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Eusociality has evolved independently in two genera of bathyergid mole-rats – but occurs in no other subterranean mammal

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Summary. Extensive field and laboratory studies show that Damaraland mole-rats, like naked mole-rats, have an extreme form of vertebrate sociality. Colonies usually contain 2 reproductives and up to 39 non-breeding siblings, 90% of whom live a socially-induced lifetime of sterility; they remain in the natal colony, forage for food, defend the colony and care for successive litters. Although there is heightened dispersal following good rainfall, the majority of adult non-reproductives remain in their natal colony and failure to disperse is not directly attributable to habitat saturation or unfavourable soil conditions. A major dispersal event follows the death of a reproductive. Differences in colony cohesion, ethology and the hormonal profiles of non-reproductive animals suggests that eusociality evolved along different pathways in these two phylogenetically divergent genera of the Bathyergidae.

Key words: Mammalian-eusociality – Mole-rats – *Cryptomys* – *Heterocephalus* – Bathyergidoe

Introduction

Cooperative breeding, in which adult animals forego reproduction and assist others in the care of the young, has been documented for many species of birds and mammals (Krebs and Davies 1983 for review). In most, group size is small and the non-breeding helpers will eventually attempt to disperse and breed. Group living and cooperative breeders are found in a variety of habitats but rarely underground. Worldwide, subterranean insectivores and rodents are typically xenophobic – a single animal occupying and aggressively defending its system of burrows (Nevo 1979; Jarvis and Bennett 1991) and Nevo (1979) examines the reasons for this. It is surprising therefore, that the most extreme form of vertebrate sociality yet described occurs in the Bathyergidae, a family of subterranean rodents endemic to Africa.

Over a decade has passed since it was first reported that the naked mole-rat, *Heterocephalus glaber* was eusocial (Jarvis 1981). A large body of research has further substantiated this claim (Sherman et al. 1991) and has conclusively shown that these unusual mammals meet all the criteria for eusociality (Michener 1969; Wilson 1971): they have a reproductive division of labour, an overlap of at least two generations and cooperative care of the young. Colonies are large (up to 300 individuals) and the majority of non-breeding colony members never disperse or breed (Brett 1986, 1991; Sherman et al. 1992).

Since 1988 we have been conducting extensive field and laboratory studies on another social bathyergid, the Damaraland mole-rat, *Cryptomys damarensis*. These mole-rats are hairy, have a mean body mass of 131 g and occur primarily in red Kalahari sands in the hot arid regions of southern Africa. They subsist on the storage organs of plants and live in colonies numbering of 2–41 individuals in which there is reproductive division of labour (Bennett and Jarvis 1988a; this paper). The data presented in this paper show unequivocally that Damaraland mole-rats are also eusocial. Thus, two of the five genera of the Bathyergidae show an extreme form of sociality, while the remaining three genera are solitary.

Methods

The study area. Since April 1988 we have been studying the dynamics of a population of *Cryptomys damarensis* at Dordabis, Namibia (22°58'S 17°41'E). The study site has red Kalahari sands which support a rich diversity of geophytes on which the mole-rats feed. The rain falls in summer (November – April) and is very unpredictable.

In April 1988 our study commenced with marking and releasing individuals from three neighbouring colonies. Subsequently, to obtain information on dispersal, we trapped colonies peripheral to the original three. By July 1990 our study area was 124800 m^2 and by November 1991 it had increased to 175000 m^2. Because

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this is an expanding study the number of colonies in our study area is constantly changing; however, we have 2 or more years of capture and recapture data from 11 "established" colonies: ones containing a number of adults and juveniles ($\bar{x} = 14$) on first capture. Additionally we have been following 17 colonies since they were first founded.

Individuals in the colonies in our study area are live-trapped at least twice yearly (in summer and mid-winter). They are marked the first time they are caught and the sex, body mass and reproductive condition noted on first and subsequent captures.

The abundance and distribution of geophytes (mainly bulbs of *Dipcadi glaucum*) was examined on the grid by means of 10 × 4 m transects and also randomly chosen 1-m^2 plots. These were used in assessing habitat quality in and outside the home ranges of the colonies.

