

# Eusociality in African mole-rats: new insights from patterns of genetic relatedness in the Damaraland mole-rat (*Cryptomys damarensis*)

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After the discovery of eusociality in the naked mole-rat, it was proposed that inbreeding and high colony relatedness in this species were the major underlying factors driving cooperative breeding in African mole-rats. By contrast, field and laboratory studies of the eusocial Damaraland mole-rat (*Cryptomys damarensis*) have raised the possibility that this species is an obligate outbreeder, although the build-up of inbreeding over several generations could still occur. Using microsatellite markers, we show that most breeding pairs in wild colonies of the Damaraland mole-rat are indeed unrelated ( $R = 0.02 \pm 0.04$ ) and that mean colony relatedness ( $R = 0.46 \pm 0.01$ ), determined across 15 colonies from three separate populations, is little more than half that previously identified in naked mole-rats. This finding demonstrates that normal familial levels of relatedness are sufficient for the occurrence of eusociality in mammals. Variation in the mean colony relatedness among populations provides support both for the central role played by ecological constraints in cooperative breeding and for the suggestion that inbreeding in naked mole-rats is a response to extreme constraints on dispersal. Approaches that determine the relative importance of an array of extrinsic factors in driving social evolution in African mole-rats are now required.

**Keywords:** inbreeding; outbreeding; African mole-rat; relatedness; microsatellite; Bathyergidae

## 1. INTRODUCTION

The African mole-rats (family: Bathyergidae) are a fascinating mammalian taxon, incorporating both strictly solitary species and social species that display a wide variety of cooperative breeding strategies. Two species within the family (the naked mole-rat, *Heterocephalus glaber*, and the Damaraland mole-rat, *Cryptomys damarensis*) are particularly notable in that they fit the classical definition of eusociality formulated for social insects (Wilson 1971). Both form stable and long-lasting colonies, consisting of a single breeding female, one or more breeding males and non-breeding colony members, who undertake both cooperative care of young and colony maintenance (Jarvis 1981; Jarvis & Bennett 1993). Extremely high levels of skew in lifetime reproductive success, comparable with some social insects, have been estimated, with less than 1% of naked mole-rat and 8% of Damaraland mole-rat individuals ever achieving direct reproductive success (Jarvis *et al.* 1994). Following Sherman *et al.* (1995), the term eusocial is not used to imply a behaviour totally distinct from other cooperative breeding strategies in vertebrates, but instead distinguishes these two species on the basis of their extraordinarily high levels of skew in lifetime reproductive success.

Molecular phylogenies based on both mitochondrial (Allard & Honeycutt 1992; Faulkes *et al.* 1997a) and

nuclear genes (Walton *et al.* 2000) suggest that the two eusocial mole-rat species are evolutionarily divergent within the family. As such, their extreme form of cooperative breeding appears to have evolved independently on at least two occasions. Understanding the underlying factors driving this convergence may give clues to the prerequisites for the evolution of eusociality both in this family and in other mammalian species. However, this requires detailed knowledge of many aspects of the species' biology, including their ecology and patterns of mating and colony relatedness.

The ecology of the two eusocial African mole-rat species is relatively well understood and provides some clues as to why they evolved this highly social lifestyle. While many other species of the family are found in mesic landscapes, the two eusocial species are found in habitats with low and unpredictable rainfall and low food density, resulting in a high energetic cost of burrowing and high risk of unsuccessful foraging (Lovegrove 1991; Jarvis *et al.* 1994; Faulkes *et al.* 1997a). Natal philopatry, group living and cooperative foraging may therefore be an adaptive response to limited opportunities for dispersal and independent breeding (the aridity food distribution hypothesis; Jarvis *et al.* 1994). Cooperative breeding could then have resulted from a lack of potential mates due to inbreeding avoidance and/or suppression of reproductive function by the breeding female (Faulkes & Bennett 2001), coupled with kin selection for helping behaviour among colony members. Some support for the role of ecological constraints on dispersal has been provided from cross-species

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comparisons of group size with levels of rainfall and food density within the family (Faulkes *et al.* 1997a), although group size *per se* is only an indirect measure of natal philopatry and cooperative breeding (Burda *et al.* 2000).

