Short communications

An example of burrow system architecture of dispersing Damaraland mole-rats

Cornelia Voigt*

Department of Zoology and Entomology, University of Pretoria, Pretoria, 0028 South Africa

Received 28 May 2013. Accepted 21 October 2013

The Damaraland mole-rat (*Fukomys damarensis*) is a social, subterranean rodent that occurs in the red Kalahari sands. This species exhibits extreme reproductive skew with a single breeding female whereas reproduction in subordinate group members is completely blocked. Rainfall, as it greatly facilitates burrowing, provides the opportunity for individuals to disperse from their natal colony and hence, to overcome reproductive suppression. However, because rainfall is scarce, optimal conditions for burrow system construction are restricted to very short periods of the year. In order to observe the construction of a new burrow system of dispersing individuals, I released a small group (two females, one male) following heavy rains, and monitored their burrowing activity in the form of mound production during the following weeks. Recapture revealed that a new male had joined the group. Over a period of one month the four individuals extruded 127 mole hills and constructed a tunnel system with a total length of approximately 100 metres. Mound production ceased after 30 days due to the lack of subsequent rain. The study provides an example of dispersal in Damaraland mole-rats and gives new insights into the method of burrow system construction of this species. It further highlights the high costs associated with dispersal.

Key words: Bathyergidae, dispersal, Damaraland mole-rat, burrow system, reproductive suppression.

Dispersal can have substantial effects on the dynamics and the genetic structure of populations. In the majority of mammals natal dispersal is male-biased (Greenwood 1980). In mole-rats, several of the social species in the genus *Cryptomys* and *Fukomys* are obligate outbreeders (Bennett & Faulkes 2000). There, dispersal is crucial to colony genesis as well as for extra-pair copulations in colonies and thus ensuring genetic variability in colonies (Bishop *et al*. 2004; Burland *et al*. 2004). The Damaraland mole-rat (*Fukomys damarensis*) is a eusocial subterranean rodent that occurs in arid regions of southern Africa (red Kalahari sands) in colonies of up to 41 individuals (Bennett & Jarvis 1988; Jarvis & Bennett 1993). Wild colonies consist of a single breeding female (queen), her non-breeding offspring of both sexes and a few unrelated males of which one or two are breeders (Bennett & Jarvis 1988; Burland *et al*. 2002). Furthermore, immigrants of both sexes and offspring unrelated to the colony breeding male have been identified (Burland *et al*. 2004). Non-breeding females are physiologically suppressed from reproducing (Bennett *et al*. 1996). Dispersal constitutes the opportunity to escape from social suppression and to subsequently pair with an unrelated male to form a new colony (Jarvis & Bennett 1993). Indeed, experimental removal of those females from the confines of their natal colony in captivity lifts this physiological suppression as evident by the occurrence of spontaneous ovulation (Molteno & Bennett 2000; Snyman *et al*. 2006).

The burrows of established colonies consist of a complex network of tunnels and chambers. The latter are used as food stores, toilet areas and nests (Bennett & Faulkes 2000). Tunnels excavated to locate food are usually less deep than those which lead to chambers and the main nest (Bennett & Faulkes 2000). Mole-rats are herbivorous and owing to their subterranean lifestyle depend almost entirely on roots and tubers as food source, which they locate while excavating foraging tunnels. The amount of food resources within the home range constitutes the major factor that influences survival of a colony (Jarvis *et al*. 1998). During dry conditions the soil is difficult to excavate, and burrowing costs are high (Lovegrove 1989). Therefore, many new colonies are formed following the rains when the soil is easily worked (Bennett & Faulkes 2000). The sporadic rainfall in

*E-mail: cvoigt@zoology.up.ac.za

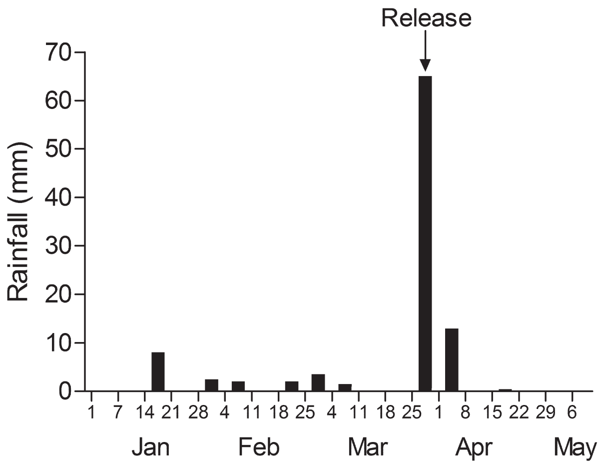

Fig. 1. Weekly rainfall (mm) from January to May 2013 recorded in the area were the new group of mole-rats was released.

