fukomys* mole-rat siblings will readily mate after a prolonged period of separation (Burda 1995; Kelley et al. 2019), suggesting kin recognition requires prior association. Whether recognition is based on familiarity or phenotype matching, there is clear evidence that subterranean rodents discriminate conspecifics using olfactory cues. However, the extent to which odour cues inform social decisions such as those related to mating, remains unclear.

In this study, we investigate whether Damaraland mole-rats *Fukomys damarensis* use odour cues to discriminate between individuals that offer alternative fitness outcomes from social interaction. Damaraland mole-rats are widely distributed across southern Africa, occurring in areas of arid thornveld where annual rainfall is low and unpredictable. They live in groups of 2-41 individuals (Jarvis and Bennett 1993) comprising a dominant breeding pair and their descendent non-breeding offspring, which contribute towards burrow excavation and maintenance, group defence and pup care (Bennett and Faulkes 2000; Zöttl et al. 2016). As in most cooperative breeders, dispersal is thought to be limited by ecological constraints on independent reproduction, including a high mortality risk associated with leaving the group, such that natal philopatry presents a better option than emigration (Faulkes et al. 1997). They are xenophobic, obligate outbreeders (Cooney and Bennett 2000), and in contrast to several other cooperative breeders, non-breeding residents rarely inherit the breeding position after the loss of a breeder (Jarvis and Bennett 1993). Instead, groups remain inactive and finally fragment during periods of heavy rainfall when dispersal conditions are most favourable (Hazell et al. 2000; Young et al. 2010). Both sexes disperse, with males dispersing slightly earlier than females, and although successful immigration of both sexes is very rare (Torrents-Ticó et al. 2018), genetic analyses have identified active groups containing immigrant males and extra-group offspring (Burland et al. 2004).

Although dispersal has never been observed directly, the relatively large dispersal distances (mean ± SD in males: 738.6 ± 1067.3m, females: 924.8 ± 1067.1m, Finn 2017), and the finding of mole-rat remains in owl scats and open water (Hazell et al. 2000) suggest that dispersal occurs principally above ground. Upon settlement, dispersers dig below the surface to access occupied burrow systems or establish new burrows, suggesting that dispersal is an active process, which may involve substrate-borne external cues. However, very little is known about how dispersers locate conspecifics, or what happens when unfamiliar conspecifics are encountered during dispersal, and much of our understanding of inter-group interactions comes from captive populations. On the one hand, encounters with breeding groups present an opportunity to reproduce; resident males and females readily mate with intruders of the opposite sex in captivity (Jacobs et al. 1998). On the other hand, dominant individuals can be highly aggressive towards intruders (Cooney 2002), and resident subordinates of either sex attack intruders when groups are breeding (Jacobs et al. 1998). In contrast, dispersers that encounter solitary individuals of the opposite sex are presented with a breeding opportunity without the risk of injury or death through aggressive disputes with same-sex residents, and one might expect dispersers to preferentially target single, opposite-sex individuals if appropriate cues are available for them to do so.

In a series of two-choice behavioural experiments, we investigate whether Damaraland mole-rats can use odour cues to discriminate between members of the same and opposite sex, and between individuals or groups, that represent alternative breeding opportunities with varying levels of competition. We focused on odour cues in sand because this is likely to be the external substrate-borne cue used by overground dispersers to identify conspecifics. Indeed, odour cues in the extruded sand of a burrow system may provide a means for solitary females to advertise themselves to dispersing males (Braude 2000). We predicted that both male and female mole-rats would discriminate between sand collected from the tunnel systems of males and females. We also predicted that mole-rats would discriminate between sand collected from solitary non-breeders of the opposite-sex, that represent a potential breeding opportunity, and sand from unfamiliar breeding groups, that represent potential breeding opportunities with competition.

METHODS

Study Animals and Husbandry

Data were collected from a captive population of Damaraland mole-rats maintained between October 2013 and April 2020 at the Kuruman River Reserve in the Northern Cape, South Africa. The captive population originated from 25 wild groups trapped in the reserve and surrounding area between February and October 2013 (mean ± SD wild group size = 8.16 ± 5.0, range = 2-26). Since 2013, the captive population was expanded through the pairing of unrelated individuals. Groups were housed in standardized artificial tunnel systems made of polyvinyl chloride (PVC) pipes, with windows of transparent plastic through which behaviour could be observed. Each self-contained tunnel system contained a nest box, a toilet, a food store and a waste box. Individuals were identified using a unique coloured dye mark applied to their head patch and a passive integrated transponder tag implanted in early life. Animals were provisioned with sweet potatoes and cucumbers twice daily (*ad libitum*) and fresh sand was provided daily through vertical pipes, which individuals swept through their tunnel system. The fresh sand was taken from a dune close to the laboratory that housed the captive population. As wild mole-rats are not found on this part of the reserve, this sand was also used as a control stimulus in our experiments.

Previous studies have shown that Damaraland mole-rats of both sex disperse during adulthood (Hazell et al. 2000). Individuals have the potential to reproduce as early as 1.5 years of age and over 90g in females and 100g in males (Thorley et al. 2018). Experimental subjects (n = 12 males, n = 13 females) were subordinate, non-breeding mole-rats of reproductive age (males: mean ± SD = 2.90 ± 0.95yrs; females: 2.62 ± 0.90yrs) and weight (males: mean ± SD = 155.33 ± 35.60g; females: 109.08 ± 25.53g), selected from a captive population of 554 individuals from 101 groups (mean ± SD captive group size = 5.49 ± 4.44, range = 1-17). All experimental subjects were considered to be pre-dispersive because they had temporarily escaped their tunnel system on more than five occasions in the six months prior to the start of the experiment (pipes occasionally open or individuals gnaw holes in the plastic).

