

# Intercolonial encounters and xenophobia in the common mole rat, *Cryptomys hottentotus hottentotus* (Bathyergidae): the effects of aridity, sex, and reproductive status

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The ecological constraints prevalent in arid environments have promoted the evolution of social groups with a high reproductive skew in mole rat species occurring there. Outbred social bathyergids face conflict between maintaining colony integrity to enhance personal foraging success and hence survival, and dispersal to maximize individual lifetime reproductive success (LRS). This conflict will be a crucial determinant of the response of colony members to the presence of foreign conspecifics. We investigated how ecological constraints, sex, and reproductive status influence the outcome of meetings between foreign common mole rats (*Cryptomys hottentotus hottentotus*) in a series of dyadic encounters. Individuals from two localities, at the extremes of an aridity gradient, were used to assess the effects of aridity. The effects of sex and reproductive status were investigated by trials between individuals of differing sex and status. The arid population revealed substantially higher levels of rejection than the mesic population. Sex and status played a significant role in moderating individual response. For both populations, encounters between different-sexed individuals produced lower levels of rejection than those between same-sexed individuals. For the mesic site, rejection was greatest for encounters between reproductive animals. Conversely, for the arid site, the levels of rejection were comparatively high and comparable for all combinations of reproductive status. Ecological constraints, sex, and reproductive status are significant factors in interactions between foreign common mole rats, ultimately influencing individual survival, colony integrity and the differential LRS of all colony members. Our results provide insight into the evolution and maintenance of family groups within the bathyergids. *Key words*: colony integrity, common mole rat, *Cryptomys hottentotus hottentotus*, intercolony encounters, outbreeding, xenophobia. [*Behav Ecol* 9:354–359 (1998)]

The level of social development evident in the African mole rats (Bathyergidae) is unparalleled among subterranean mammals. Most subterranean mammals are solitary and strongly xenophobic to conspecifics (Nevo, 1979). Bathyergid sociality is thought to have evolved via natal philopatry, as an adaptation to high foraging and dispersal risks in arid environments (Jarvis, 1985; Jarvis et al., 1994; Lovegrove, 1991; Lovegrove and Wissel, 1988). There are several factors that increase foraging costs in arid regions. Low and sporadic rainfall reduces suitable burrowing opportunities, as edaphic conditions are rarely energetically optimal for excavation (Jarvis et al., 1994; Vleck, 1979). Furthermore, the location of food is restricted by the low density and highly dispersed nature of food resources in arid habitats, and because foraging animals do not use sensory cues to locate food items (Jarvis et al., 1994, 1997; Lovegrove, 1991). Together these factors substantially increase the risks associated with foraging, effectively constraining dispersal and promoting cooperative foraging (Jarvis et al., 1994; Lacey and Sherman, 1997; Lovegrove, 1991). As a consequence of these constraints, the colony burrow system and the resources it contains represent critical assets for the continued survival of all colony members (Bennett, 1988; Jarvis et al., 1994; O’Riain and Jarvis, 1997). O’Riain and Jarvis (1997) suggest that, in naked mole rats (*Heterocephalus glaber*), the importance of protecting these re-

sources has selected for a highly efficient defense system and a reliable mechanism of colony-member recognition, whereby all foreigners are vigorously excluded from the natal burrow system; ergo the intensive degree of xenophobia evident in this species (O’Riain and Jarvis, 1997).

Reproduction within mole rat colonies is highly skewed, typically being monopolized by a reproductive pair (Bennett, 1989; Bennett and Jarvis, 1988; Bennett et al., 1994; Jarvis, 1985). However, whereas naked mole rats routinely inbreed (Faulkes et al., 1990; Honeycutt et al., 1991; Jarvis, 1991b; O’Riain et al., 1996; Reeve et al., 1990), the remaining social bathyergids appear to be obligate outbreeders, and nonbreeding colony members can only maximize their lifetime reproductive success (LRS) by leaving the natal colony and mating with foreigners (Bennett et al., 1997; Burda, 1995; Jarvis et al., 1994; Rickard and Bennett, 1997). Consequently, intercolony encounters in these outbred species cannot merely be assessed in the context of resource defense, but must also be viewed in relation to the outbreeding opportunities they may represent. Acceptance or rejection of foreigners during such encounters will have significant ramifications for the direct fitness of the interactants. Consequently, we predict a diminished xenophobic response in outbred social mole rat colonies relative to *H. glaber* to facilitate pair-bond formation and outbreeding.