Laboratory studies. Behavioural and hormonal studies on colony structure and reproduction were done on colonies maintained in the laboratory. Details of maintenance procedures are described in Bennett and Jarvis (1988a).

The degree of reproductive suppression in colonies of *C. damarensis* was investigated in three ways:

1. By examination of the histology of the gonads and the concentrations of circulating reproductive hormones of a colony of 25 freshly captured mole-rats (Bennett 1988).
2. Through monitoring the changes in the concentrations of circulating reproductive hormones in a colony of 12 captive animals through three reproductive cycles (Bennett 1988).
3. By measuring changes in the plasma luteinising hormone (LH) concentrations after injecting single 2-μg doses of gonadotrophic releasing hormone (GnRH) into the animals from two entire wild colonies ($n = 31$ animals) and an additional freshly captured 12 reproductive and 5 non-reproductive animals (Bennett et al. in press). Plasma samples were obtained immediately prior to injecting GnRH (the basal LH level) and 20 min after injection (the resultant LH level from the GnRH challenge).

Steroid hormones were measured using standard radioimmunoassays previously described by Abraham (1976) and validated for mole-rats (Bennett and Jarvis 1988a; Bennett 1988). LH was measured using an *in vitro* bioassay based on the production of testosterone by dispersed mouse Leydig cells (Van Damme et al. 1974) and previously described and validated in the mole-rat (Faulkes et al. 1990c).

Results and discussion

A total of 716 mole-rats were marked and released at Dordabis between April 1988 and February 1993. Many of these were recaptured a number of times. The maximum colony size at Dordabis was 41 animals ($\bar{x} = 16$) and colony growth is slow with recruitment almost matching the loss of colony members through predation and dispersion. Growth rates of animals first captured as juveniles weighing <40 g (around 3 months old, Bennett et al. 1991) show that they attain a mass of >125 g in a year. A body mass of 125 g has been used in this study to separate yearlings from older animals.

The tunnels of neighbouring colonies can come to within 1 m of each other. When the soil is dry minor changes are made by the mole-rats to their burrow systems and excavated soil is shunted into disused sections of the system. Damaraland mole-rats only throw up mounds and make appreciable extensions to their burrow systems after the rain has penetrated at least 25 cm below ground. For this to happen 25 mm of rain has to fall over a short period. In years of poor rainfall this may only occur once or twice in the season and the mole-rats' search for new patches of food and their potential to disperse are severely curtailed.

Rainfall during the study period was below average (270 mm), except during the summer of 1990–1991 when 263 mm fell. The poorest wet seasons were 1989/1990 (115 mm) and 1991/1992 (170 mm). The 1992/1993 rainfall was also well below average (161 mm).

Evidence for eusociality in Cryptomys damarensis

1. There is a reproductive division of labour. Each colony contains one reproductive female. She is clearly identifiable by her prominent nipples and often also by her large size and elongate body. In the laboratory, the oestrous female initiates courtship behaviour (Bennett and Jarvis 1988a). Reproductive males are less easy to identify in the field but are among the largest males in the colony (Bennett and Jarvis 1988a) and are individuals in which the outlines of the inguinal testes are visible through the abdominal skin; however, a few non-reproductive males may also have enlarged testes. In the laboratory behavioural interactions with the reproductive female and their position at the top of the dominance hierarchy further identify the reproductive males (Bennett 1990; Jacobs et al. 1991). Using these criteria, usually one, but in the laboratory occasionally up to three, males in the colony may be reproductively active. Therefore, a colony will usually be composed of 2 breeding animals and up to 39 non-breeding animals.