Olfactory Stimuli

Focal subjects were presented with four categories of odour stimuli: sand collected from the tunnel systems of solitary, non-breeding males (*n* = 4), sand collected from the tunnel systems of solitary, non-breeding females (*n* = 4), sand collected from the tunnel systems of active breeding groups (*n* = 17), or control sand (see above). For the experimental stimuli, sand was collected from the waste box of mole-rat groups at least 12 hours after the fresh sand had been provided, so all group members had the opportunity to interact with sand prior to its use in the experiments. All solitary individuals were non-breeding adults of reproductive age and weight. These animals were either evicted from their natal group as a subordinate non-breeder ($n = 3$), part of a social pair whose partner died or emigrated before breeding ($n = 3$), or the only remaining subordinate member of a once larger group ($n = 2$). In all cases, animals were solitary for at least two months before the experiment began. Breeding groups were defined as groups with a breeding pair that had produced at least one litter within the six month period prior to the start of the experiment, and contained at least one male and one female non-breeder. All solitary individuals and breeding groups were unfamiliar to the test subject. Subjects were presented with a two-way choice of experimental or control stimuli in a series of experimental treatments:

1. Same-sex non-breeder (SSN) versus solitary, opposite-sex non-breeder (SON).
2. Breeding group versus SON.
3. Control sand versus SON.
4. Control sand versus breeding group.

Experimental Procedure

The research carried out in this study was approved by the University of Pretoria Animal Ethics Committee (permit numbers EC089-12 and SOP-004-13). Trials were conducted in a T-maze made from the same PVC pipes used to build the artificial tunnel systems (Fig. 1, Supplementary Fig. S1.). The maze contained a starting chamber (30 x 20 x 14cm) with a metal sliding door leading into a 64 x 7cm entrance tunnel followed by two 80 x 7cm side tunnels (arms) fitted with windows of transparent film. The end of each arm was filled with a 30cm plug of sand (total volume = 1154.5cm^3), with a ratio of 2:1 control sand to group sand for the experimental stimuli or 30cm control sand for the control stimulus. Any detritus in the experimental sand (e.g. pieces of food, faeces) was removed and, if necessary, control sand was wetted with distilled water so that the two sand stimuli being used in a single trial were of equivalent dampness, thus equally moveable. The first 40cm of each arm was fitted with a metal grate in order to dispel cleared sand and minimize the movement of sand from one arm to the other.

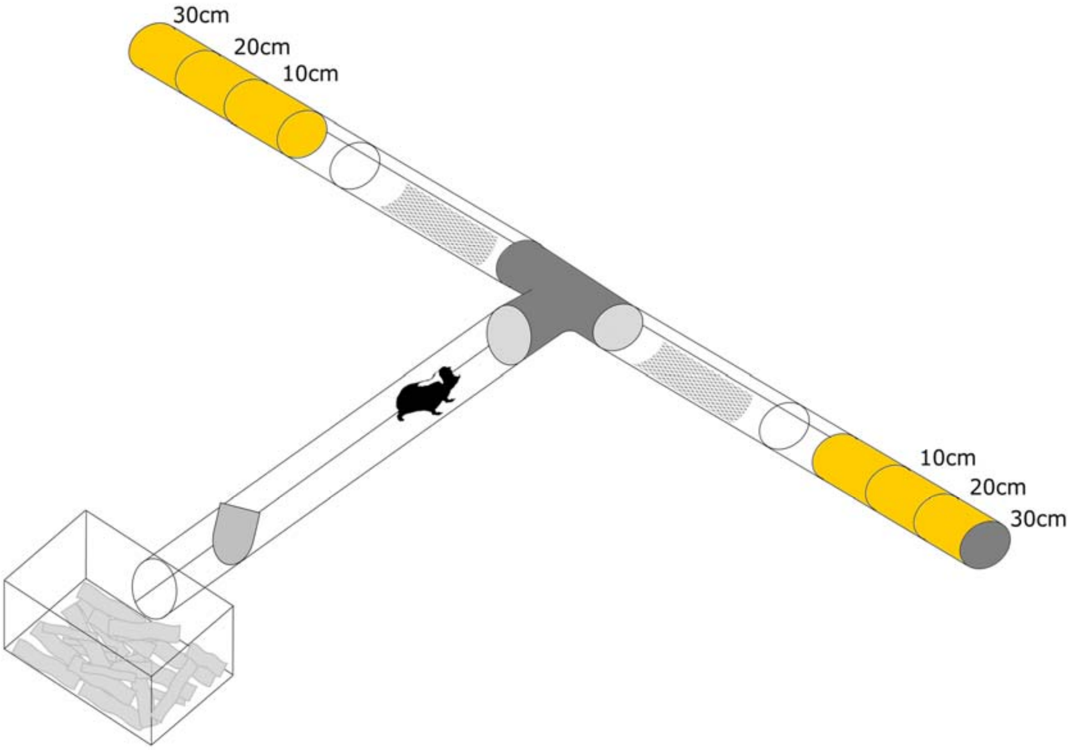

Figure 1. Experimental T-maze set-up. After entering the T-maze Damaraland mole-rats had a choice of nosing and moving two 30cm plugs of sand that each contained a different olfactory stimulus. Any sand removed from the maze arm would pass through a metal grid incorporated in the bottom side of a pipe, preventing the mixing of the stimuli. Digging effort was measured in 10cm increments. A single trial lasted 10 minutes, or until mole-rats completely cleared both arms of sand.