Mating patterns and levels of genetic relatedness are less well characterized across the family. The relative importance of genetic factors in the evolution and maintenance of cooperative breeding in this species has therefore remained elusive. Colony relatedness estimates for the naked mole-rat from one geographical region, based on multilocus DNA fingerprinting, have revealed that colonies can show extremely high levels of mean relatedness (0.81; Reeve *et al.* 1990), although other populations could be more outbred (Braude 2000). By contrast, both field and laboratory studies have indicated that the Damaraland mole-rat actively avoids breeding with relatives (Jarvis & Bennett 1993; Bennett *et al.* 1996; Cooney & Bennett 2000). However, such observations cannot discount the build-up of high levels of inbreeding over several generations as a result of limited dispersal distances and/or breeding with unfamiliar but related individuals.

The aim of this study was to quantify, for the first time, to our knowledge, the level of genetic relatedness between breeding pairs of wild Damaraland mole-rats and the resultant levels of relatedness within colonies. Results from this study, in combination with recent behavioural studies of naked mole-rats, provide further insights into the underlying causes of cooperative breeding in African mole-rats.

## 2. MATERIAL AND METHODS

### (a) *Study sites and sample collection*

Damaraland mole-rats were live trapped (as described in detail for the common mole-rat by Spinks *et al.* (2000)) between January 1995 and September 1996 at three separate locations (Hotazel, Northern Cape Province, South Africa, 27°17' S, 23°0' E; Dordabis, Namibia, 22°58' S, 17°41' E; and Waterberg, Namibia 20°46' S, 17°15' E). Toe tips, taken as a by-product of mark-release-recapture studies, were placed into salt/dimethyl sulphoxide preservation buffer and stored on return to the laboratory at -20 °C. Between four and seven colonies were sampled at each site. In total, 190 individuals from 15 colonies were sampled. Colony size ranged from five to 19.

### (b) *Genotyping*

DNA was extracted and individuals genotyped as previously detailed in Burland *et al.* (2001) for the following 10 microsatellite loci: DMR 2-5, 7, CH1-3 (Burland *et al.* 2001); NCAM (Moore *et al.* 1998); and LV25 (Walker *et al.* 2000), using the following re-designed PCR primers: F 5'-CACCTTTACCT-ACCAGTCGGG-3', R 5'-GCAAGTACTTGTGCTTATCT-AGG-3'.

### (c) *Identification of mother-offspring and breeding pairs*

Before assessing levels of relatedness among breeding pairs, it was necessary to determine which individuals in each colony were breeders. The colony breeding female, who is recognized by the presence of prominent teats (Jarvis & Bennett 1993), was sampled in 12 of the 15 colonies. However, identification of colony breeding males using morphological characteristics is less straightforward. Parentage was therefore assigned from the

multilocus genotypes using the program CERVUS 2.0 (Marshall *et al.* 1998). This program uses population allele frequencies to determine a likelihood score for each offspring-candidate parent pairing. It then determines, through simulation, the minimum difference in likelihood score required between the most likely and second most likely parent, for parentage to be assigned at a given level of confidence (delta criteria).

For each colony where the breeding female was sampled, those colony members who were her offspring were identified using the delta criterion for 95% confidence. This was determined by simulating two candidate parents, of which only one was typed (the breeding female), with 99% of loci typed (the actual figure was above this) and an error rate of 0.01 (no known mother-offspring data were available to determine the true error rate, hence this is the default value). Calculations of allele frequencies and delta criteria were performed separately for each geographically isolated population. Once mother-offspring pairs had been identified, the male within the colony who was most likely to have fathered each offspring was determined.

