

## Colony member recognition and xenophobia in the naked mole-rat

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(Received 14 February 1995; initial acceptance 1 September 1995;  
final acceptance 26 April 1996; MS. number: 4850R)

**Abstract.** The ability of naked mole-rats, *Heterocephalus glaber*, to discriminate between familiar and unfamiliar conspecifics and their response to intruders was investigated. Odour cues used by mole-rats in recognition contexts were identified in a three-way choice apparatus and 'decision rules' for accepting or rejecting conspecifics were explored in a series of odour manipulation experiments. Naked mole-rats were highly xenophobic, even to closely related foreign conspecifics, and a division of labour existed amongst the non-breeders in colony defence. The principal mechanism of recognition appeared to be distinct colony odour labels, contributed by each colony member and distributed among, and learned by, all colony members. Differences in the mixture of these odours may provide even genetically similar colonies with a unique odour label. These odours persisted despite controlling for exogenous cues. Fitness consequences of these phenomena are interpreted with respect to the need for closely related neighbouring colonies to maintain autonomy and the importance of excluding foreign competitors from within-colony rivalry for reproductive succession.

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Kin bias is a feature of social organization in many species (Gadagkar 1985; Sherman & Holmes 1985; Fletcher & Michener 1986; Blaustein & Porter 1990; Hepper 1991; Pfennig & Sherman 1995) and can occur for a number of reasons, some involving kin discrimination, others reflecting incidental consequences of discrimination at other levels (Barnard 1991). In social organisms bias towards close kin in the form of colony mates is particularly important where it serves to facilitate cooperation amongst colony members and to decrease the chances of social parasitism, theft of brood and food stores or killing of the colony (Michener 1974; Crosland 1990; Fishwild & Gamboa 1992). Social insects typically have well-developed nestmate recognition abilities, by which they admit nestmates to, and exclude non-nestmates from, their colony (Buckle & Greenberg 1981; Fletcher & Michener 1986; Gamboa et al. 1986; Venkataraman et al. 1992). In these instances discrimination may be effected at the level of group member recognition rather than the degree of kinship (Barnard 1991). If groups tend to be composed of relatives (e.g.

parent/offspring associations) such discrimination will necessarily be correlated with genetic similarity. According to Grafen (1990) kin discrimination at this level does not represent kin recognition (see, however, Blaustein et al. 1991; Byers & Bekoff 1991; Stuart 1991).

Evolutionary explanations for kin bias are often based on the assumption that the animals discriminate between conspecifics according to their genetic relatedness (Hepper 1991). It is argued that it is only by responding differentially on the basis of genetic similarity that individuals can obtain the fitness benefits as espoused by Hamilton's kinship theory (Hamilton 1964a, b). Experimental tests of this assumption and the mechanisms that enable such genetic discrimination are thus essential to theories on kin selection.

Colonies of the naked mole-rat, *Heterocephalus glaber*, a cooperatively breeding subterranean rodent (Jarvis 1981), are highly xenophobic to foreign conspecifics in the laboratory (Lacey & Sherman 1991). Intriguingly, neighbouring colonies, the most likely source of foreign conspecifics within naturally occurring populations, are also close genetic relatives (Faulkes et al. 1990; Reeve et al. 1990). Such high inter-colony relatedness is due in part to the high viscosity (low vagility) of naked mole-rat populations,

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with limited dispersal and the apparent formation of new colonies by fissioning (Brett 1991). Their close physical proximity makes them the most likely competitors in any interactions while their extremely high relatedness would suggest a limited potential for the use of genetic cues in inter-colony recognition. This raises interesting questions as to the mechanisms used by naked mole-rats to recognize colony members and reject genetically similar (i.e. siblings), but foreign, conspecifics.

Our aims in this study were to investigate (1) the ability of the naked mole-rat to discriminate between foreign conspecifics and resident members of a colony in a homogeneous environment, (2) how kinship and familiarity affect recognition ability, and (3) the possible sources of cues used in discrimination and the maintenance of colony integrity.

## METHODS

All animals used in these experiments were captive born and all experiments were performed in the laboratory. Except where noted, housing and maintenance procedures are the same as those given in Jarvis (1991a).

### Transfer Experiments

We investigated the behavioural responses of resident mole-rats to a foreign mole-rat by transferring individuals from one experimental colony to another. The transferred mole-rat is referred to as the foreigner and the colony into which it is transferred as the resident colony. We chose foreigners at random (amongst non-breeders) from their colony and then introduced them into the toilet chamber of the resident colony within 1 min of their removal. We chose the toilet chamber as the site of introduction as it was the least frequented location within the resident burrow system thus enabling us to introduce the foreigner with minimal disturbance to resident colony members. In addition, the latency time for foreigners leaving the toilet chamber was much less than for foreigners leaving either food chambers or digging arenas. This effectively decreased the time from introduction to contact between foreigner and resident mole-rats, minimizing the duration of each trial.