Trials were conducted between 07:00 and 16:00 SAST during 12 February – 7 April 2020. Subjects were removed from their groups and placed in an isolation box with standardised food, sand, paper and enrichment for 12-24hrs prior to each trial to simulate emigration from the group. All subjects were exposed to each treatment twice, in a controlled sequence, except for one female that was exposed to treatment one once, before being replaced by another female of similar age and weight for the remaining treatments. This generated 192 trials of 4 treatments on 25 subjects. For each subject, the group used for each experimental stimuli type (e.g. unfamiliar breeding group) was randomly assigned, and subjects were not presented with sand from any tunnel system more than once (full trial design presented in Supplementary Table S1). For each trial, stimuli were randomly placed into the left or right arm of the T-maze.

Before each trial, the subject was placed into the starting chamber. The door was opened and the trial began as soon as the subject moved into the entrance tunnel and the door was then closed. Subjects typically emerged from the starting chamber as soon as the door was opened and none remained in the starting chamber for more than a few seconds. Subjects were placed back in their groups for 2-3 days between each trial in order to retain familiarity with group members. The maze was disassembled and cleaned with 70% ethanol between trials. Data were collected in real time and inputted onto an Android tablet (Pendragon Software Corporation, Chicago, USA). Trials were also recorded using a Sony HDR CX240 camcorder for cross-checking. Trials lasted 10 minutes, with pilot studies indicating that this gave individuals the opportunity to interact frequently with sand in both tunnel arms whilst also allowing for the possibility that individuals would clear all the sand in the tunnel system. Accordingly, the mean number of alternations between left and right arms across all trials was 0.91 alternations/minute (median ± SD = 19.9 ± 27.3). Subjects cleared both arms of sand on 24 occasions (n = 192 trials).

Behavioural Response

Mole-rat responses were recorded by behavioural assay. The full ethogram is presented in Supplementary Table S2. Briefly, behaviour was recorded continuously as: dig, gnaw, nose sand, retreat, sniff, sweep and miscellaneous. Whether these behaviours were observed in the neutral tunnel, the left arm or the right arm was recorded, allowing the recovery of complete time budgets. In addition, as a measure of digging effort, the time taken to move 10cm, 20cm, or 30cm of sand from each tunnel arm were recorded as instantaneous events. Subjects were considered to exhibit discrimination between the two presented stimuli if one or more of the following differed between maze arms: (i) the proportion of time spent in the arm, (ii) the proportion of time spent nosing sand, which is a display of investigative behaviour, (iii) the proportion of time spent moving sand (summed duration of digging and sweeping) or (iv) the amount of sand removed by the end of the trial. Traditional preference test set-ups, such as the ‘habituation-generalization paradigm’, can elucidate whether individuals discriminate odours by quantifying differences in the time spent interacting with them, but whether this is motivated by the scent’s novelty, or by some attractive or repulsive property of the producer, is not always clear. By using sand as the experimental stimulus, and by separating behavioural parameters into investigative and digging behaviour, we try to address motivation to engage with an odour, as well as interest. In our study, subjects were considered to exhibit a preference for the experimental stimulus if they spent proportionally more time moving sand from the arm containing the experimental stimulus compared to the control, and/or removed more experimental sand.

Statistical Analysis

All analyses were performed in R version 3.6.1 (R Core Team 2020). To test whether different combinations of sand stimuli affect behavioural time budgets, we fitted a series of multinomial logistic regressions. These models capture the multinomial nature of our behavioural observations, whereby the more time an individual spends engaged in one behaviour, the less time it has to engage in other behaviours. We used these models to investigate whether mole-rats discriminated between sand stimuli based on the following behavioural responses: (i) the proportion of time spent in each arm of the T-maze, (ii) the proportion of time spent moving sand, and (iii) the proportion of time spent nosing sand. In all cases, the behavioural responses of males and females were grouped to allow comparisons by sex, and models were fitted in a Bayesian framework to include random effects for the individual and the trial.

To investigate the effect of sand stimulus on the time spent in each arm of the T-maze, we fitted a multinomial model to quantify the probability per unit time of being in a given arm, i.e. the proportion of time spent in that arm. The response variable represented the per-second location of each individual within each trial (n = 25 individuals, 48 trials). Thus, for a 10-minute observation, a single individual has 600 rows of data denoting its location during each trial (mean trial duration = 591.02s ± 33.95 SD, median = 600s, range = 367 – 600s). Setting the reference category as the neutral arm of the T-maze, the log-odds that individual *i* in trial *j* is in the arm with sand stimuli 1 (*k* = 2) or sand stimuli 2 (*k* = 3) instead of the neutral arm (*k* = 1) at time *t* is given as:

$$\log\left(\frac{\pi_{1ijt}}{\pi_{2ijt}}\right) = \beta_{1ijt} + \beta_{3ijt} + \gamma_{1i} + \gamma_{1j}$$

$$\log\left(\frac{\pi_{1ijt}}{\pi_{3ijt}}\right) = \beta_{2ijt} + \beta_{4ijt} + \gamma_{2i} + \gamma_{2j}$$