Simulations to obtain the delta criteria for assigning paternity with 95% confidence were performed separately for each colony. The percentage of loci typed and the typing error rate were as above. To allow for the possibility of inbreeding, all males within the colony over 100 g when caught, including those previously identified as offspring of the breeding female, were considered candidate fathers. Males under 100 g are unlikely to be sexually mature (Jarvis & Bennett 1993; Bennett & Faulkes 2000). The total number of candidate fathers detailed in each simulation assumed that the number of typed candidate males was 90% of the total candidate males. It is believed that this is a reasonable reflection of the true proportion sampled, as capture effort at each colony was high and did not cease until capture rate had slowed and no further individual had been caught in the trap for at least 72 h. The number of candidate fathers in each colony previously identified as offspring of the breeding female was also detailed in the simulation, specifying a relatedness level of 0.5 to the offspring. This correction is necessary as it is otherwise assumed that candidate fathers and offspring are unrelated, which could lead to an overestimation of parentage assignment confidence (Marshall *et al.* 1998).

### (d) *Analysis of relatedness*

Using the program RELATEDNESS 5.08 (<http://gsoft.smu.edu/GSoft.html>), which uses the calculation by Queller & Goodnight (1989), mean levels of relatedness were estimated among the following categories of individuals: all colony members; mother-offspring pairs; colony females; colony males; breeding pairs; among individuals from different colonies. The mother-offspring and breeding pairs were those identified from the parentage analysis (described in § 2c). Breeding pairs consisted of the colony breeding female and any male identified as a father of any of her offspring with 95% confidence. As such, more than one breeding pair was possible for each colony.

Background allele frequencies were calculated separately for each population. In addition, a bias-corrected allele frequency value, which excluded members of the same colony as those being tested, was incorporated into each calculation of relatedness (Queller & Goodnight 1989). This was necessary so that the presence of close relatives within the same colony did not lead to an underestimation of relatedness. Estimates of relatedness averaged across colonies within each population and across all colonies were calculated by weighting colonies equally.

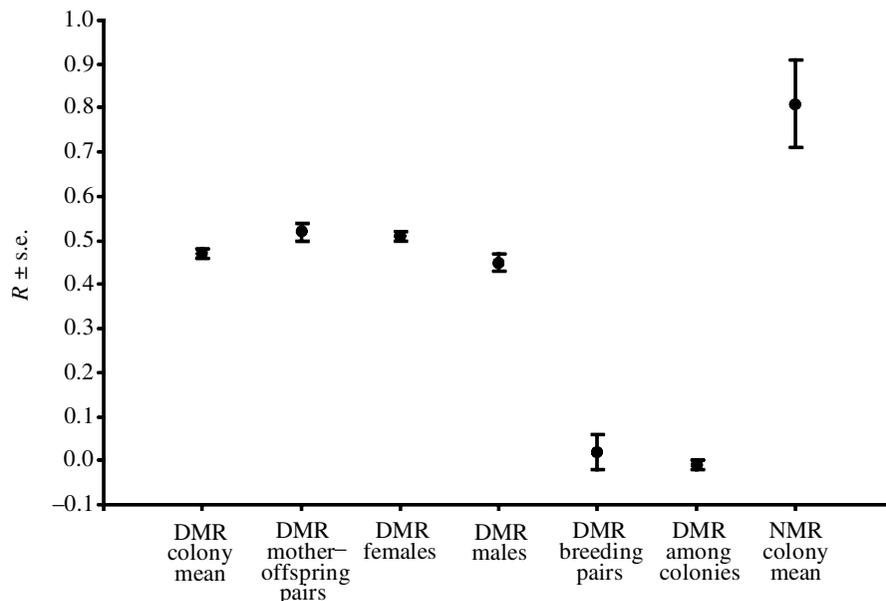


Figure 1.  $R \pm s.e.$  calculated across 15 Damaraland mole-rat (DMR) colonies. The mean colony  $R (\pm s.e.)$  for naked mole-rats (NMR) calculated by Reeve *et al.* (1990) is also shown.

Standard errors and 95% confidence intervals were calculated by jackknifing over loci.