From the hormonal and histological studies we have verified that non-reproductive female *C. damarensis* are anovulatory and reproductively suppressed. The follicles in the ovaries of non-reproductive females do not mature, but the secondary and early tertiary follicles luteinise and fill the stroma of the ovaries (Bennett 1988). The concentrations of urinary progesterone and oestrogen of non-reproductive *C. damarensis* are detectable but are significantly different from those of reproductive females (Table 1a) and their anterior pituitaries are significantly less sensitive to a GnRH challenge (Table 1b). By contrast, the reproductive and non-reproductive males show few histological and hormonal differences. The testes of both groups are undergoing spermatogenesis, and all adult males have comparable levels of circulating testosterone and responses to GnRH (Table 1a, b). However, the testes of non-reproductive males are smaller than those of the reproductive male and the two groups differ behaviourally.

In *C. damarensis* colonies the reproductive female remains the sole reproductive throughout her stay in the colony, which can exceed 5 years (the maximum time for which we currently have field data). She breeds throughout the year, has one to six ($\bar{x} = 3$) pups in a litter and a maximum of three litters a year. Apart from the founder members, all the individuals in the colony are her progeny. On the death or experimental removal of the reproductives, the colony fragments, the non-reproductive adults become sexually active and new colonies are founded. Thus the lifespan of a colony appears

Table 1a. Urinary sex steroid concentrations in a captive colony of *Cryptomys damarensis* collected over 18 months (incorporating 3 pregnancies)

Hormone	Status	Sex	Concentration (nmols/mmol creatinine)	*n*	
Testosterone	RM	M	3.8 ± 3.7	25	n.s.
Testosterone	NR	M	4.4 ± 5.3	114	
Oestradiol 17B	RF	F	95.0 ± 151.0	17	*
Oestradiol 17B	NR	F	2.2 ± 4.6	133	
Progesterone	RF	F	63.3 ± 70.1	14	*
Progesterone	NR	F	10.7 ± 8.8	85	

NS, not significant, $P>0.05$; *significant, $P<0.05$; Wilcoxon matched pairs sign test. The sequential hormone concentrations of the reproductive animal were tested independently against each non-reproductive animal

Table 1b. Plasma luteinising hormone (LH) concentrations for 2.0 μg exogenous gonadotrophic releasing hormone (GnRH) challenges conducted on 2 complete wild colonies and 12 other reproductive animals in the field

Status	Sex	Pre-GnRH challenge (mIU/ml)	Post-GnRH challenge (mIU/ml)	*n*	
RM	M	5.1 ± 1.8	21.3 ± 3.5	7	n.s.
NR	M	3.4 ± 0.3	21.4 ± 1.8	21	
RF	F	7.6 ± 1.0	37.7 ± 6.2	9	*
NR	F	4.3 ± 0.6	11.8 ± 1.0	11	

NS, not significant, $P>0.05$; * = significant, $P<0.05$; Student's *t*-test

to be dependent on the continued presence of the founding reproductive pair of mole-rats. We have limited evidence from three colonies at Dordabis that this fragmentation following the death of a reproductive is delayed until the next good rains. In one colony (colony A, Table 2) the reproductive male was last caught in January 1990; recruitment ceased but the colony only fragmented following good rainfall in January 1991. Two others (colonies E and H, Table 2) have been without either reproductive for at least 12 months (as of February 1993); there has been no recruitment but also no dispersal, the summer rains of 1991/1992 and 1992/1993 having failed. In the laboratory the reproductive females were removed from two actively breeding colonies. Recruitment ceased and no new reproductive female emerged until 5 years later when a foreign male was added to each colony. Both colonies then resumed breeding and rearing pups.

Of the 17 newly founded colonies studied at Dordabis 14 were begun by a pair of adult animals. In all but one of these, the pairings were of animals from different colonies. The maximum distance moved by a marked animal forming a new colony was 217 m. The remaining 3 colonies were founded by an adult female and a small group of sub-adults and adults (the latter all males); however, within a year all but one adult male and all the sub-adults disappeared, leaving a breeding pair of animals. Thus most, if not all, colonies are composed of the offspring of a pair of reproductive animals. Corrobative data have been obtained from mtDNA analyses of entire colonies from Dordabis which show that one male in the colony is not the offspring of the reproductive female (R.L. Honeycutt, J.U.M. Jarvis and N.C. Bennett, in prep).