where the probability of observing each category is π_k, and $\pi_1 + \pi_2 + \pi_3 = 1$, following the generalized Bernoulli distribution. Here, β_{1ijt} and β_{2ijt} are the intercepts that contrast the two sand stimulus categories against the neutral category, β_{3ijt} and β_{4ijt} are the fixed effects of sex on each behaviour, and Υ_n are the individual-level, *i*, and trial level, *j*, random effects. Models were fitted in the 'brms' package (Bürkner 2018) with three chains of 3000 iterations, of which 600 were dedicated to the warm-up. Model diagnostics and posterior predictive checks highlighted adequate mixing of chains and appropriate choice of priors. Because multinomial models provide odds ratios, coefficients are not straightforward indicators of the effect of a predictor on the probability of doing behaviour *k,* so their interpretation should make use of predicted probabilities. In our results, we therefore emphasize cases where the 95% credible intervals (CI) of the predicted probabilities do not overlap.

To investigate the effect of sand stimulus on the time spent moving and nosing sand we repeated the above framework, but here, the response variable was the behaviour being performed. We fitted a multinomial model to quantify the probability per unit time of nosing or moving sand, i.e. the proportion of time spent performing these behaviours, in each arm. For each model, the response represented one of $k = 5$ behavioural categories: Moving sand stimulus 1, Moving sand stimulus 2, Nosing sand stimulus 1, Nosing sand stimulus 2 and Other. Here, 'Other' refers to any other behaviour observed irrespective of stimuli, and was set as the reference category. Sex was fitted as a fixed effect and as before, biological importance was determined by the difference in CIs for the predicted probabilities of moving and nosing sand between the two stimuli. Full model outputs are presented in Supplementary Tables S3-S7.

To quantify digging effort, we measured the amount of sand removed during the trial and, when any arm was cleared of sand before the trial finished, which arm was cleared first. To test the effect of sand stimulus on the amount of sand removed, we carried out ordinal logistic regressions (cumulative link mixed models, CLMM) fitted in the R package 'ordinal' (Christensen 2019). In short, ordinal logistic regressions model the cumulative probability of ordered categories, where each cumulative probability reflects the probability of a given categorical value or lower. In our case, data from each treatment were analysed in separate models, and for each model, the distribution of outcomes (four factor levels: 0cm, 10cm, 20cm, 30cm) was parameterised on the log-cumulative-odds scale, giving three intercepts that represent 'cut-points' at 0-10cm, 10-20cm, and 20-30cm of sand moved. Sand stimulus was included as an explanatory variable throughout to estimate the change in log-cumulative-odds at each intercept, allowing for an overall shift in the probability mass towards higher or lower amounts of sand clearing according to the contrast in response to different sand stimuli. Trial ID nested within subject ID were fitted as random effects throughout. In the results, we report the effect of sand stimuli in the different treatments as an indicator of significance, and include full model tables (including intercepts) in Supplementary Table S8.

Finally, we performed a series of one-sample tests for equality of proportions with continuity correction to determine whether sand stimulus affected which arm was cleared first (Supplementary Table S9). For all non-Bayesian analyses we interpreted all effects below an alpha threshold of 0.05 as being biologically important, but also note cases where alpha < 0.1 as being indicative of a trend in the data.

RESULTS

Time Budgets

Individuals of both sexes spent more time nosing the sand taken from the tunnel systems of mole-rat groups (whether SON or breeding) than control sand, as indicated by the significant contrasts in Fig. 2, demonstrating that individuals can identify mole-rat odours in the sand. Females spent more time moving the sand taken from the tunnels of solitary males (Fig. 3), and more time in the maze arm containing sand from the tunnels of solitary (Fig. 4) when compared with breeding groups. Although an increase in time spent moving sand from solitary females was also detected in males presented with the same treatment, the contrasts only reached statistical significance in females (Fig. 3; full model outputs in Supplementary Tables 3-7).

Digging Effort

Males removed more sand from arms containing sand from the tunnels of solitary females when presented with sand from solitary females versus breeding groups (CLMM: estimate ± SE = 1.35 ± 0.63, $Z = 2.14$, $P = 0.03$) and control sand (CLMM: estimate ± SE = 1.82 ± 0.72, $Z = 2.51$, $P = 0.01$). Males also removed more sand from breeding groups when presented with sand from breeding groups versus control sand (CLMM: estimate ± SE = -1.39 ± 0.66, $Z = -2.12$, $P = 0.03$), and exhibited a tendency to move more sand from arms containing sand from solitary male tunnels when presented with sand from the tunnels of solitary males versus solitary females (CLMM: estimate ± SE = 1.14 ± 0.63, $Z = 1.80$, $P = 0.07$, Table 1). In contrast, sand stimulus had little effect on the amount of sand moved in females, although there was a tendency for females to move more sand in arms containing sand from solitary male tunnels when presented with sand taken from solitary male tunnels versus control sand (CLMM: estimate ± SE = 1.21 ± 0.69, $Z = 1.76$, $P = 0.08$, Table 1).

Males cleared the arm containing sand from breeding groups first when presented with sand from breeding groups versus control sand ($\chi^2_1 = 4.9$, $P = 0.02$), and solitary male sand first when presented with sand from the tunnels of solitary males versus solitary females ($\chi^2_1 = 4.08$, $P = 0.04$). There was also a tendency for males to clear the arm containing sand from solitary females first when presented with sand from solitary female tunnels versus breeding groups ($\chi^2_1 = 2.76$, $P = 0.09$, Table 2). However, sand stimulus type had no effect on which arm females cleared first (Table 2).