We examined the outcome of meetings between foreign common mole rats, *Cryptomys hottentotus hottentotus*, in a series of dyadic encounters. We predicted that the reaction of individuals during encounters between foreign conspecifics would be influenced by ecological constraints and the sex and reproductive status of interactants, such that (1) the fitness

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penalties for failing to exclude foreigners should be substantially more severe in populations from arid, relative to mesic, areas, and this will heighten xenophobia in the former, (2) opposite-sexed interactants should be more willing to accept one another to facilitate outbreeding, and (3) animals of both reproductive and nonreproductive status should be equally likely to reject foreigners as these may represent a dilution of reproductive output and kin relatedness. Clearly, the effects of sex and status on the outcome of encounters between foreign conspecifics should be moderated by the overriding ecological constraints.

### Study animals

The common mole rat is a cooperative breeder living in colonies of 2–14 individuals (Bennett, 1989). It is widely distributed throughout southern Africa and occurs in both mesic and arid areas (Skinner and Smithers, 1990). In addition, *C. h. hottentotus* exhibits a reproductive division of labor similar to that found in naked (*Heterocephalus glaber*) and Damaraland (*C. damarensis*) mole rats, reproduction typically being restricted to the largest male and female within a colony (Bennett, 1989, 1992; Rosenthal et al., 1992; Spinks et al., 1997). The common mole rat appears to conform to the pattern observed in other cryptomids in being an obligate outbreeder (Burda, 1995; Rickard and Bennett, 1997). This contention is supported by both field and laboratory observations: nascent colonies are always formed from dispersing animals from separate colonies, and colonies in the laboratory become reproductively quiescent upon the removal of either breeding animal (Spinks AC, Bennett NC, unpublished data). *Cryptomys h. hottentotus* thus provides an excellent model to investigate the effects of aridity, sex, and reproductive status in intercolonial encounters between outbred batherygids.

### MATERIALS AND METHODS

We investigated animals from two populations in this study. Animals were collected near Sir Lowry's Pass (18°55' E, 34°07' S) in the Western Cape, and Steinkopf (16°50' E, 29°20' S) in the Northern Cape, South Africa. Both sites occur in winter rainfall areas (May–August), but are situated at opposite extremes of an aridity gradient; Sir Lowry's Pass is a mesic region with an annual rainfall of  $652 \pm 175$  mm (coefficient of variation,  $CV = 27\%$ ), while Steinkopf is an arid region with an annual rainfall of  $145 \pm 96$  mm ( $CV = 63\%$ ).

The mole rats were captured using modified Hickman (1979) live-traps. A colony was considered to be completely trapped out if no animals came to the traps for 3 consecutive days after the capture of the last animal. All colonies were considered functionally complete because both the reproductive female and reproductive male were caught in each study colony. Moreover, the majority of the colonies had formed part of a long-term demographic study and were recaptured on several occasions. Consequently, we knew with some confidence when we had captured the complete colony. We used 86 animals from 26 colonies in this investigation: 25 individuals from 6 colonies at Steinkopf and 61 individuals from 20 colonies at Sir Lowry's Pass. Although exact age could not be established without sacrificing the study animals, all the individuals used in this study were sexually mature adults, with males weighing between 57 and 132 g and females between 43 and 87 g. Postmortem examination of sacrificed individuals indicates that males weighing in  $>50$  g and females  $>40$  g are sexually mature (Spinks AC, unpublished data).

We transferred the study colonies to the laboratory and housed them in transparent acrylic plastic burrow systems with wood shavings and paper toweling provided as nesting

material (Jarvis, 1991a). Mole rats were fed ad libitum on a variety of vegetables, supplemented with a high protein cereal (Pronutro).