arid regions restricts burrowing activities, and hence dispersal, to short periods of the year. However, the minority of newly founded colonies survive the dry periods mainly because the few individuals (usually a pair or a small group) fail to excavate long enough tunnels to locate sufficient food, which would sustain them until the next rains (Jarvis & Bennett 1993).

While in solitary species individuals disperse as juveniles, in the social species they remain within the natal colony until suitable conditions arise and, thus, dispersers are usually adults (Hazell *et al*. 2000). Very little is known about dispersal and new colony formation in mole-rats mainly because observing such events is difficult in a subterranean animal. There is some evidence from Damaraland mole-rats and naked mole-rats (*Heterocephalus glaber*) that individuals travel above ground (De Graaff 1972; Hazell *et al*. 2000; Braude 2000). In the latter species, field observations confirmed travel distances of over 2 km and new colonies appear to be established by one or few animals who then try to attract other dispersers (Braude 2000). A case of underground dispersal has been reported recently in a study on giant mole-rats (*Fukomys mechowii*). There, a single female settled in an abandoned part of an existing burrow system, presumably 'waiting' for an above-ground disperser (Lövy *et al*. 2013).

The aim of the present study was to experimentally induce the formation of a new colony and subsequently monitor the construction of their burrow system. In Damaraland mole-rats there is evidence that newly formed colonies do not only consist of pairs but also of small groups including adult non-reproductive individuals (Jarvis & Bennett 1993; C. Voigt, pers. obs.). Therefore, I decided to release a group consisting of a reproductively active female together with two non-reproductive conspecifics.

Mole rats were trapped near the village of Black Rock, Northern Cape, South Africa (27°7′S, 22°50′E) with Hickman live-traps, and kept in captivity for two months before their release. They were fed sweet potato, pumpkin and squash, daily. Mole rats were released in the evening of 29 March 2013 after two days of heavy rain, which constituted the major rainfall for the last three months (Fig. 1). I released two females and one male. They were toe-clipped for identification and toe-clips were collected for a future genetic study. All three individuals originated from different colonies. Female 1 (132 g) was considered a disperser as she was initially trapped alone and was in reproductive condition as indicated by a perforated vagina. Female 2 (80 g) was a non-reproductive female (vagina not perforated, teats not visible) that was caught as part of a whole colony. The male (105 g) was caught together with other colony members and was considered a non-breeder since larger males were present within the colony. The group was kept together for several days prior to release to ensure that there were no aggressive interactions. The release site was chosen to be at least 500 m away from other colonies and to contain several patches of geophytes (Gemsbok cucumber, *Acanthosicyos naudinianus*; Eland's bean, *Elephantorrhiza elphantina*), known to be consumed by mole-rats. The mole-rats were released through a 50 cm long plastic tube, which was buried tilted into the sand and covered with a plastic lid once all three animals had been released. The release site was visited daily and the number of fresh mounds produced as well as their distance and orientation were recorded after 5, 10 and 30 days. Mole-rats were recaptured after 30 days to verify their body condition and to confirm the number of animals within the burrow system. Upon capture their body mass was recorded and the animals were released again.