The non-reproductive individuals in Damaraland mole-rat colonies constitute two loosely defined working groups, namely frequent and infrequent workers. These groups each contain both sexes and are generally identifiable by size differences and the amount of work (burrow maintence behaviour) that they perform (Bennett and Jarvis 1988a; Jacobs et al. 1991).

2. There is overlap of two generations. From our field studies we have documented an overlap of two generations in all our colonies. Furthermore, more than a third (37%) of animals under 1 year old on first capture remain with their natal colony for at least 16 months (54 of 146 mole-rats); 13 (12.9%, $n=101$) have survived for at least 2–2.5 years and 2 (8%, $n=22$) for more than 3 years. Extensive trapping of the study area indicates that disappearance from the natal colony is predominantly through predation and other forms of mortality rather than inter-colony migration. Thus only 16 (11%) of the above 146 animals have been captured as founder members of new colonies and only 34 (8.4%) of the 403 animals (of all ages on first capture) which have disappeared since the inception of our study have been found in new colonies. It would appear therefore that the majority of colony members forego reproduction for their entire lives.

3. There is cooperative care of the young. Damaraland mole-rats are central-place foragers and storers. Colony members contribute to the extension of the burrow system and store portable food that they encounter whilst foraging, in a central store sited close to a very deep (1.6–2.4 m, $n=3$) and protected nest (Bennett et al. 1992). The pups are weaned when 28 days old but only become efficient diggers when about 3 months old. Until then they depend on the communal food store for sustenance. The colony members care more directly for the pups by keeping them from straying far from the safety of the colony nest, grooming them, providing warmth by huddling with them and feeding them caecotrophs. More than a third of the non-reproductives remain in the colony long enough to help care for four or more litters of siblings and 13% long enough to help rear up to seven litters.

Facultatively or truly eusocial?

In terms of the size and composition of the colonies, and the extent of reproductive suppression, naked and Damaraland mole-rats are at the most extreme eusocial end of a continuum of cooperatively breeding vertebrates which includes some other species of *Cryptomys* (Bennett 1989; Burda 1990). Although the non-breeders of both genera of mole-rats retain the potential to breed, our data and also field studies on naked mole-rats (Sher-

Table 2. History of selected colonies of *C. damarensis* showing: recruitment (bold number) and survival (subsequent numbers in column)

Capture Dates	Colony (A) Animals <125 g on first capture (bold) and their survival					Total Colony Size	(B)									
Survival																
April 88	**4**					15										
Dec 88		colony not found				***	**4**									
July 89	2	**7**				17	3	**3**								
Jan 90	1	8	**5**			19	2	3	**2**							
July 90	0	5	4	**6**←		18	2	3	2	**9**						
Jan 91	0	4	3	5	**0**	15	1	2	1	7	**6**					
July 91		colony fragments				5	0	**0	0	1	5	**1**				
Nov 91		Breeding female founds					0	0	0	0	4	1	**2**			
March 92		new colony									3	1	2	**6**		
Nov 92											2	1	2	6	**5**	
Feb 93											1	1	2	5	4	**0**
Longest survival (months)	21m	18m	12m	6m			25	18	12	12	25	20	15	11	3	
Survival of dispersing reproductives		+43	+36	20 +31		55										
Survival of colony reproductives					B♂ 21m	B♀ +58										

Capture Dates	(E)								Total Colony Size	(F)				Total Colony Size	(G)	
Survival																
April 88																
Dec 88																
July 89																
Jan 90	**6**								□13							
July 90	5	**4**							17							
Jan 91	5	3	**3**						*17							
July 91	3	2	2	**2**					13						**3**	
Nov 91	1	2	1	2	**4**				14	**1**				3	Colony not	
March 92	1	1	1	2	3	**2**			14	1	**2**			5	1	
Nov 92	1	1	1	1	2	2	**0**←		10	1	2	**2**		7	0	
Feb 93	1	1	1	1	2	2	0	**0**	11	1	2	2	**0**	7	0	
Longest survival (months)	+37	+31	+25	+20	+15	+11	0	0		+16	+11	+3			8	+1

The only good (average) rainfall in the study is indicated by the broken line (---). □ next to totals = colony not completely trapped out because reproductive female was very gravid and had to be released; whereas + next to longevity figures indicates minimum number of months the reproductive animals have maintained this position ← = indicates where in colonies A, E and H at least one

man et al. 1992) show that more than 90% of non-breeders have a socially-imposed lifetime of sterility.