We used two 'relatedness classes' of foreigners in all experiments to explore the effects of familiarity versus relatedness: (1) foreign kin, which were mole-rats that had been removed from their natal colony (the resident colony) at least 6 months prior to the onset of these experiments and housed together in small groups of same-sexed individuals; and (2) foreign non-kin, which were mole-rats that were born and reared in a completely separate colony to resident mole-rats. Whilst the exact degree of relatedness between foreign non-kin and resident mole-rats was not measured (i.e. by DNA fingerprinting) previous studies (Faulkes et al. 1990; Reeve et al. 1990) have shown that intra-colony relatedness is consistently higher than inter-colony relatedness.

We performed 80 trials on four resident colonies. These included 16 foreign kin trials (four foreign kin to each of four resident colonies), 44 foreign non-kin trials (11 foreign non-kin to each of four resident colonies) and 20 control trials (five resident mole-rats to their respective resident colonies). The latter experiment was designed to control for the experimental effects of handling and transferring mole-rats. The overall experimental design ensured that all resident colonies were exposed to a similar cross-section of foreigners, to minimize the possible effects of variation in inter-colony recognition/aggression. In addition, the random selection of individuals within source colonies ensured variation in the body mass of foreigners thus allowing us to analyse the effects of body size on the acceptance or rejection levels.

Diet and nest-bedding were the same in all colonies, minimizing the possible influence of exogenous odour sources and thus allowing us to assess recognition responses in a relatively homogeneous odour environment.

We recorded the behaviour of the transferred individual, as well as its interactions with the colony residents it encountered, for a maximum of 10 min. Only three of the 60 trials involving foreigners lasted longer than 30 s, and in all these trials the foreign mole-rat was accepted. Acceptance or rejection of the transferred animal in each trial was noted on the basis of either aggressive (i.e. biting and toothfencing, sensu Lacey & Sherman 1991) or non-aggressive interactions (i.e. sniffing and ignoring) by resident colony members. Each introduced mole-rat was usually tested against several members of the resident colony because more than one animal was usually active

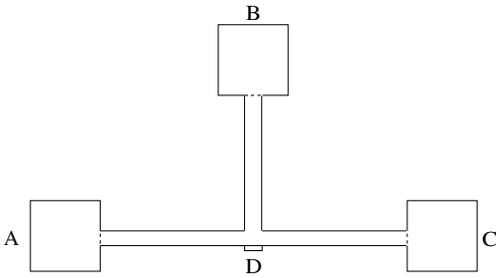


Figure 1. Odour choice apparatus. Individual mole-rats were introduced into the apparatus at D. A, B and C represent chambers into which the different odour sources were introduced. Perforations at the end of each arm enabled olfactory detection of the odour sources in each chamber. The arms of the apparatus were all interchangeable.

in the burrow system at the time of introduction. We performed control experiments by removing an individual (for less than 1 min) and then reintroducing it to its own colony.

Although it was not possible to control for behavioural idiosyncrasies of the introduced mole-rats, their behaviour was not observed to vary much. Foreign mole-rats typically advanced cautiously along the section of burrow that led directly from the toilet chamber and it was here that all aggressive interactions between them and resident colony members were observed to take place.

### Odour Choice Experiments

Nestmate recognition cues were investigated in a three-way choice test employing a T-maze (Fig. 1). All the non-breeders from two colonies (colonies 100 and 7400,  $N=45$  and  $N=37$ , respectively) were used in this study. Each trial involved removing an individual from its colony and placing it in a clean glass terrarium. After a 5-min adjustment period we introduced the mole-rat into the T-maze. Each mole-rat was presented with the choice of an odour source from its own colony, a foreign colony and a blank (a chamber containing nesting or toilet material that had not previously been in contact with any mole-rats). Two colony odour sources were used separately: the soiled litter of the communal toilet and the soiled bedding material of the nest. Each test lasted 10 min during which preference was inferred from the frequency and duration of attempts to gain access

(by gnawing at the perforated partition) to an odour source. We tested each animal once only, to minimize the effects of familiarity and learning on the results. We randomized the position of the different odour sources relative to one another to control for any directional bias amongst members of the two colonies. The entire apparatus was cleaned, wiped down with 70% alcohol and then rinsed with water, between each trial to remove residual odours from previous animals.

### Odour Manipulation Experiments

To investigate the relative importance of an individual's odour versus the colony odour in nestmate recognition experiments we manipulated the odour of individual non-breeding mole-rats. We altered the odours of individuals by exposing them to different odour sources. We conducted 45 trials (15 per colony) using 15 individuals from each of three colonies. Individuals from each colony were subjected to three different odour environments, two experimental and one control. Experimental odours involved exposing individuals (five individuals per odour) to either a foreign colony odour source or a blank colony odour source for 12 h and then reintroducing them into their natal burrow system. We exposed a mole-rat to a foreign colony's odour source by introducing it to a section of the burrow system of a foreign colony that was temporarily sealed-off from its inhabitants (to prevent physical contact). We introduced a mixture of soiled material from both the nest and toilet of the foreign colony to this sealed section to ensure the animal was exposed to a diverse compliment of foreign colony odour cues. We obtained blank colony odour sources by placing the mole-rat into a section of previously unused burrow provided with clean toilet (wood-shavings) and nesting material (wood-wool). We performed control experiments by confining an animal to a section of its own burrow system and thus exposing it to its own colony odour sources. When we returned these animals, who had been exposed to these three different odour environments in separate trials, to their colony, we recorded the behavioural response of the resident mole-rats to these individuals. The aggression rate (and acceptance/rejection) was determined as the number of aggressive acts (i.e. shoving) per manipulated individual per trial.