### 3. RESULTS

#### (a) Identification of mother-offspring pairs

In the 12 colonies investigated, the breeding female was confirmed with 95% confidence as mother of all other females and the majority (on average 85%) of males. However, in all but one colony, pairings between the breeding female and between one to four males returned negative likelihood scores, and mismatches at up to six out of the 10 loci were observed. As negative likelihood scores suggest that the breeding female is less likely to be the true mother than a randomly selected female (Marshall *et al.* 1998), these males were not considered to be her offspring.

#### (b) Identification of breeding males

Breeding males (males identified as siring at least one offspring with 95% confidence) were identified in 10 of the 12 colonies investigated. For each colony, just one or, in a single case, two breeding males were identified; all had previously been excluded as offspring of the breeding female. Patterns of paternity and skew in male reproductive success are now being investigated in more detail for this species.

#### (c) Patterns of relatedness

Mean values of relatedness ( $R \pm s.e.$ ) calculated across the 15 Damaraland mole-rat colonies are shown in figure 1 and individual estimates for each colony and population are given in table 1. The overall values obtained for both colony relatedness ( $0.46 \pm 0.01$ ) and mother-offspring relatedness ( $0.52 \pm 0.02$ ) were no greater than that expected for outbred, diploid first-order relatives (0.5). Furthermore, mean colony relatedness was little more than half that previously determined for naked mole-rat colonies ( $0.81 \pm 0.1$ ; figure 1). Individual estimates of

colony relatedness were highly variable (table 1). However, an absence of overlap in the 95% confidence intervals for the overall mean value at Hotazel compared with that at Dordabis and Waterberg (table 1) suggested that colony relatedness was significantly lower at this site.

Mean relatedness among breeding pairs ( $0.02 \pm 0.04$ ) was close to the population average (which is, by definition, zero (Queller & Goodnight 1989)). Low levels of relatedness among breeding pairs were also observed in the majority of individual colony estimates (table 1). However, for two colonies (Hotazel F and Dordabis C; table 1) there was some indication that the breeding pair were more closely related than the average in the population.

### 4. DISCUSSION

Identifying the selective forces that drive the evolution and maintenance of cooperative breeding and, at its extreme, eusociality, is a major challenge to evolutionary biologists. While early studies on social insects focused mainly on the importance of high genetic relatedness, it has been increasingly recognized that explanations based wholly on such intrinsic factors cannot account for the evolution and maintenance of cooperative breeding strategies (Bourke 1997). Instead, the occurrence of reproductive altruism is determined both by patterns of genetic relatedness and by the relative costs and benefits of reproductive altruism, compared with independent breeding. Reproductive altruism is expected when  $c < Rb$  (Hamilton 1964), where  $c$  is the cost to the altruist,  $b$  is the benefit to the beneficiary and  $R$  is relatedness among individuals. Thus, a reciprocal relationship exists, such that when benefits are high, levels of relatedness among participating individuals can be reduced. Current approaches to the study of cooperative breeding strategies therefore consider an array of extrinsic factors that determine the costs and benefits, including ecological constraints on independent breeding, group productivity, dominant control of reproduction and the relative fighting ability of group members

Table 1.  $R \pm$  s.e. for each category of individuals for each colony and population.

(Numbers of individuals or pairs tested in colony for each category are given in parentheses. The 95% confidence intervals (CI) for the mean of each population are also shown.)