We conducted behavioral tests in November/December 1995 for the Sir Lowry's Pass population and in November 1995 and October 1996 for the Steinkopf population. The period October–December coincides with the breeding season for both populations (Spinks et al., 1997).

### Behavioral trials

The experimental apparatus consisted of two plastic containers ( $16 \times 12 \times 8.5$  cm) containing wood shavings, connected by a 1-m long acrylic plastic tunnel ( $5 \times 5$  cm). We chose this design to simulate a below-ground encounter between mole rats from neighboring colonies. Three expanded metal gates were fitted to the tunnel. One gate, situated in the middle of the tunnel, enabled the apparatus to be separated into two. The other gates, one at the entrance to each chamber, allowed the interactants to be confined to their respective chambers.

Behavioral trials were conducted in the laboratory and consisted of dyadic encounters. Initially interactants were confined to their respective chambers for a 5-min period of habituation to the apparatus. We then initiated trials by first lifting the chamber entrance gates and, after both interactants had entered the tunnel, lifting the mid-tunnel gate. Each encounter lasted 10 min. We scored the outcome of each trial as a categorical variable with two mutually exclusive states, accept or reject. Trial outcome was scored as accept if both interactants exhibited nonaggressive interactions (i.e., sniffing and ignoring). The trial was scored as reject if (1) one or both of the interactants displayed aggressive behaviors (i.e., biting and tooth-fencing), or (2) one or both of the interactants exhibited overt avoidance behavior (i.e., interactant actively avoided contact with its dyadic "competitor" by retreating from it). We terminated all encounters before the interactants sustained any physical injury. The apparatus was thoroughly washed with chlorinated water between trials to remove odors.

We conducted 206 trials, including 51 controls. Experimental trials consisted of dyadic encounters between individuals from different colonies collected at the same study site. Controls consisted of encounters between individuals from the same colony. Individuals were assigned to local, gender, and status groups, and trials were then chosen deliberately to test the effects of locality, sex, and reproductive status. Within any treatment, we randomly selected individuals to control for intercolony variation affecting trial outcome. The effects of aridity were explored through dyadic encounters between individuals from different colonies captured at the same site—either Steinkopf (arid) or Sir Lowry's Pass (mesic). To assess the effects of sex and reproductive status, we conducted encounters between all combinations of sex and status from each study site. Reproductive females could readily be identified by their perforate vaginas and prominent teats. The heaviest male in each colony was identified as the reproductive male (criteria in Bennett, 1989, 1992; Rosenthal et al., 1992). Whenever possible animals were only used in a single trial. Where individuals were used more than once, they were immediately returned to their natal colony after the initial trial, and a minimum of 3 h was allowed to elapse before they were used in any subsequent trial. On reintroduction to their natal colony, individuals settled down rapidly, there were no aggressive interactions with colony mates, no physical injuries were sustained by any individuals, and within 10 min colony activity and individual behavior had returned to normal. Consequently, when an animal was used in more than a single trial, we considered 3 h more than sufficient time to ensure independence of trial outcomes.

**Table 1**  
Results of the bivariate logistic regression analysis between four independent variables and experimental trial outcome

Variable	Estimate	SEM	<i>t</i>	<i>p</i>
Locality	1.239	0.418	2.961	<.0001
Size differential	0.009	0.008	1.058	.291
Sex <sub>1</sub> <sup>a</sup>	1.796	0.507	3.554	.001
Sex <sub>2</sub> <sup>a</sup>	-0.304	0.505	-0.603	.547
Status <sub>1</sub> <sup>a</sup>	1.880	0.500	3.761	<.0001
Status <sub>2</sub> <sup>a</sup>	1.197	0.520	2.300	.023
Constant	-2.778	0.600	-4.636	<.0001

Maximum likelihood estimates (coefficients) are indicated for each variable. Standard error measurements (SEM) and significance levels (*p*) for each estimate are provided.