## Data Analyses

We recorded acceptance or rejection of foreigners in transfer experiments as a categorical variable with two states, accept or reject. Here a single attack on the foreigner was sufficient for a trial to be categorized as reject. We could not accurately record the aggression rate because of ethical considerations: to avoid any mole-rat being physically harmed we intervened whenever the potential for serious injury existed (see below). Differences in the proportion of rejected versus accepted foreign kin and foreign non-kin, and males and females, were collated for all colonies and tested using Fisher's exact test for comparing proportions (Zar 1984). We explored differences in the body mass of accepted versus rejected mole-rats using the Mann-Whitney U-test for unpaired samples.

The reduced severity of aggressive encounters between interactants in odour manipulation trials enabled us to assess the rate of aggression. We analysed these latter data using a multifactorial ANOVA with aggression rate as the dependent variable, odour treatment, colony and sex as factors and the manipulated individuals' body mass as a covariate. To determine the effects of an intruder on the general activity levels within the colony we used a paired *t*-test to compare the levels of activity of all non-breeders within the colony before the introduction and immediately after the removal of a foreign individual. We analysed the relationship between the behaviour of resident mole-rats and their body mass using Spearman's rank correlation tests. We analysed all odour trials using the Friedman's analysis of variance model for related samples. In all the above analyses we used parametric tests when the distribution of data, transformed where necessary, permitted. Otherwise, we used non-parametric tests.

## Ethical Note

We performed preliminary experiments to determine the most effective and yet least stressful means of testing the proposed hypotheses. Given the potentially harmful design of the transfer experiments it is important to point out that we considered alternatives before proceeding with the final protocol and, once adopted, precautions were taken to prevent the physical injury of animals in all trials.

We first attempted placing foreign individuals in separate containers that could be placed in olfactory but not physical contact with resident colonies. However, the results from these trials showed that there was no measurable response to either controls or foreigners. Resident mole-rats gnawed at the perforated dividing wall for both controls and foreign conspecifics. There was no evidence of threats (i.e. open mouthed gaping), and obviously no chance of mole-rats performing any other aggressive interactions in their natural repertoire. Furthermore, while mole-rats chose their own colony odours over foreign odours in the odour choice trials they never displayed any agonistic response to the foreign odour. Given these limitations we decided to adopt a more direct method of measuring inter-colony aggression, but not without ensuring that no individuals were subjected to physical harm.

Of paramount importance was our ability to terminate any experiment at the point when the foreigner and the residents had initiated the ritualized act associated with conspecific aggression but prior to the occurrence of any potentially injurious aggression. The former took the form of shoving, open mouthed gapes, incisor fencing, toothlocking and biting, typically followed by a rapid retreat by the foreign individual. Here biting as defined by Lacey et al. (1991, page 237; 'the jaws of one animal close over the body of another animal') does not imply that the skin is broken. By ensuring that we had immediate access to interactants (by removing the roof of the burrow) at all stages during the experiment we were able to intervene prior to the escalation of ritualized aggression. When the roof of the burrow is removed all mole-rats freeze, enabling us to terminate immediately any interactions. We intervened in every experiment in which we witnessed an escalation in the ritualized form of aggression (i.e. all rejections). In this way no individual in any of the experiments sustained any physical injuries (i.e. the skin was never broken).

The apparently excessive duration of transfer trials (maximum of 10 min) was a function of the fact that foreign mole-rats, in preliminary trials, occasionally remained undetected in the resident colony for up to 7 min. The decision to make the total time 10 min was thus an attempt to cater for these instances. Once olfactory/physical contact had been made between a foreigner and a

resident then the trial was invariably terminated within 30 s.

Transferred individuals in odour manipulation trials were typically shoved following their return to their natal colony. Other behaviour included biting (see above) and toothfencing. No physical injuries were sustained by any individuals. We always monitored transferred individuals as this was an integral part of the experiment. We terminated observations once colony activity and the behaviour of the transferee had returned to normal (usually within 10 min of reintroduction). A further point was that mole-rats exposed to foreign odours were not observed to show any overt signs of distress and all their exhibited behaviour patterns were part of their behavioural repertoire when in their natal burrow system.

## RESULTS

### Transfer Experiments

Naked mole-rats were highly xenophobic to foreign conspecifics. Resident mole-rats aggressively rejected foreign mole-rats (non-kin) in 93.2% of all trials (Fig. 2). There was no significant effect of sex (Fisher's exact test:  $Z=0.514$ ,  $P>0.05$ ) on acceptance or rejection. Similarly there was no significant difference in the body mass of rejected versus accepted mole-rats (Mann-Whitney  $U$ -test:  $U=0.102$ ,  $N_1=41$ ,  $N_2=3$ ,  $P=0.978$ ).