population	colony	all colony members	females	males	mother-offspring pairs	breeding pairs
Hotazel	A	0.34 ± 0.09 (14)	0.39 ± 0.05 (7)	0.40 ± 0.14 (7)	0.47 ± 0.07 (9)	-0.02 ± 0.14 (2)
	B	0.33 ± 0.06 (5)	0.38 ± 0.10 (2)	0.26 ± 0.12 (3)	0.40 ± 0.06 (4)	—
	C	0.32 ± 0.06 (7)	0.39 ± 0.06 (4)	0.25 ± 0.06 (3)	0.41 ± 0.08 (5)	-0.24 ± 0.14 (1)
	D	0.35 ± 0.07 (8)	0.37 ± 0.07 (6)	0.34 ± 0.07 (2)	0.47 ± 0.07 (6)	-0.06 ± 0.14 (1)
	E	0.55 ± 0.05 (10)	0.66 ± 0.10 (2)	0.54 ± 0.04 (8)	0.56 ± 0.07 (8)	—
	F	0.51 ± 0.05 (18)	0.71 ± 0.08 (5)	0.47 ± 0.05 (13)	0.61 ± 0.09 (15)	0.23 ± 0.14 (1)
	G	0.34 ± 0.05 (17)	0.43 ± 0.09 (7)	0.30 ± 0.05 (10)	0.39 ± 0.07 (15)	-0.10 ± 0.16 (1)
	mean (95% CI)	0.4 ± 0.02 (0.36–0.44)	0.45 ± 0.02 (0.41–0.49)	0.39 ± 0.03 (0.32–0.46)	0.48 ± 0.02 (0.42–0.54)	-0.07 ± 0.04 (-0.17–0.17)
Dordabis	A	0.33 ± 0.1 (15)	0.39 ± 0.08 (7)	0.27 ± 0.12 (8)	—	—
	B	0.50 ± 0.08 (16)	0.58 ± 0.07 (7)	0.48 ± 0.07 (2)	0.48 ± 0.12 (14)	-0.13 ± 0.18 (1)
	C	0.71 ± 0.09 (15)	0.74 ± 0.10 (8)	0.72 ± 0.09 (7)	0.76 ± 0.10 (13)	0.36 ± 0.23 (1)
	D	0.57 ± 0.03 (18)	0.57 ± 0.04 (12)	0.57 ± 0.05 (6)	0.54 ± 0.11 (16)	0.15 ± 0.18 (1)
	mean (95% CI)	0.54 ± 0.04 (0.44–0.62)	0.56 ± 0.04 (0.5–0.66)	0.50 ± 0.04 (0.41–0.59)	0.60 ± 0.07 (0.44–0.76)	0.13 ± 0.13 (-0.17–0.43)
Waterberg	A	0.47 ± 0.07 (12)	0.56 ± 0.09 (4)	0.47 ± 0.09 (8)	—	—
	B	0.56 ± 0.05 (9)	0.57 ± 0.05 (6)	0.64 ± 0.08 (3)	0.55 ± 0.07 (7)	0.02 ± 0.14 (1)
	C	0.43 ± 0.03 (19)	0.42 ± 0.05 (11)	0.46 ± 0.07 (8)	—	—
	D	0.57 ± 0.05 (7)	0.60 ± 0.04 (5)	0.58 ± 0.07 (2)	0.52 ± 0.07 (5)	0.16 ± 0.13 (1)
	mean (95% CI)	0.51 ± 0.02 (0.46–0.56)	0.54 ± 0.01 (0.51–0.57)	0.52 ± 0.03 (0.44–0.60)	0.54 ± 0.04 (0.45–0.63)	0.10 ± 0.09 (-0.09–0.29)

(reviewed in Keller & Reeve 1994; Clutton-Brock 1998; Reeve *et al.* 1998).

We have demonstrated that wild colonies of the eusocial Damaraland mole-rat consist of a single breeding female, her non-breeding offspring of both sexes and a few (up to four) unrelated males, of which one or two may be breeders. This finding supports inferences from field studies that breeding pairs originate from different colonies (Jarvis & Bennett 1993). Outbreeding and normal familial levels of relatedness were identified in all three populations investigated, with mean relatedness among breeding pairs similar to that identified among individuals from different colonies (figure 1). However, breeding pairs more closely related than the population average may occasionally occur (table 1). It is therefore apparent that eusociality in the Damaraland mole-rat is not reliant on systematic inbreeding or extraordinarily high levels of relatedness. Instead, the benefits of reproductive altruism appear sufficiently high in this species that normal familial levels of genetic relatedness are adequate to maintain their extreme pattern of cooperative breeding. Eusociality therefore probably arose as a result of the offspring of unrelated parents remaining in the natal colony, in response to one or more extrinsic factors.