<sup>a</sup> Design (dummy) variables used to parameterize the threefold permutations of reproductive status and sex in dyadic encounters between individuals.

As outlined in the introduction, we investigated the conflict between maintaining colony integrity to enhance personal foraging success and hence survival, and dispersal to maximize individual lifetime reproductive success. Conflict between these factors should be maximal when conditions are not suitable for dispersal, and consequently most insight will be gained by investigating aggression when the interactants have not experienced appropriate dispersal cues. Accordingly, the animals used in this investigation were not primed for dispersal by the pertinent triggers (i.e., precipitation). Furthermore, laboratory trials were conducted between October and December, a period coinciding with the dry summer period in the field.

#### Data analysis

We recorded acceptance or rejection in dyadic encounters as a categorical variable with two states, accept or reject. It was not possible to accurately record the intensity of aggression due to ethical considerations requiring that no physical harm be experienced by any of the interactants. This necessitated that the observer intervene whenever the potential for serious injury existed, effectively preventing an assessment of the aggression rate.

We used bivariate logistic regression analysis (Hosmer and Lemeshow, 1989) to find the best fitting model to describe the relationship between the dyadic behavioral outcome (a binary response variable) and the set of independent covariates (body weight, locality, status, and sex). Body weight was expressed in terms of the size difference between pairwise interactants. A given difference in body weight between two interactants could influence the outcome of an encounter in a manner that depended on the absolute value of their respective size. To control for such a scaling effect, we calculated a dimensionless ratio, similar to that used by Beacham (1988) and Beaugrand et al. (1991). The size differential between contestants in each dyadic encounter was expressed as a percentage of the body weight of the smaller individual:

#### Size differential

$$= \left( \frac{\text{larger body weight} - \text{smaller body weight}}{\text{smaller body weight}} \right) \times 100\%.$$

Size differential was coded as a continuous variable (size differential, Table 1), and locality as a binary variable (locality, Table 1) in the logistic regression model. We used design (dummy) variables to parameterize the threefold permuta-

tions of both reproductive status and sex in dyadic encounters between individuals (status<sub>1</sub> and status<sub>2</sub>, and sex<sub>1</sub> and sex<sub>2</sub>, respectively; Table 1). An interaction term between the sex and status variables was similarly coded. All logistic regression analyses were run on Statistica software using the nonlinear estimation module (Statistica, 1995). In addition we examined the interaction between reproductive status and locality post-hoc using a chi-square goodness-of-fit test (Zar, 1984).

To control for the effects of the experimental apparatus, we tested the results from control trials against results from experimental trials using a chi-square goodness-of-fit test (Zar, 1984). The control trial results differed significantly from the experimental trial results (0% rejection in control trials versus 52.9% rejection in experimental trials;  $\chi^2 = 47.61$ , *df* = 1, *p* < .0001). This effectively excludes experimental apparatus design as a determinant of experimental trial outcome.

## RESULTS

Maximum likelihood estimates of the covariates in the subset model are provided in Table 1. The null hypothesis that the estimated covariate coefficients in the model were equal to zero was tested against a chi-square distribution with six degrees of freedom. The results reveal a significant model fit ( $\chi^2 = 57.951$ , *df* = 6, *p* < .0001). In a saturated model (where all independent variables had been included), the maximum likelihood estimate of the interaction term was nonsignificant (coefficient  $\pm$  SE = 0.8334  $\pm$  0.845, *t* = 0.987, *p* = .325). In addition, the predictive power of the model including the interaction term did not differ significantly from the model presented here ( $\chi^2 = 58.912$ , *df* = 6, *p* < .0001). Hence, the interaction between sex and reproductive status was excluded from the model selection.

The results indicate a significant effect of locality, sex combination, and reproductive status combination on the outcome of experimental trials. In contrast, the size differential had no significant impact. To aid interpretation, the patterns of rejection for dyadic encounters between individuals of different sex and of differing reproductive status are presented graphically in Figures 1a and 1b, respectively, and are detailed below.