We found no evidence from our field studies that Damaraland mole-rats were merely facultatively social due to habitat saturation or adverse climatic conditions. Thus, suitable vacant sites close to numerically large non-dispersing colonies were not immediately occupied by potential breeders from the colony – some of these sites were later successfully colonised by pairs migrating from other areas, whilst others have remained unoccupied. Furthermore, although we found a heightened incidence of outbreeding and colony formation following the first average rainfall since the inception of this study, the majority of adult non-breeders remained in their natal colonies (Table 2). Thus only 13 (14%) of the 91 adult non-breeders captured in July 1990, prior to the summer rains, had dispersed and bred before the soil was dry again in July 1991. Three of these came from of young (< 125 g); total colony size and instances of successful dispersal to found new colonies (*)

Total Colony Size	(C)								Total Colony Size	(D)						Total Colony Size
□11																
□11																
□12	**7**								□ 8							
22	7	**2**							11	**16**						24
23	6	1	**1**						12	11	**5**					22
11	4	1	1	**2**					10	**Could not find colony						
10	2	1	1	2	**7**				16	4	4	**9**				*26
18	2	0	0	2	5	**7**			19	*2	2	8	**2**			□25
21	1	0	0	2	5	7	**5**		23	2	2	8	0	**7**		□29
18	1	0	0	2	5	7	4	**3**	□25	2	2	8	0	7	**11**	41
	+37	18	10	+19	+16	+11	+3		+3	1	+25	+16		+3		
+25																+15
B♀♂ +50									B♂♀ +37							B♂♀ +31

			Total Colony Size	(H)					Total Colony Size	(I)		Total Colony Size	(J)			Total Colony Size
																2
													3			5
													3	**4**		8
													3	2	**0**	7
			5	**1**					3			2	Colony not found			
found				1	**2**				6	**3**		5	1	0	1	3
6			9	1	2	**3**			6	**3**	4	9	0	0	0	2
5	**4**		11	1	2	3	**1**←		7	0	0	0				1
2	4	**4**	12	1	2	3	1	**0**	7							
1	+3			+20	+18	+1	+3			4m			23m	8m		

reproductive disappeared and recruitment ceased. In A the colony split on first good rainfall; insufficient rainfall has apparently prevented E and H from fragmenting. Animals disappearing from the colonies after the good rains have either dispersed or been predated; extensive trapping both within and outside the study area suggests the latter factor to be more important

colony A (Table 2) which had lost the reproductive male. When dispersal does occur it appears to be rapid, and single "floating" animals are rarely captured ($n=3$).