Resident mole-rats showed similar levels of rejection (Fisher's exact test:  $Z=0.916$ ,  $P>0.2$ ) of both foreign non-kin and foreign kin (Fig. 2). These results suggest that acceptance or rejection is dependent on recent association and familiarity of odours and not genetic relatedness.

Given that naked mole-rats live in the dark, have poor visual acuity, and that introduced animals were always sniffed following physical contact, it seems likely that discrimination was achieved through olfaction. In all colonies discrimination and aggressive rejection of foreigners was positively correlated with the body mass of the aggressors (Spearman rank correlation test:  $P<0.05$ , for data presented in Fig. 3), most foreigners being rejected by a small group of highly aggressive, physically robust individuals. Interestingly, despite being the principal colony defenders, these larger individuals were seldom the first to encounter introduced animals (see also Lacey &

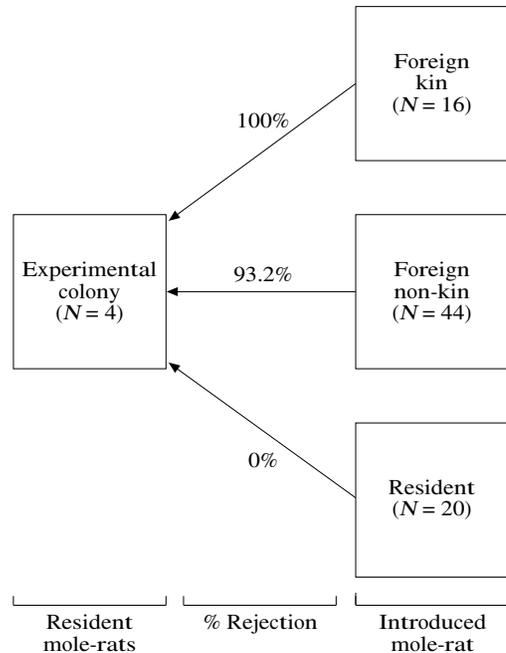


Figure 2. The percentage rejection of introduced mole-rats by resident colonies. The number of foreign and control mole-rats for each 'relatedness/familiarity' class is provided in parentheses.

Sherman 1991). Smaller more active colony members were responsible for the majority of first encounters, a probabilistic outcome of their heightened activity in the burrow (Jarvis et al. 1991). Upon encountering a foreigner these individuals typically (92% of trials) retreated and alarm-called (described by Pepper et al. 1991). Alarm callers invariably returned directly to the communal nest to alert colony members to the presence of an intruder. This behaviour resulted in a significant increase (paired  $t$ -test:  $P<0.05$  for all colonies) in the number of mole-rats actively patrolling the burrow system (Fig. 4), in addition to mobilizing the colony defenders.

Reproductive animals, despite being amongst the largest individuals in the colony, were not observed to engage in colony defence against foreigners in three of the four study colonies (Fig. 3a, c and d). In contrast, the reproductive female in colony 7400 (Fig. 3b) was responsible for the majority of aggressive acts associated with the ousting of intruders.

Controls for all transfer experiments indicate that introduction procedures did not significantly