#### Locality

Locality was identified in the model as being a significant variable in accounting for variation in the level of rejection (Table 1). Levels of rejection were substantially higher for trials between mole rats from the arid site (63%, *n* = 70) than between those from the mesic site (45%, *n* = 85).

#### Sex combination

The sex combination of dyadic interactants had a marked effect on the pattern of rejection (Table 1, Figure 1a). For both arid and mesic populations, encounters between males and females produced lower levels of rejection than those between individuals of the same sex (Figure 1a). Consistent with the locality results, the percentage of rejection was higher for the arid site than for the mesic site, for all combinations of sex.

#### Reproductive status combination

Although the model revealed that reproductive status combination was an important determinant of trial outcome (Table 1), trends in the level of rejection for different combinations of reproductive status were equivocal (Figure 1b). There was a significant interaction between reproductive status and locality ( $\chi^2 = 22.04$ , *df* = 2, *p* < .001), suggesting that the pat-

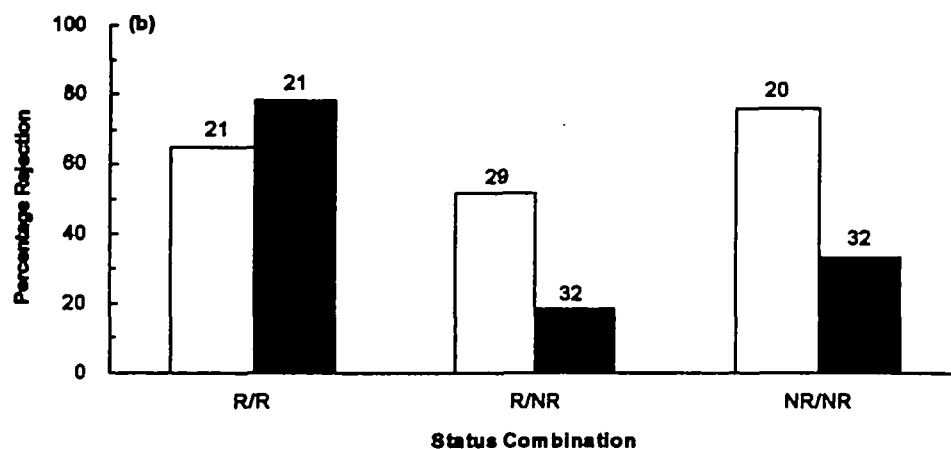
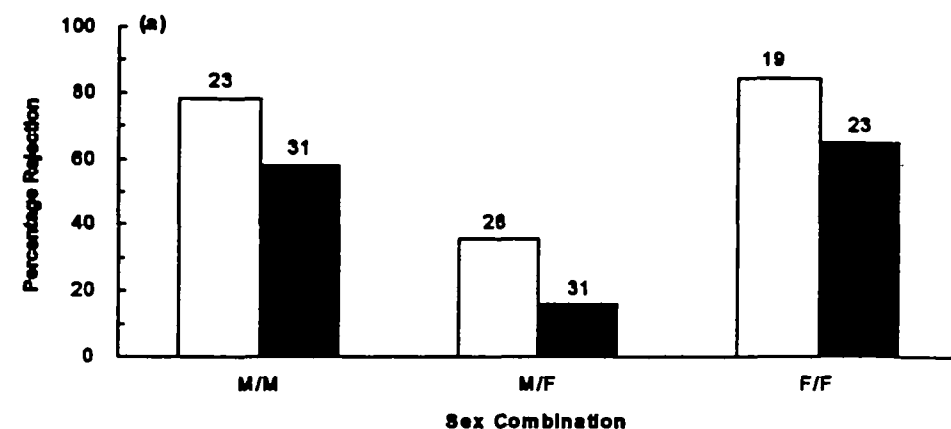


Figure 1

Percent rejection for dyadic encounters between (a) different-sex combinations and (b) different reproductive status combinations of *C. h. hottentotus* from arid (open bars) and mesic (filled bars) localities. Numbers of trials for each category are shown above each bar. For sex combination, M/M, male versus male; M/F, male versus female; F/F, female versus female. For status combination, R/R, reproductive animal versus reproductive animal; R/NR, reproductive animal versus nonreproductive animal, NR/NR, nonreproductive animal versus nonreproductive animal.