The finding that mean relatedness may vary among geographical locations lends weight to the role played by an ecological constraint to dispersal from the natal colony and independent breeding. While the data are preliminary, the population with the lowest mean relatedness value, Hotazel, also experiences both the highest mean annual rainfall and highest mean number of months per year when total rainfall is above 25 mm (T. M. Burland, N. C.

Bennett, J. U. M. Jarvis and C. G. Faulkes, unpublished data). The latter value is the level of rainfall necessary to allow new burrow formation (Jarvis *et al.* 1994). As dispersal may, at least in part, be dependent on new burrow formation (Jarvis *et al.* 1994), opportunities for leaving the natal colony and either forming a new colony or joining an existing colony, may therefore be greater at this site. The finding that relatedness among females, in particular among those in Hotazel colonies, is higher than among males (table 1) supports earlier suggestions based on field observations (Hazell *et al.* 2000) that dispersal into existing colonies is male biased. Further investigation into patterns of parentage, relatedness and dispersal is now required across this species' range to quantify the extent to which flexibility in cooperative breeding may occur with varying environmental conditions at the intra-specific level.

The results of this study also contribute to the understanding of mechanisms driving eusociality in naked mole-rats. After eusociality was described in the naked mole-rat (Jarvis 1981), it was suggested that this species' capacity to inbreed and the resultant high colony relatedness values were fundamental to their extreme cooperative breeding system (Reeve *et al.* 1990). However, the central role played by inbreeding has been widely questioned in this species (Jarvis *et al.* 1994; Braude 2000). In particular, studies on captive populations have demonstrated that they are facultative, rather than obligate, inbreeders and, should the opportunity arise, outbreeding is preferred (Clarke & Faulkes 1999; Ciszek 2000). Furthermore, while both field (Brett 1991) and genetic (Reeve *et al.* 1990; Faulkes *et al.* 1997b) data indicate that new colonies

may be formed by budding and recruitment of breeders from within, patterns of outbreeding and new colony formation similar to those identified in Damaraland mole-rats have also been reported (O'Riain *et al.* 1996; Braude 2000). Our finding that eusociality can occur within the Bathyergidae at normal familial levels of relatedness further strengthens the suggestion that inbreeding and high relatedness in naked mole-rats, a feature unique within the family, is a derived trait that evolved after cooperative breeding, possibly in response to severe constraints on dispersal and opportunities to meet unrelated individuals (Faulkes *et al.* 1997a).

## 5. CONCLUSIONS

Our results demonstrate that explanations based on exceptionally high colony relatedness cannot account for the convergent evolution of cooperative breeding in African mole-rats. Instead, a more integrated approach, which unites both genetic and extrinsic factors, is necessary to fully understand the mechanisms driving social evolution in this unique vertebrate family. The central role played by ecological constraints to dispersal and independent breeding (Jarvis *et al.* 1994; Faulkes *et al.* 1997a) is supported by this study. However, ecological constraints are unlikely to fully explain the occurrence of cooperative breeding (reviewed for birds in Hatchwell & Komdeur (2000)). The relative importance of other factors in promoting cooperative breeding and eusociality in African mole-rats, including social control of reproduction (Faulkes & Bennett 2001), life history and physiological traits (reviewed for mole-rats in Bennett & Faulkes (2000)), evolutionary constraints (Burda *et al.* 2000), kin discrimination ability (Perrin & Lehmann 2001) and the direct benefits of cooperation, such as helping behaviour (Clutton-Brock *et al.* 2001; Kokko *et al.* 2001), remain to be determined.

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## REFERENCES

Allard, M. W. & Honeycutt, R. L. 1992 Nucleotide sequence variation in the mitochondrial 12S rRNA gene and the phylogeny of African mole-rats (Rodentia: Bathyergidae). *Mol. Biol. Evol.* **9**, 27–40.