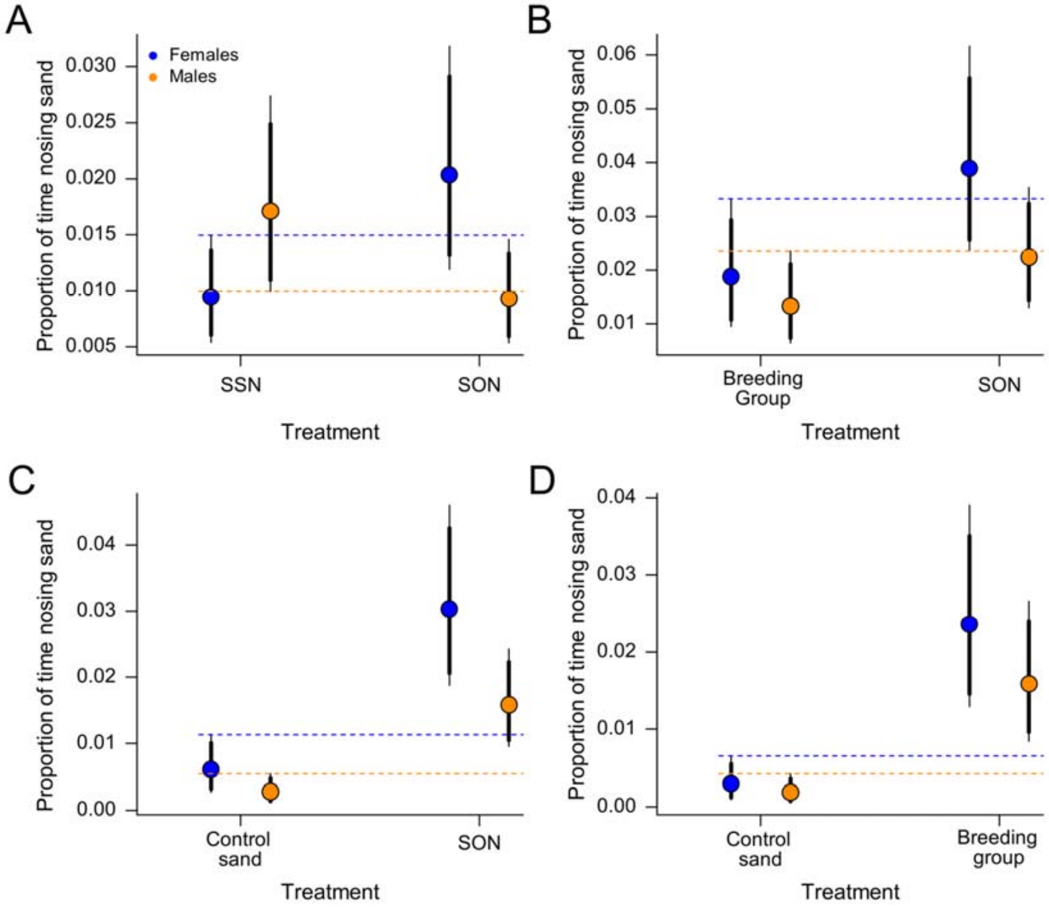

Figure 2. Proportion of time spent nosing sand in each arm. Model predictions of mole-rat time budgets across four two-choice experimental treatments (n = 24): (A) same-sex non-breeder (SSN) versus solitary, opposite-sex non-breeder (SON), (B) breeding group versus SON, (C) control sand versus SON, (D) control sand versus breeding group. Points display the predicted mean proportion of time spent nosing sand for males (orange) and females (blue), with 89% (thick line) and 95% (thin line) credible interval (CI). Horizontal dotted lines mark upper and lower CIs of contrasting stimuli .