tern of rejection differed between the arid and mesic populations, and this is evident in Figure 1b. In trials between individuals from the mesic site, rejection was greatest for encounters between reproductive animals (Figure 1b). Furthermore, encounters between reproductive and nonreproductive animals and between nonreproductive dyads from the mesic population produced a relatively low level of rejection. In contrast, for individuals from the arid site, the levels of rejection were comparatively high and comparable for all combinations of reproductive status (Figure 1b).

## DISCUSSION

Emlen (1995) postulated that family groupings will be unstable and disintegrate when acceptable reproductive opportunities materialize elsewhere. This would appear to be true for outbred mole rat families, in which dispersal and outbreeding typically occur when rainfall provides optimal digging conditions (Jarvis and Bennett, 1990, 1991, 1993; Jarvis et al., 1994; Lovegrove, 1991). For the majority of the time, however, conditions are unfavorable for dispersal, and social mole rats may satisfy their inclusive fitness requirements indirectly by helping closely related kin within the familial group (Jarvis et al., 1994). During this nondispersal period the survival of all col-

ony members will ultimately depend on maintaining colony integrity and protecting the burrow system and its associated resources against foreigners. Thus, conflict between maintaining group cohesion and outbreeding must arise when foreigners, encountered in the natal burrow system, provide an opportunity for the maximization of the LRS requirements of the nonbreeding colony members.

As predicted, *Cryptomys h. hottentotus* individuals from the arid area revealed significantly higher levels of rejection in dyadic encounters than those from the mesic area. As previously suggested, the costs of foraging in arid habitats are higher than in mesic ones (Jarvis and Bennett, 1990, 1991; Jarvis et al., 1994; Lovegrove, 1991). Given the restrictions on foraging, there should thus be strong selection to reduce these costs in arid environments. Foreign animals may elevate costs, threatening colony, and hence individual, survival by increasing pressure on limited food resources and parasitizing the colony workforce (i.e., consuming colony food resources but not assisting in their location). In addition, foreign animals may disrupt colony integrity through the breeding opportunities they present to the subordinate members of the colony they invade. Consequently, adaptation to arid environments may have selected for high levels of kin discrimination and the rejection of foreigners. In mesic areas, reliable precipita-

tion translates into improved foraging predictability, and consequently the penalties for failing to exclude foreign conspecifics should be reduced. Individuals from mesic areas are thus more likely to accept foreign conspecifics and the opportunities for independent reproduction that they represent.

It could be argued that interhabitat differences in aggression are a consequence of differences in predation pressure rather than aridity. Higher rates of predation in arid areas may theoretically select for individuals which are more aggressive toward predators and as a by-product toward foreigners. Predation rates are difficult to assess, as predation is never directly observed, and it is difficult to distinguish between disappearance due to mortality, predation or dispersal. However, evidence available from long-term demographic studies (Spinks AC, unpublished data) suggests that individuals from the arid site remain resident within their natal colony for a substantially longer time period than those from the mesic site, indicating that the rates of predation are not higher in the arid area. Moreover, Nevo (1979, 1982) suggests that the subterranean niche is well buffered against high levels of predation. These observations do not correlate with substantial interhabitat differences in predation rates, nor with predation pressure as an explanation for interhabitat divergence in aggression.

In their investigation of aggression in the solitary Israeli mole rat, *Spalax ehrenbergi*, Ganem and Nevo (1996) and Nevo et al. (1986, 1992) suggested that, due to physiological constraints, aggression is curtailed in arid areas. They went on to propose that ecological constraints may have been a major proximate determinant of the evolution toward pacifism, and subsequent sociality, observed in bathyergids inhabiting harsh environments. Although aggression rates were not measured in our study, the results do suggest that, for the common mole rat, levels of aggression are higher in arid areas. Once sociality has evolved, one may expect differentiation in agonistic behavior. Selection should favor colony members that are aggressive to foreigners who threaten colony integrity and colony resources, but that are unaggressive toward colony members, thereby promoting the cooperative behaviors essential to survival in arid regions. Clearly, aggression toward both foreigners and colony mates will be moderated by the selfish desire to maximize LRS and the concomitant need to outbreed.