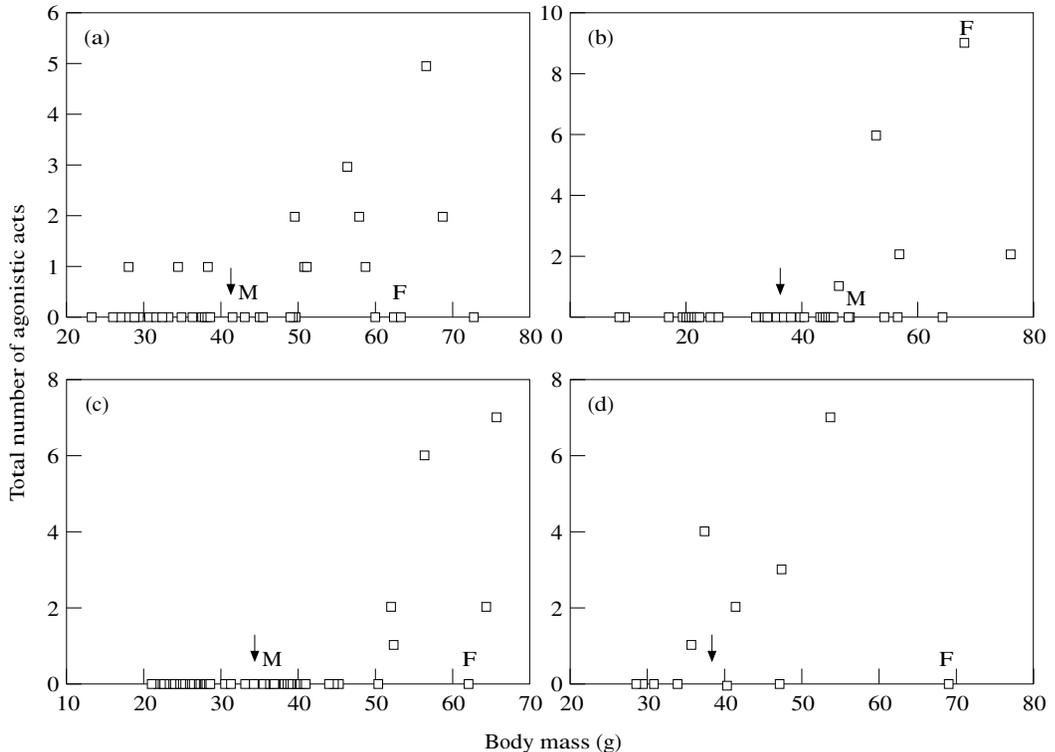


Figure 3. The relationship between aggression towards foreigners and the body mass of resident mole-rats. (a) Colony 100,  $r_s=0.46$ ,  $N=45$ ,  $P=0.0023$ ; (b) colony 7400,  $r_s=0.48$ ,  $N=37$ ,  $P=0.0067$ ; (c) colony 1000,  $r_s=0.55$ ,  $N=44$ ,  $P=0.0008$ ; (d) colony 2000,  $r_s=0.644$ ,  $N=12$ ,  $P=0.0416$ . The mean body mass for each colony is indicated by the arrow. F: breeding female; M: breeding male. There was no breeding male in colony 2000 (d).

influence the behaviour of the resident colony members (paired  $t$ -test:  $P>0.05$  for all colonies).

#### Odour Choice Experiments

Mole-rats spent significantly more time (Friedman ANOVA:  $P<0.001$  for all trials) attempting to access their own colony odours than foreign colony odours. Results were consistent for both colonies and for both experimental odour sources (Fig. 5). Mole-rats in both colonies spent more time on average attempting to access the odour source from the nest than that of the toilet. Close olfactory contact with soiled toilet material appeared to cause mild irritation of the mole-rats' nasal region with many individuals grooming their nose between efforts to access the odour source. This behaviour reduced the total amount of time that mole-rats spent attempting to access this odour source, as reflected in Fig. 5c, d.

#### Odour Manipulation Experiments

There were no significant interaction effects between odour treatment, colony or sex and consequently the main effects were calculated without them. Furthermore body mass did not covary significantly ( $F_{1,44}=0.005$ ,  $P=0.947$ ) and was thus excluded from the analysis. There was a significant difference in the aggression rate between odour treatments ( $F_{2,44}=20.46$ ,  $P<0.0001$ ) with mole-rats subjected to foreign and blank odour environments being shoved significantly more frequently than mole-rats exposed to their own colony odour (Fig. 6; Tukey multiple range test). There was no significant difference in the aggression rate of individuals exposed to either foreign or blank odour sources (Fig. 6; Tukey test). There was also a significant difference in the rate of aggression ( $F_{2,44}=4.308$ ,  $P=0.02$ ) between colonies 100 and 1000 (Tukey test), with the latter