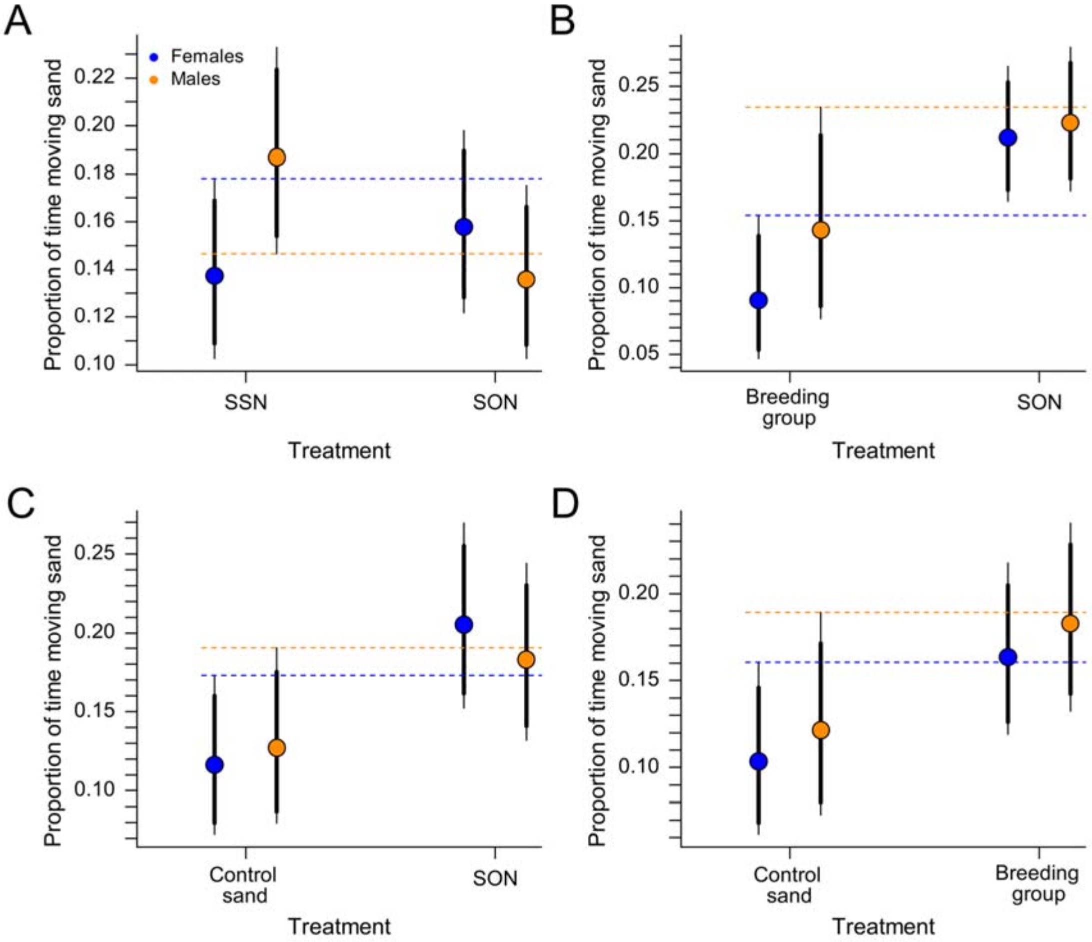

Figure 3. Proportion of time spent moving sand in each arm. Model predictions of the mole-rat time budgets across four two-choice experimental treatments (n = 24): (A) same-sex non-breeder (SSN) versus solitary, opposite-sex non-breeder (SON), (B) breeding group versus SON, (C) control sand versus SON, (D) control sand versus breeding group. Points display the predicted mean proportion of time spent moving sand for males (purple) and females (green), with 89% (thick line) and 95% (thin line) credible interval (CI). Horizontal dotted lines mark upper and lower CIs of contrasting stimuli .

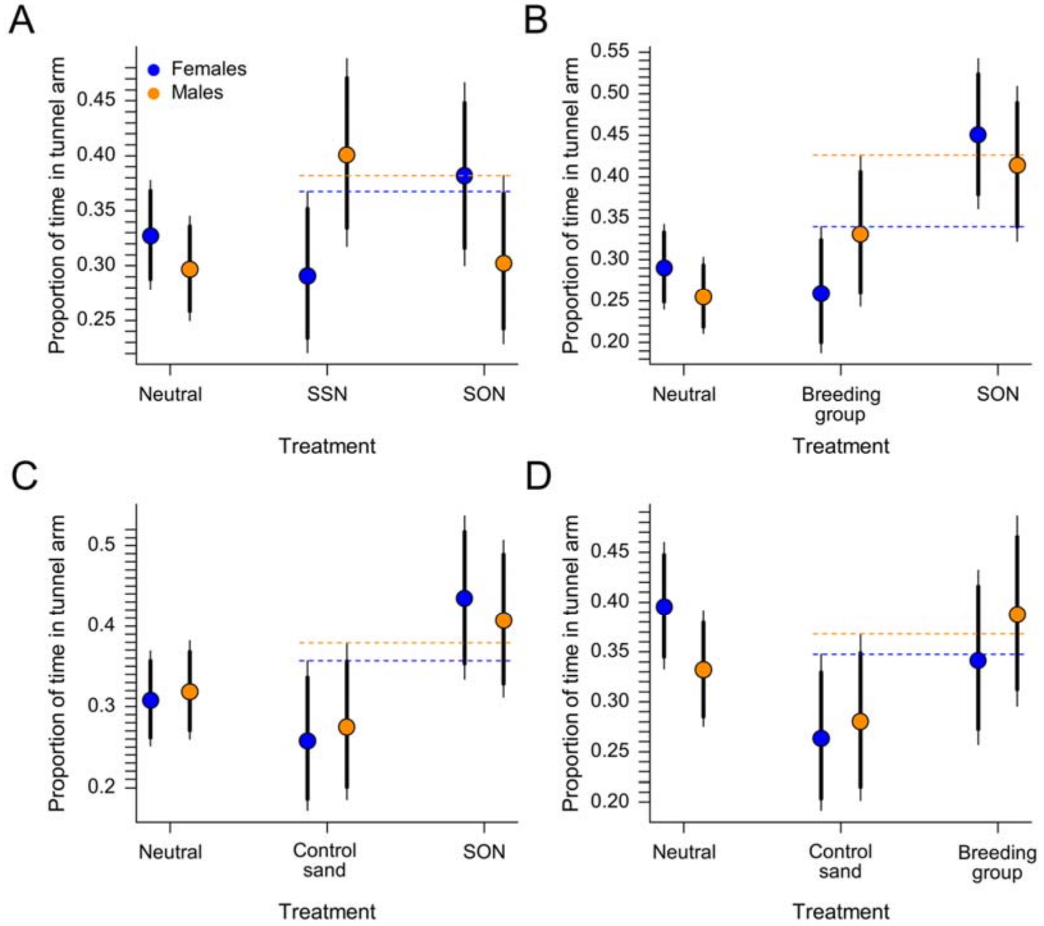

Figure 4. Proportion of time spent in each arm. Model predictions of mole-rat time budgets across four two-choice experimental treatments (n = 24): (A) Same-sex non-breeder (SSN) versus solitary opposite-sex non-breeder (SON), (B) breeding group versus SON, (C) control sand versus SON, (D) control sand versus breeding group. Points display the predicted mean proportion of time in each arm for males (orange) and females (blue), with 89% (thick line) and 95% (thin line) credible interval (CI). Horizontal dotted lines mark upper and lower CIs of contrasting stimuli.