Group size and composition

Recapture after 30 days confirmed the originally released three individuals and, in addition, the presence of a new male (127 g). Body measurements showed that the large female (Female 1) had lost substantial mass (132 g *vs* 110 g), while the two non-breeders maintained approximately the same body mass (Female 2: 80 g *vs* 85 g, Male: 105 g *vs* 99 g). Damaraland mole-rats exhibit a behavioural division of labour, and among non-breeding colony members two castes can be distinguished, which are also reflected in body size: smaller individuals form a 'frequent worker' group while larger individuals are grouped as 'infrequent workers' (Bennett & Jarvis 1988). There is evidence that the latter constitute a distinct disperser caste, thereby building up their fat reserves rather than contributing to colony work (Scantlebury *et al*. 2006). Such a disperser morph has been discovered in the only other eusocial mole-rat species, the naked mole-rat (O'Riain *et al*. 1996). The characteristics would fit with the new male, which moved into the colony, as well as the larger of the two females (Female 1) that I released. The latter had initially increased body size and signs of reproductive readiness compared with Female 2. In the beginning, her presence most likely guaranteed that a new colony was established at the release site. Adult non-reproductive individuals not 'ready' for dispersal might simply disappear when experimentally released. However, it would probably pay a disperser to recruit 'frequent workers' from the colony as they would make a major contribution during the short period available for burrow system construction. There is indeed evidence that new colonies are founded by small groups (and not only pairs; Jarvis & Bennett 1993), and in a case study in Namibia, dispersing animals were found to be both reproductives and non-reproductives of either sex (Hazell *et al*. 2000). However, it remains unclear how dispersing individuals locate new colonies. The present case of the newly immigrated male demonstrates that dispersing animals travel above ground for at least several hundred metres as I did not detect burrowing activities in the vicinity of the released colony. This observation confirms previous reports on above-ground dispersal in other social and solitary mole-rat species (Braude 2000; Patzenhauerova *et al*. 2010; Bray *et al*. 2012).

Burrow construction

Burrowing activity started immediately after release. Several large mounds were produced at the release site, which could indicate the construction of a transient chamber. More mounds were produced in the following weeks, and it remained the place with the most excavated soil and possibly the centre of the burrow system. During the first 5 days burrowing activity radiated out in all geographic directions, resembling a star-like structure. In total 29 mounds were produced. During the following days the burrow system was mainly extended in northeasterly and southeasterly directions and after 10 days 45 mole hills were counted. Mound production ceased 30 days after the release. By this time 127 mounds had been produced and the total length of the burrow system was estimated to be approximately 100 metres (Fig. 2). Towards the northeast the mole-rats had excavated a long, rather straight tunnel with few side branches, while in southwesterly and southeasterly directions many mounds in close proximity where produced, which indicate a network of tunnels. Those could be more superficial secondary burrows for harvesting food resources as patches of geophytes occurred within these areas (Lovegrove & Painting 1987; Bennett & Faulkes 2000). To extend the primary burrow system as long straight tunnels as long as the soil is damp would be the optimal strategy for ensuring access to food resources during dry periods (Sumbera *et al.* 2003). In my study, because of the lack of subsequent rainfall the period for optimal digging was very short (30 days) and probably precluded further expansion of the home range. However, it is known that during the dry season mole-rats can continue to enlarge their burrow system by depositing the excavated soil into unused portions of the tunnel system (Jarvis *et al*. 1998; Skliba *et al*. 2009). Further, the mass loss of the large female in the group that I released reflects the high energetic demands of burrowing that the group was facing. A long-term field study in Namibia revealed that 50% of the newly formed colonies that consisted of