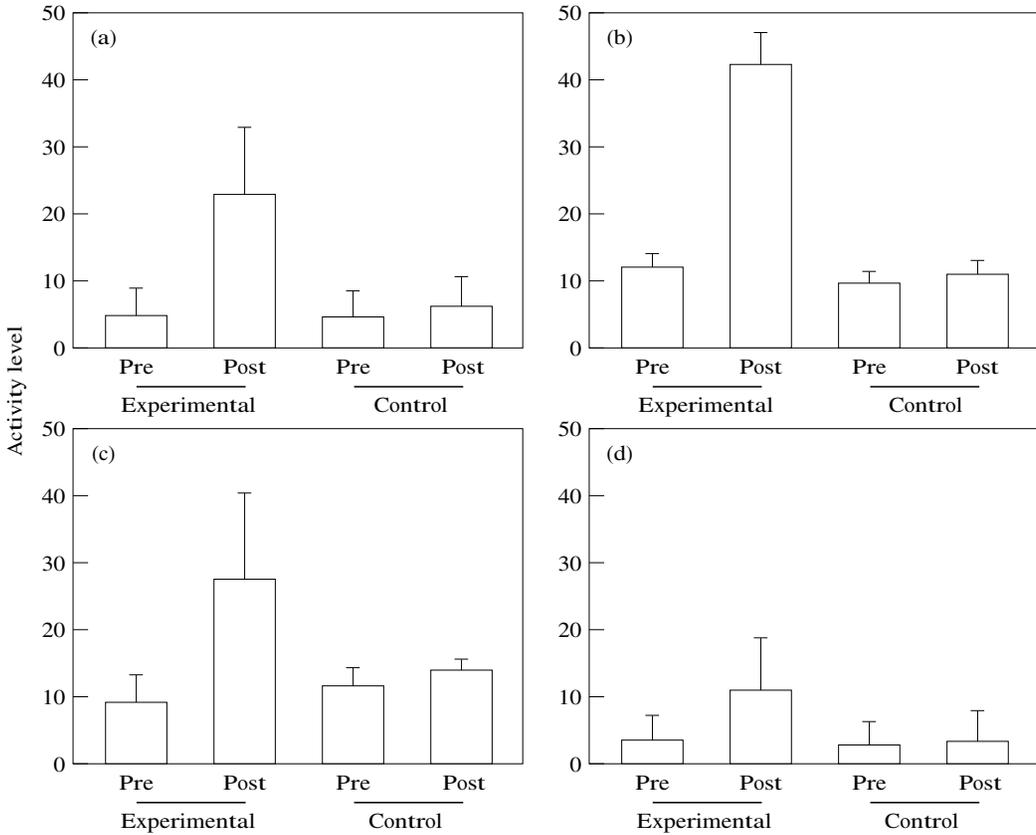


Figure 4. The mean number ( $\pm$ SD) of mole-rats active within the burrow system before and after the introduction of a foreign (experimental) and resident (control) mole-rat. Experimental data: (a) colony 7400,  $t_{18} = -5.17$ ,  $P < 0.001$ ; (b) colony 100,  $t_{20} = -14.68$ ,  $P < 0.001$ ; (c) colony 1000,  $t_{16} = -6.69$ ,  $P < 0.001$ ; (d) colony 2000,  $t_{18} = -13.56$ ,  $P < 0.001$ . Control data:  $t$ -test,  $P > 0.05$  for a, b, c and d.

exhibiting the highest levels of aggression. The sex of the manipulated individuals did not have a significant effect on aggression rates ( $F_{1,44} = 2.97$ ,  $P = 0.09$ ). All experimental animals were accepted back into their resident colony within 10 min (i.e. no more shoving or tugging at the skin).

## DISCUSSION

These results demonstrate that naked mole-rats recognize colony members and aggressively discriminate against foreign conspecifics. This ability persisted despite controlling for exogenous cues in all colonies. Naked mole-rats, however, failed to discriminate between foreign kin (siblings no longer resident in the colony) and foreign non-kin, and rejected both. This indicates that genetic

similarity per se is not the criterion used for discrimination. It is possible that because inter-colony relatedness in populations of naked mole-rats is high, foreign colony recognition systems based on a direct assessment of relatedness would lead to ambiguity. Furthermore, because naked mole-rats are predictably more likely to associate spatially and/or temporally with kin, and/or more likely to be unfamiliar with non-kin, colony recognition mechanisms need not involve an ability to recognize genetic relatives (Sherman 1980; Davis 1982; Barnard 1991). Our finding that colony members interact aggressively even with kin that have been removed from their natal burrow system for a short period (12 h), suggests that odour familiarity in naked mole-rats needs to be continually reinforced if it is to serve as an effective mechanism of colony member recognition.