Table 1: Total amount of sand removed. Mole-rat digging effort measured in the amount of sand removed from T-maze arms across four two-choice experimental treatments (n = 24): (A) same-sex non-breeder (SSN) versus solitary, opposite-sex non-breeder (SON), (B) breeding group versus SON, (C) control sand versus SON, (D) control sand versus breeding group. Sand removed (cm) is binned into 10cm increments to a maximum of 30cm. Trials lasted 10 minutes.

		Treatment A		**Treatment B**		**Treatment C**		**Treatment D**	
Sex	**Sand removed (cm)**	SSN	SON	Breeding group	SON	Control sand	SON	Control sand	Breeding group
Female	0	2	1	7	2	4	2	8	3
	10	8	12	6	8	7	7	6	9
	20	9	7	8	6	8	7	6	8
	30	5	4	3	8	4	8	4	4
Median		*20*	*10*	*10*	*20*	*15*	*20*	*10*	*15*
Male	0	4	5	5	0	3	2	4	2
	10	5	5	7	7	8	5	12	9
	20	5	11	6	6	9	6	4	4
	30	10	3	6	11	4	11	4	9
Median		*20*	*20*	*15*	*20*	*20*	*20*	*10*	*20*

Table 2: First arm to clear of sand. The number of trials in which the first arm mole-rats cleared contained sand from a same-sex non-breeder (SSN), opposite-sex non-breeder (SON), breeding group or control sand (n = 24) across four two-choice experimental treatments: (A) SSN versus SON, (B) breeding group versus SON, (C) control sand versus SON, (D) control sand versus breeding group. In some treatments, no arm was cleared. Trials lasted 10 minutes.

Sex		**Treatment A**	**Treatment B**	**Treatment C**	**Treatment D**
Male	SSN	10	-	-	-
	SON	2	10	8	-
	Breeding group	-	3	-	9
	Control sand	-	-	3	1
	Not cleared	12	11	13	14
Female	SSN	3	-	-	-
	SON	3	8	8	-
	Breeding group	-	2	-	3
	Control sand	-	-	2	4
	Not cleared	18	14	14	17

DISCUSSION

This study shows that Damaraland mole-rats are able to discriminate between sand taken from the tunnel systems of other mole-rat groups and control sand, suggesting they have the capacity to identify conspecifics using olfactory cues. Both sexes spent more time investigating sand taken from mole-rat tunnels when compared with control sand, irrespective of whether the sand was taken from solitary, opposite-sex non-breeders (SONs) or breeding groups (Fig. 3). Mole-rats also tended to move more sand from maze arms containing sand from mole-rat tunnels when compared with control sand (Table 1), indicating that odour cues in sand could potentially be used by dispersing individuals to locate non-natal groups. To date, only a handful of studies have investigated the use of olfactory cues for social recognition in bathyergid mole-rats (Heth et al. 2002a; Toor et al. 2015), despite other aspects of their behaviour and physiology receiving much attention (Sherman et al. 1991, Bennett and Faulkes 2000; Buffenstein 2008). Our experimental results therefore form an important step in guiding future studies on social recognition in this clade.

When presented with a choice of sand taken from the tunnels of SONs or breeding groups, females spent more time moving the sand from solitary males (Fig. 3). Although males did not spend significantly more time moving sand, they did remove a higher volume of sand taken from solitary females in this treatment (Table 1). This suggests that males expended greater effort per unit time when moving sand from solitary females. Another possibility is that because males are larger they are able to clear sand at faster rates (Zelová et al. 2010), and that as a consequence, any contrasts in digging effort are accentuated when considered in terms of the amount of sand moved, especially when this amount was measured on categorical rather than continuous scale. Considering both sexes together, these results suggest a preference for SONs over breeding groups. Our results are supported by field data showing that immigration of dispersers of either sex into active breeding groups is very rare, with females being most likely to settle alone after natal dispersal where they are often joined by unfamiliar dispersing males (Finn 2017). Indeed, repeated captures of wild individuals have shown that once a new tunnel system has been excavated, solitary females can remain there for years, rather than attempting a secondary dispersal to join an active breeding group (Finn 2017). A similar pattern of dispersal has been identified in naked mole-rats, in which nascent groups are formed in a two-step process, whereby lone females disperse from their natal group and settle in isolated burrow systems, then are subsequently joined by dispersing males with whom they will breed (Braude 2000). Laboratory studies have also shown that Damaraland mole-rats are highly xenophobic (Jacobs et al. 1998). Aggression by residents towards immigrants is sex-specific, with females directing aggression towards females and males directing aggression towards males (Cooney and Bennett 2000), and is mostly initiated by the dominant breeder (Cooney 2002). Although laboratory studies have shown that attempts to join established groups often result in severe or fatal injury (Jacobs et al. 1998), wild groups can contain immigrants and extra-pair offspring, suggesting that immigration is occasionally successful, if only for a brief time (Burland et al. 2004; Torrents-Ticó et. al. 2018). However, our findings are consistent with dispersers avoiding active breeding groups and the risk of costly disputes with same-sex residents, via olfactory cues.