Bennett, N. C. & Faulkes, C. G. 2000 *African mole-rats: ecology and eusociality*. Cambridge University Press.

Bennett, N. C., Faulkes, C. G. & Molteno, A. J. 1996 Reproductive suppression in subordinate, non-breeding female Damaraland mole-rats: two components to a lifetime of

socially-induced infertility. *Proc R. Soc. Lond. B* **263**, 1599–1603.

Bourke, A. F. G. 1997 Sociality and kin selection in insects. In *Behavioural ecology: an evolutionary approach*, 4th edn (ed. J. R. Krebs & N. B. Davies), pp. 203–227. Oxford: Blackwell Science.

Braude, S. 2000 Dispersal and new colony formation in wild naked mole-rats: evidence against inbreeding as the system of mating. *Behav. Ecol.* **11**, 7–12.

Brett, R. A. 1991 The population structure of naked mole-rat colonies. In *The biology of the naked mole-rat* (ed. P. W. Sherman, J. U. M. Jarvis & R. D. Alexander), pp. 97–136. Princeton University Press.

Burda, H., Honeycutt, R. L., Begall, S., Locker-Grütjen, O. & Scharff, A. 2000 Are naked and common mole-rats eusocial and if so, why? *Behav. Ecol. Sociobiol.* **47**, 293–303.

Burland, T. M., Bishop, J. M., O'Riain, C. & Faulkes, C. G. 2001 Microsatellite primers for the African mole-rat genus *Cryptomys* and cross-species amplification within the family Bathyergidae. *Mol. Ecol. Notes* **1**, 311–314.

Ciszek, D. 2000 New colony formation in the 'highly inbred' eusocial naked mole-rat: outbreeding is preferred. *Behav. Ecol.* **11**, 1–6.

Clarke, F. M. & Faulkes, C. G. 1999 Kin discrimination and female mate choice in the naked mole-rat *Heterocephalus glaber*. *Proc R. Soc. Lond. B* **266**, 1995–2002. (DOI 10.1098/rspb.1999.0877.)

Clutton-Brock, T. H. 1998 Reproductive skew, concessions and limited control. *Trends Ecol. Evol.* **13**, 288–292.

Clutton-Brock, T. H., Russell, A. F., Sharpe, L. L., Brotherton, P. N. M., McIlrath, G. M., White, S. & Cameron, E. Z. 2001 Effects of helpers on juvenile development and survival in meerkats. *Science* **293**, 2446–2449.

Cooney, R. & Bennett, N. C. 2000 Inbreeding avoidance and reproductive skew in a cooperative mammal. *Proc R. Soc. Lond. B* **267**, 801–806. (DOI 10.1098/rspb.2000.1074.)

Faulkes, C. G. & Bennett, N. C. 2001 Family values: group dynamics and social control of reproduction in African mole-rats. *Trends Ecol. Evol.* **16**, 184–190.

Faulkes, C. G., Bennett, N. C., Bruford, M. W., O'Brien, H. P., Aguilar, G. H. & Jarvis, J. U. M. 1997a Ecological constraints drive social evolution in the African mole-rats. *Proc R. Soc. Lond. B* **264**, 1619–1627. (DOI 10.1098/rspb.1997.0226.)

Faulkes, C. G., Abbot, D. H., O'Brien, H. P., Lau, L., Roy, M. R., Wayne, R. K. & Bruford, M. W. 1997b Micro- and macrogeographical genetic structure of colonies of naked mole-rats *Heterocephalus glaber*. *Mol. Ecol.* **6**, 615–628.

Hamilton, W. D. 1964 The genetical evolution of social behaviour I, II. *J. Theor. Biol.* **7**, 1–52.

Hatchwell, B. J. & Komdeur, J. 2000 Ecological constraints, life history traits and the evolution of cooperative breeding. *Anim. Behav.* **59**, 1079–1086.

Hazell, R. W. A., Bennett, N. C., Jarvis, J. U. M. & Griffin, M. 2000 Adult dispersal in the cooperatively breeding Damaraland mole-rat (*Cryptomys damarensis*): a case from the Waterberg region of Namibia. *J. Zool. Lond.* **252**, 19–25.