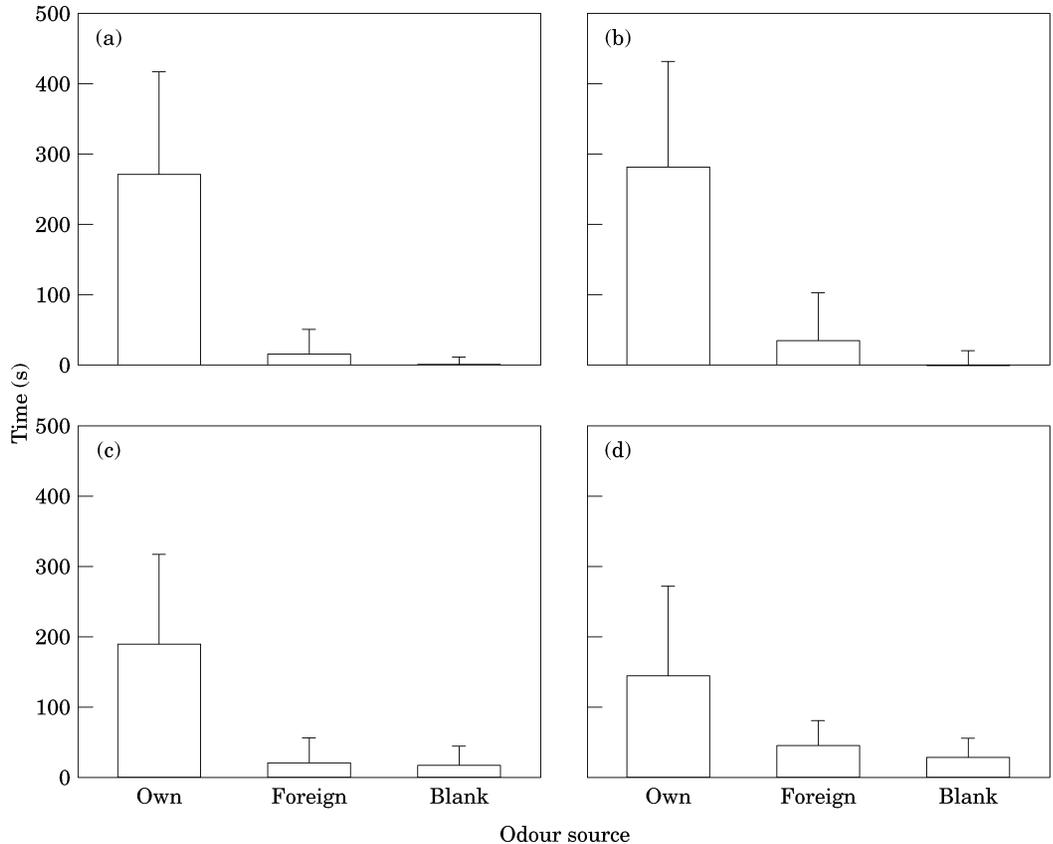


Figure 5. The mean amount of time (+SD) mole-rats spent actively attempting to gain access to the respective odour sources. (a) and (b) show data for individuals from colony 100 (Friedman ANOVA:  $\chi^2_{T,2,132}=65.899$ ,  $P<0.001$ ) and 7400 (Friedman ANOVA:  $\chi^2_{T,2,96}=50.0$ ,  $P<0.001$ ), respectively, when presented with soiled nesting material. (c) and (d) show data from colony 100 (Friedman ANOVA:  $\chi^2_{T,2,132}=41.0556$ ,  $P<0.001$ ) and 7400 (Friedman ANOVA,  $\chi^2_{T,2,96}=32.758$ ,  $P<0.001$ ), respectively, when presented with soiled toilet material.

This may be mediated by some of the communal behaviour patterns of naked mole-rats. Thus all colony members depend on the communal nest for efficient thermoregulation and routinely use the communal toilet area. In both these places they may contribute to and acquire distinctive colony odours.

These results suggest, therefore, that colony member recognition in the naked mole-rat is achieved through the mixing of individual odours to form a unique and dynamic recognition cue between colonies of closely related individuals. Thus, physically separated groups of siblings will contribute to and acquire a unique colony odour or 'badge' (sensu Linsenmair 1987). Similarly, newly acquired foreign odours are capable of inducing aggression in otherwise non-aggressive

colony members. Similar findings have been reported for the spiny mouse, *Acomys cahirinus* (Porter & Wyrick 1979) and house mouse, *Mus musculus* (Hurst et al. 1993). In contrast, in the absence of familiarity, both Richardson's ground squirrels, *Spermophilus richardsonii* (Davis 1982) and white-footed mice, *Peromyscus leucopus* (Grau 1982) can still recognize their siblings.

The odour choice experiments suggested that both the nest and toilet areas are distinctively marked with colony odours. When individuals were given a choice between their own and a foreign colony odour, they were able to distinguish between them and preferentially chose their own colony odours. Because these odour sources are derived from all members of the colony, it is likely that colony odours themselves are a

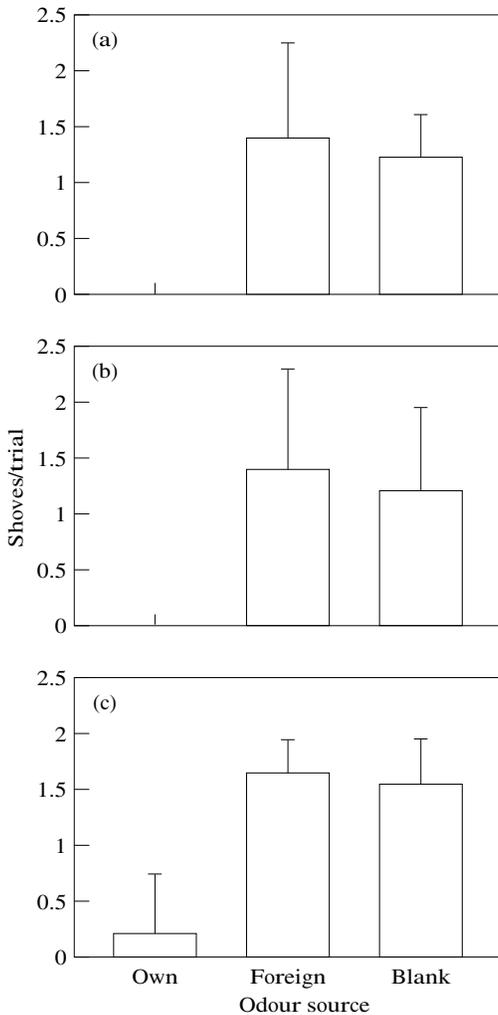


Figure 6. The mean number (+SD) of agonistic acts (shoves) performed by resident mole-rats on individuals that were returned to their colonies after separate exposure to three different odour sources. (a) Colony 100; (b) colony 7400; (c) colony 1000.

combination of individual odour cues. This 'cocktail' of odours is shared among all members of a colony but would appear to be different from that of other, even closely related, colonies (such as those formed by siblings). The colony-specific group labels are thus reliable cues for the recognition of familiar colony members but convey no direct information on genetic relatedness.