One unexpected result from our study was the tendency for both males and females to exhibit a greater response to male odour, as we had predicted that both sexes, when given the choice, would prefer opposite-sex non-breeders that provided a mating opportunity without competition. Though not always receiving statistical support, one possible explanation for this tendency is that the sand from males was more odiferous. However, if odour strength was the basis on which the choice was made then we may have also expected to see a stronger response towards sand from breeding groups when contrasted with sand from solitary individuals, which was not borne out in our results. An alternative explanation is that the greater response of either sex to male odour might reflect competing drives. For females, the response to male odour may indeed reflect the benefits of a mating opportunity, whereas in males, the response towards males might be driven by intrasexual competition, to the point where this overrides any competing preference for a potential mating. Though speculative, the possibility for competition to mediate the sex difference in response, with males being more strongly inclined towards agonism with conspecifics, is supported by data showing that males have shorter breeding tenures than females (Young and Bennett 2013), as well as being substantially larger. In general though, sexual selection in mole-rats has received little attention and whether this presents a plausible explanation for this specific result warrants further study.

The use of odour cues for social recognition is well-documented, particularly in rodents (e.g. Johnston 2003; Stockley et al. 2013; Roberts et al. 2018). Whether odour profiles in Damaraland mole-rats differ between males and females, or breeders and non-breeders is currently not known, but differential odour profiles, or 'signatures', that signal sex or reproductive status have been identified in several rodent species, such as house mice *Mus musculus*, Syrian golden hamsters *Mesocricetus auratus* and meadow voles *Microtus pennsylvanicus* (reviewed by Ferkin 2018). Analyses of volatile odour compounds using gas chromatography have revealed that the relative proportions of common volatiles in the odour profile convey information about identity (Singer et al. 1997). It is possible that olfactory cues associated with breeding status could provide a mechanism by which Damaraland mole-rats recognise breeding groups. Alternatively, it may be the case that odour cues from breeding groups are simply more complex than those from solitary individuals and that this is enough to aid in decision making. Although the proximate basis for olfactory recognition in Damaraland mole-rats is beyond the scope of this study, further advances in methods for sampling volatile compounds (Weiß et al. 2018) offer a promising approach for testing whether odour signatures exist in Damaraland mole-rats, which may mediate the discriminatory behaviour we observed in our experiments.

In previous mole-rat studies, focal individuals have been presented with urine, faeces or anogenital secretions collected from conspecifics (Heth et al. 2002a; Toor et al. 2015). In this study, the presentation of odour cues is indirect: we present individuals with sand taken from different categories of mole-rat group, and the sand is assumed to contain odour cues that permit discrimination between these categories due to the differences discussed above. A further assumption of our experiment is that olfactory cues, if present in the sand, are strong enough to elicit a response. That more direct odour stimuli, such as urine, or indirect stimuli which may contain more olfactory compounds, such as nesting material, could elicit a stronger response than sand is a possibility. However, we selected sand as our experimental stimulus for three reasons. First, it is more ecologically relevant to dispersal behaviour in the wild, whereby the first conspecific odour a disperser encounters is within the mounds of sand extruded by other groups. Only after entering a novel burrow system will individuals have the opportunity to sniff other individuals or locate the nest, the consequences of which could be fatal because of the xenophobic nature of mole-rats (Jacobs et al. 1998). Second, food exudates in the sand are used to locate food sources in the closely related Ansell's mole-rat (Heth et al. 2002b), suggesting that odours cues in sand could also be effective in social contexts. Finally, by using sand we argue that it is possible to assess the motivation of individuals to engage with an odour, as measured by the amount of time spent digging and the amount of sand removed. Our finding that mole-rats spent more time investigating sand from other mole-rat groups than control sand, and that both sexes increase their digging effort in sand taken from solitary, opposite-sex individuals over breeding groups, indicate that conspecific odour cues are present in sufficient quantities to elicit behavioural responses.

Despite our focus on olfaction, it is worth considering whether social recognition may involve cues of other sensory modalities. In naked mole-rats, vocalisations are used frequently in social interactions (Pepper et al. 1991; Yosida et al. 2007), and recent work has also identified group level dialects that can facilitate group recognition (Baker et al. 2021). Elsewhere, a study on the spalacid mole-rat *Tachyoryctes daemon* suggests that seismic signals propagated through the environment may also be used for communication (Hrouzkové et al. 2013), but the precise function of seismic signals, and whether they convey producer identity, remain to be determined. Generally, although odour may still operate in combination with other phenotypic cues, olfaction appears to have a primary role in social recognition in this clade.

CONCLUSIONS

By their subterranean nature it will always remain challenging to investigate social behaviour of mole-rats in the wild. Genetic analyses of natural populations can further our understanding of some aspects of social recognition, such as whether breeders pair assortatively (e.g. Meléndez-Rosa et al. 2018). Alongside field data, laboratory experiments will be crucial for investigating the cues that facilitate intra-specific interactions in these highly social mammals. While the reproductive physiology of social mole-rats is relatively well-studied, much remains unknown about how social behaviour is mediated, and the proximate mechanisms by which conspecifics are recognized. This study provides timely insight into the role of olfactory cues in discriminatory behaviour and reveals a putative mechanism by which mole-rats are able to make adaptive dispersal decisions.

DATA AVAILABILITY STATEMENT

Data will be made available in a suitable digital repository.

Declarations of interest: none

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