Jarvis, J. U. M. 1981 Eusociality in a mammal: cooperative breeding in naked mole-rat *Heterocephalus glaber* colonies. *Science* **212**, 571–573.

Jarvis, J. U. M. & Bennett, N. C. 1993 Eusociality has evolved independently in two genera of bathyergid mole-rats—but occurs in no other subterranean mammal. *Behav. Ecol. Sociobiol.* **33**, 353–360.

Jarvis, J. U. M., O'Riain, M. J., Bennett, N. C. & Sherman, P. W. 1994 Mammalian eusociality: a family affair. *Trends Ecol. Evol.* **9**, 47–51.

Keller, L. & Reeve, H. K. 1994 Partitioning of reproduction in animal societies. *Trends Ecol. Evol.* **9**, 98–102.

- Kokko, H., Johnstone, R. A. & Clutton-Brock, T. H. 2001 The evolution of cooperative breeding through group augmentation. *Proc. R. Soc. Lond. B* **268**, 187–196. (DOI 10.1098/rspb.2000.1349.)
- Lovegrove, B. G. 1991 The evolution of eusociality in mole-rats (Bathyergidae): a question of risks, numbers, and costs. *Behav. Ecol. Sociobiol.* **28**, 37–45.
- Marshall, T. C., Slate, J., Kruuk, L. E. B. & Pemberton, J. M. 1998 Statistical confidence for likelihood-based paternity inference in natural populations. *Mol. Ecol.* **7**, 639–655.
- Moore, S. S., Hale, P. & Byrne, K. 1998 NCAM: a polymorphic microsatellite locus conserved across eutherian mammal species. *Anim. Genet.* **29**, 33–36.
- O’Riain, M. J., Jarvis, J. U. M. & Faulkes, C. G. 1996 A dispersive morph in the naked mole-rat. *Nature* **380**, 619–621.
- Perrin, N. & Lehmann, L. 2001 Is sociality driven by the costs of dispersal or the benefits of philopatry? A role for kin-discrimination mechanisms *Am. Nat.* **158**, 471–483.
- Queller, D. C. & Goodnight, K. F. 1989 Estimating relatedness using genetic markers. *Evolution* **43**, 258–275.
- Reeve, H. K., Westneat, D. F., Noon, W. A., Sherman, P. W. & Aquadro, C. F. 1990 DNA ‘fingerprinting’ reveals high levels of inbreeding in colonies of the eusocial naked mole-rat. *Proc. Natl Acad. Sci. USA* **87**, 2496–2500.
- Reeve, H. K., Emlen, S. T. & Keller, L. 1998 Reproductive sharing in animal societies: reproductive incentives, or incomplete control by dominant breeders? *Behav. Ecol.* **9**, 267–278.
- Sherman, P. W., Lacey, E. A., Reeve, H. K. & Keller, L. 1995 The eusociality continuum. *Behav. Ecol.* **6**, 102–108.
- Spinks, A. C., Jarvis, J. U. M. & Bennett, N. C. 2000 Comparative patterns of philopatry and dispersal in two common mole-rat populations: implications for the evolution of mole-rat sociality. *J. Anim. Ecol.* **69**, 224–234.
- Walker, R. S., Farmerie, W. G. & Branch, L. C. 2000 Characterization of microsatellite loci from the mountain vizcacha *Lagidium viscacia* and their use for the plains vizcacha *Lagotomus maximus*. *Mol. Ecol.* **9**, 1672–1674.
- Walton, A. H., Nedbal, M. A. & Honeycutt, R. L. 2000 Evidence from intron 1 of the nuclear transthyretin (Prealbumin) gene for the phylogeny of African mole-rats (Bathyergidae). *Mol. Phylogenet. Evol.* **16**, 467–474.
- Wilson, E. O. 1971 *The insect societies*. Cambridge, MA: Belknap Press of Harvard University Press.