The most likely recognition mechanism in naked mole-rats would thus appear to be through the sharing of familiar odours that are spread

through close physical association. Holmes & Sherman (1983) stated that sometimes animals treat as kin those conspecifics with whom they have close association during their life. Naked mole-rats thus exhibit kin bias because, under natural conditions, there is normally a reliable correlation between genetic relatedness and the spatial/temporal component of association.

This recognition mechanism in naked mole-rats closely parallels nestmate recognition cues in some social insects. Various authors have suggested that nestmate recognition in many social insects may have both genetic and environmental components (Wilson 1971; Jutsum et al. 1979; Carlin & Hölldobler 1983; Page & Breed 1987; Hölldobler & Wilson 1990; Gastreich et al. 1991; Venkataraman et al. 1992), and that colony odours, derived from the mixing of individual odours or a common environmental odour, may have evolved as the simplest and most effective means of facilitating nestmate recognition (Hölldobler & Michener 1980).

If the penalties for failing to exclude foreign conspecifics were trivial, colony-specific recognition and colony defence would have a limited selective advantage. However, both the existence of a highly efficient defence system in naked mole-rat colonies and the existence of a reliable colony member recognition mechanism suggest that protection of the burrow system and its resources from potential usurpers (irrespective of their relatedness) is of paramount importance to their continued survival. Indeed the existence of a defence-based division of labour with small individuals recruiting large colony defenders with alarm calls suggests an evolutionary history of defence against conspecifics. Interestingly, foreigners never alarm-called whilst in the resident burrow system or following physical contact with a resident individual. These foreigners did, however (94% of all trials), alarm-call following their return to their natal burrow system, suggesting that the alarm call of the naked mole-rat is context specific, serving to alert only colony members to the presence of foreign conspecifics.

A further important selective advantage of xenophobia in naked mole-rats may be that of the selfish 'desire' to reproduce. Despite reproduction being monopolized by a minority of dominant animals in the colony, every mole-rat born to that colony has the potential to be a reproductive (Jarvis et al. 1991) and colony members are

therefore principal competitors for fulfilling this role. The acceptance of a foreign conspecific would only serve to diminish an individual's chances of attaining reproductive status, and gaining the associated direct fitness benefits. Dispersal to avoid this competition is a costly alternative for naked mole-rats and one that appears to have been selected against, judging from its rarity of occurrence (Brett 1991; O'Riain et al. 1996) and the fact that inbreeding is common both in the field (Faulkes et al. 1990; Reeve et al. 1990) and the laboratory (Jarvis 1991b).

This suggested reproductive threat is supported by our finding that colony defence against foreign conspecifics is predominantly performed by the largest/oldest members of the colony (Fig. 3). These individuals are the colony's most likely reproductive replacements in the event of the death of either of the reproductives. In another series of experiments designed to investigate reproductive succession in naked mole-rats, the new reproductives, both male ( $N=4$ ) and female ( $N=4$ ), were consistently amongst the largest (top 5%) individuals in their colony (M. J. O'Riain, unpublished data). Their large size and experience makes them worthy contestants for what is often a bloody battle to the death for reproductive rights within the colony (Jarvis 1991b). It is these individuals, therefore, that stand to lose the most, in potential direct fitness terms, by accepting a foreign conspecific into their social hierarchy. Furthermore, whilst colony defence is positively correlated with body mass in naked mole-rat colonies, the breeding female, typically one of the largest animals in the colony, rarely participates in colony defence ( $N=3$  this study,  $N=4$  personal observation). The exception to this observation was in colony 7400 (Fig. 3b) in which the reproductive female had recently acquired her sexual status through intense physical competition with colony members. This breeding female was consistently the most aggressive defender of the colony against foreigners, emphasizing the close link between colony defence and reproductive opportunity.

The ability to maintain colony integrity, in the midst of closely related neighbouring colonies, is obviously important and reflects an evolutionary history of repeated contacts between colonies. We suggest that the use of a recognition system in which the individual odours are mixed to form a unique colony odour may have evolved to func-

tion primarily as a mechanism to ensure the acceptance of colony members and the rejection of non-colony members, and as a mechanism to permit the segregation of genetically similar kin in different neighbouring colonies. This is essential for the efficient functioning of individual colonies as separate entities (Stuart 1992). Naked mole-rat colonies are essentially independent functional units with a characteristic composition of a reproductive pair, their non-reproductive offspring and other close kin. Their efficient functioning may depend on this composition, and their ability to maintain colony autonomy, in the midst of closely related neighbouring colonies, may be essential for survival.

#### ACKNOWLEDGMENTS

We thank Joseph Booysen and Mary Vosloo for assisting with the maintenance of the animals in the laboratory. We thank Nigel Bennett, Jonathon Bloomer, David Jacobs, Daniel Polakow, Paul Sherman and Andrew Spinks and two anonymous referees for comments on an early version of the manuscript. This research was supported by an FRD bursary and grant and a grant from the University of Cape Town.

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