The effect of sex on the outcome of dyadic encounters was unequivocal. For both localities, levels of rejection were, as predicted, lowest in encounters between individuals of different sex. Jacobs et al. (manuscript submitted) showed that in the Damaraland mole rat resident colony members will readily accept foreigners of the opposite sex. Similarly, Jarvis et al. (1994) noted that foreign conspecific male and female *C. damarensis* could be paired with little or no aggression. In encounters between mole rats of the opposite sex, interactants are probably influenced by the desire to outbreed and maximize personal LRS. Indeed, in several instances animals were observed attempting to copulate during the behavioral trials. It is noteworthy that even encounters between opposite-sex interactants from the arid locality revealed relatively low levels of rejection. It must be remembered that in arid areas, even when dispersal conditions are favorable, there are overwhelming odds against successful outbreeding. These relate to the low probability of finding a dispersing mate of the opposite sex. Consequently, when faced with a concrete opportunity to maximize their LRS, foreign conspecifics may accept one another, even when the risks to colony integrity and resources are high. In encounters between same-sexed individuals, few fitness benefits will accrue if combatants accept their competitors, and, in fact, as previously discussed, considerable fitness costs may result. This may explain the high levels of rejection

observed for encounters between same-sexed individuals at both localities.

The existence of fundamental asymmetries in the distribution of LRS among group members of social mammals is well established (Keller and Reeve, 1994; Vehrencamp, 1983). For example, dwarf mongooses, *Helogale parvula* (Rasa, 1973; Rood, 1980), slender-tailed meerkats, *Suricata suricatta* (Doolan and MacDonald, 1996), spotted hyenas, *Crocuta crocuta* (Frank, 1986), and wild dogs, *Lycan pictus* (Frame et al., 1979; Malcolm and Marten, 1982) exhibit a marked reproductive skew, with dominant individuals monopolizing reproduction. The same is true of social mole rats (Jarvis and Bennett, 1990, 1991, 1993; Jarvis et al., 1994). Consequently, dominance/reproductive status will have a substantial impact on realized LRS and should be an important motivational determinant of decisions during meetings between outbred social mole rats. The results from the present study are, however, enigmatic and were difficult to interpret within the context of our predictions. The consistently high levels of rejection for all combinations of reproductive status in trials between animals from the arid area reflects the fact that foreign animals, irrespective of their status, represent a substantial threat to colony integrity and resources in arid areas. Although, in contrast, the penalties for failing to reject foreign conspecifics should tend to be rather negligible in mesic areas, the exact fitness cost will depend on the dominance status of the alien animal. In encounters between dominants, the competitors are likely to recognize the threat posed by the foreigner to their reproductive position, hence the high level of rejection. In encounters between dominants and subordinates and between subordinate dyads, the subordinate status of at least one interactant will immediately eliminate the perceived threat to reproductive position.

In conclusion, the results from this study reveal a significant departure from the patterns found in the naked mole rat (O'Riain and Jarvis, 1997). This disparity is probably linked to deviations in mating strategy. In social mole rat species in general (including *H. glaber*), protection of the natal burrow system and its associated resources may have substantial implications for the survival of all colony members. However, in outbred social species like *C. h. hottentotus*, this may clash with the selfish desire to maximize LRS, especially during meetings between foreign conspecifics. Conflict between these fitness components is regulated to some degree by the sex and reproductive status of interactants, but especially by ecological constraints. For populations in arid regions, the penalties for failing to exclude foreigners will be substantially more severe than for those in mesic regions, resulting in elevated levels of xenophobia. Results from this type of study provide keen insight into understanding the evolution and maintenance of familial groups.

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