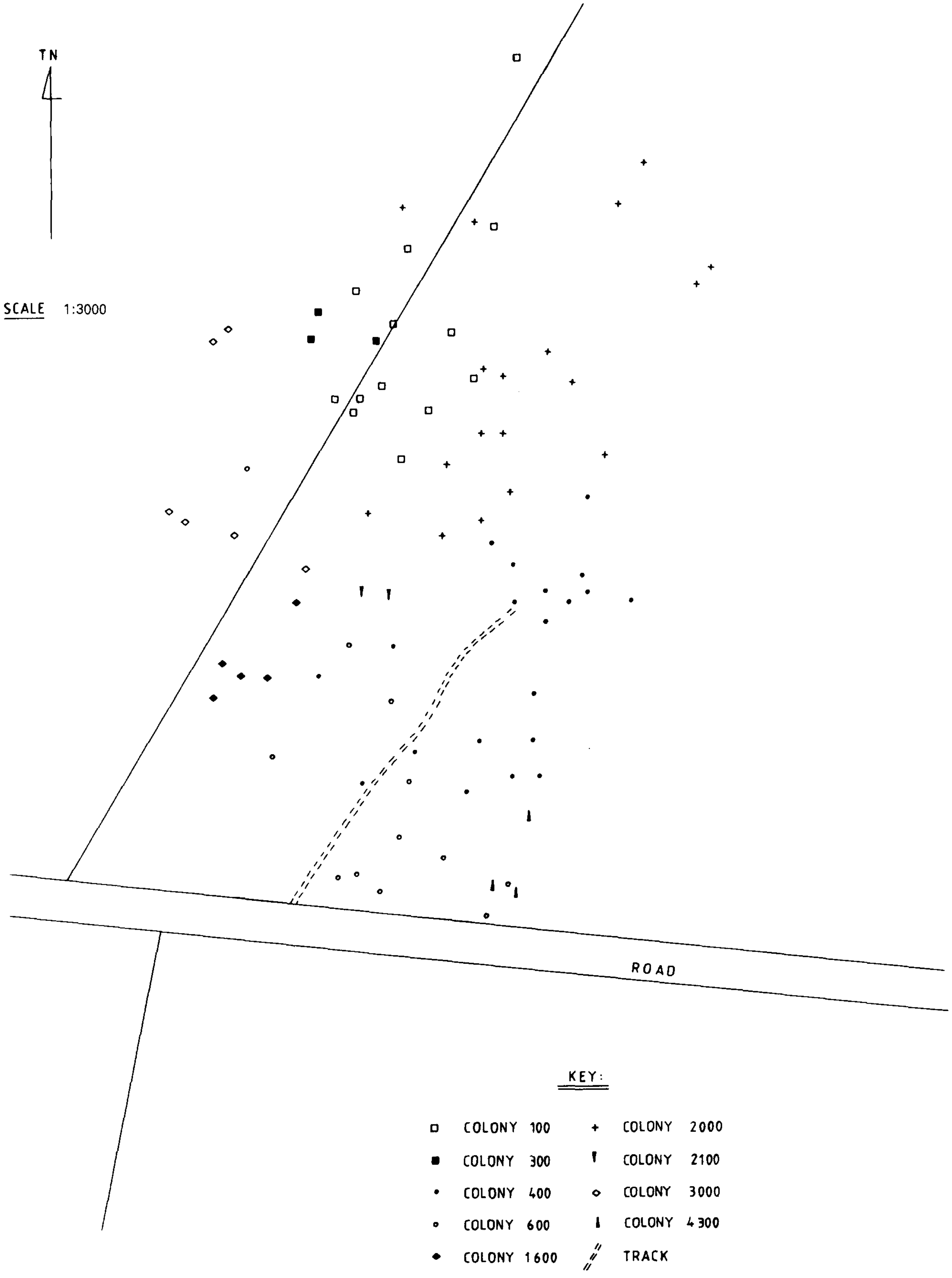
Evidence for independent evolution of eusociality in the two genera

Although naked and Damaraland mole-rats are both eusocial, there is an increasingly substantial body of evidence, from their phylogeny, colony composition, ethology and reproductive physiology, to indicate that eusociality evolved twice in this family.

Thus in the most parsimonious tree constructed for the Bathyergidae by Allard and Honeycutt (1992), the two social genera are distantly related – naked mole-rats diverged close to the base of the tree and the genus *Cryptomys* diverged after the three solitary genera.

The two species also show fundamental differences

DISTRIBUTION OF SELECTED MOLERAT COLONIES



in the composition and founding of colonies. We have shown in this paper that although colonies of *C. damarensis* are maintained for a number of years, their existence is dependent upon the continued presence of both the founding reproductive animals. In most instances a pair of breeding animals are the parents of all the non-breeding mole-rats in the colony. The death of a reproductive leads to fragmentation of the colony and, because of the close proximity of neighbouring colonies (Fig. 1), this provides an opportunity to outbreed. By contrast, naked mole-rat colonies are usually widely dispersed, outbreeding rarely occurs, succession of reproductives is from within the colony and the overall integrity of the colony is maintained during this transition. Therefore within colonies of naked mole-rats some individuals are the siblings (or more distant relatives) and not the progeny of the reigning reproductive animals, but, because they are so inbred, there is little genetic variation within a colony (Faulkes et al. 1990b) and it will not greatly decrease the inclusive fitness of the helpers.

Our data show that there is a higher probability of non-reproductive Damaraland mole-rats eventually becoming breeders than those in naked mole-rat colonies (Sherman et al. 1992). However, it also appears that Damaraland mole-rats are recaptured for longer than naked mole-rats in their natal colonies. This apparent dichotomy can perhaps be attributed to different predator pressures; for instance naked mole-rats are more exposed to predators as they form their mole-hills (Jarvis and Bennett 1991). The two species differ markedly in their response to mole-rats from other colonies. Non-reproductive Damaraland mole-rats do not fight while naked mole-rats are highly xenophobic. This difference in behaviour enables Damaraland mole-rats to outbreed, but severely limits the possibility of outbreeding in naked mole-rats and favours succession from within the colony.

Although socially induced suppression of reproduction occurs in both species its characteristics appear to differ. The ovaries of the naked mole-rat show little follicular development (Kayanja and Jarvis 1971; Faulkes 1990) and concentrations of circulating reproductive hormones are undetectable in nearly all non-breeding females (Faulkes 1990; Faulkes et al. 1990a). Follicular development occurs in non-breeding Damaraland mole-rats but the follicles fail to ovulate and instead luteinise, producing progesterone which may feed back to the neuroendocrine system to maintain a form of pseudopregnancy and thereby prevent ovulation (Bennett 1988). Likewise, significant differences are found in the males, where, although the non-reproductive males of both species undergo spermatogenesis, circulating testosterone concentrations of reproductive and non-reproductive male naked mole-rats differ significantly from each other, whereas those of the Damaraland mole-rats do not – again suggesting different methods of reproductive suppression in the non-breeders of the two species (Bennett 1988; Faulkes et al. 1991). The fact that the breeding female naked mole-rat is the most dominant animal in naked mole-rat colonies while the breeding male tops the dominance hierarchy in Damaraland mole-rat colonies may be of relevance here.

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Fig. 1. Distribution of nine neighbouring colonies at the study site at Dordabis. *Symbols* indicate different colonies. All the capture points for a colony are given the same symbol and give an indication of the home range of the colony and proximity to neighbouring colonies. Colonies F, I, J, K and L were founded from pairs following the January 1991 rainfall. Of these five colonies I, J and L have subsequently disappeared. A similar proportion of failures in new colonies has occurred throughout the study area. The *straight line* through the study area is a fence. *Key* notation: colony *100* = A, *2000* = B, *400* = C, *600* = D, *1600* = F, *4300* = I, *2100* = J, *3000* = K and *300* = L (cf. Table 2)

Independent evolution of eusociality in these two genera parallels that in the social insects, where eusociality has arisen on multiple occasions, in the Hymenoptera and in the Isoptera (Hamilton 1964). Alexander et al. (1991) have suggested that living in super-safe expandable nests, which are often subterranean, may be important precursors for the evolution of eusociality in mammals. While we would concur with many of their arguments, the fact remains that most subterranean mammals are solitary for reasons that are thoroughly examined by Nevo (1979). Attempts to determine the ecological correlates of cooperative breeding in birds and mammals are often hampered by the number of variables that have to be considered. This wide spectrum of factors has made it difficult to find a common denominator amongst cooperatively breeding species (Emlen 1982). The subterranean niche is a relatively stable environment (Bennett et al. 1988), but one which, as we have shown, normally precludes living in groups. By being the one exception to this rule the Bathyergidae provide a unique opportunity to critically examine the determinants of eusociality. Not only are there solitary and social genera in the family, but the pinnacle of social development, eusociality, has evolved twice independently in the family.

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