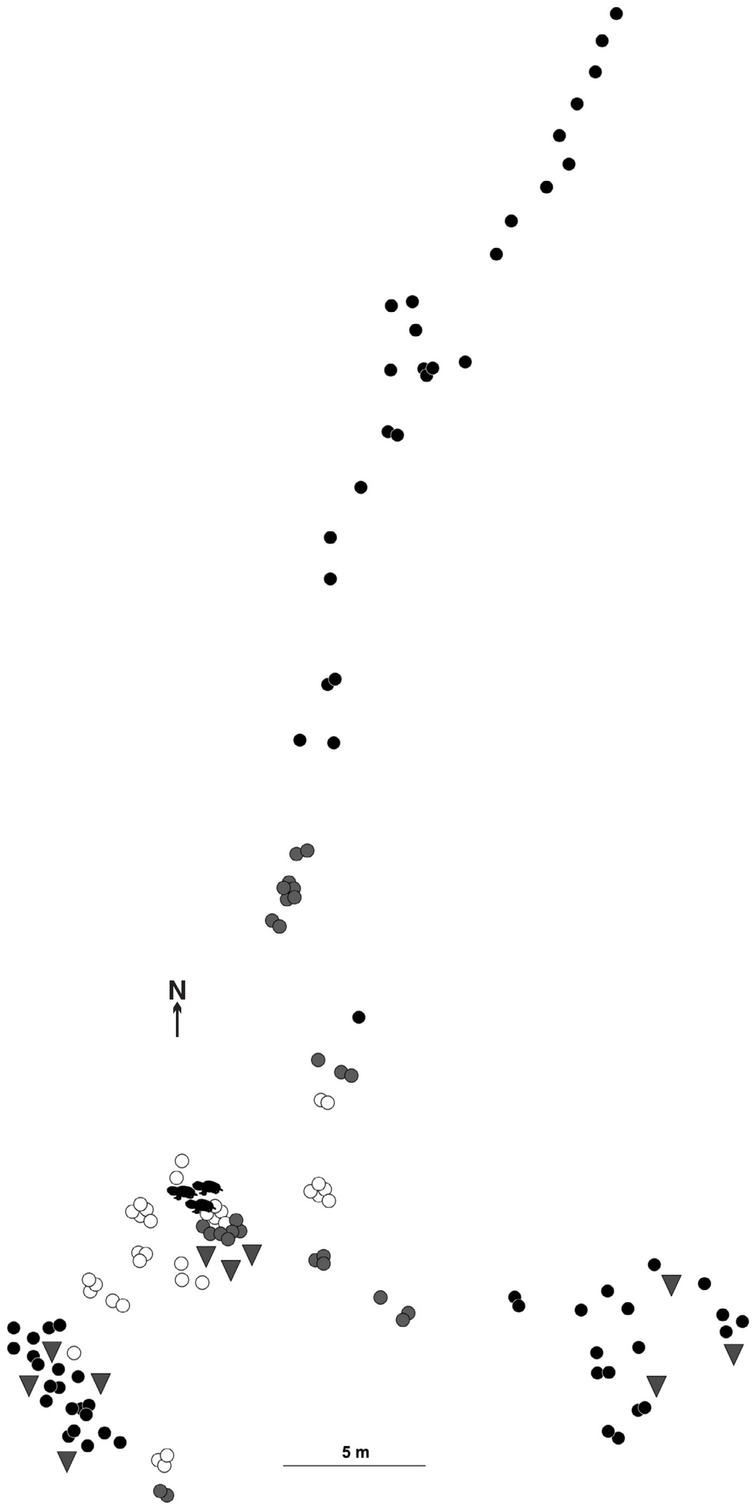

Fig. 2. Structure of the burrow system at 5 (○), 10 (●) and 30 days (●) after the release. The release site is indicated by the mole-rat symbols and the patches of geophytes by the triangles.

only 2–4 individuals, failed within two years, whereas larger colonies with an established workforce have a greater chance to survive periods of drought (Jarvis *et al*. 1994).

In conclusion, the experiment provides new insights into the pattern of dispersal and burrow system formation of Damaraland mole-rats, and it highlights the ecological constraints such as aridity on dispersal.

I thank Nigel Bennett for his advice and support. The Family Reynecke is thanked for letting me work on their farm. I am especially grateful to Paul Balayer for his great hospitality and logistical help. This work was supported by a fellowship from the University of Pretoria. Permits were obtained from the Northern Cape Department of Nature Conservation.

REFERENCES

BENNETT, N.C. 1994. Reproductive suppression in social *Cryptomys damarensis* colonies – a lifetime of socially-induced sterility in males and females. *Journal of Zoology* (London) **234**: 25–39.

BENNETT, N.C. & FAULKES, C.G. 2000. *African Mole-rats: Ecology and Eusociality.* Cambridge University Press, Cambridge.

BENNETT, N.C. & JARVIS, J.U.M. 1988. The social structure and reproductive biology of colonies of the mole-rat, *Cryptomys damarensis* (Rodentia, Bathyergidae). *Journal of Mammalogy* **69**: 293–302.

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. *Proceedings of the Royal Society B – Biological Sciences* **263**: 1599–1603.

BISHOP, J.M., JARVIS, J.U.M., SPINKS, A.C., BENNETT N.C. & O'RYAN, C. 2004. Molecular insight into patterns of colony composition and paternity in the common mole-rat *Cryptomys hottentotus hottentotus. Molecular Ecology* **13**: 1217–1229**.**

BRAUDE, S. 2000. Dispersal and new colony formation in wild naked mole-rats: evidence against inbreeding as a system of mating. *Behavioural Ecology* **11**: 7–12.

BRAY, T.C., BLOOMER, P., O'RIAIN, M.J. & BENNETT, N.C. 2012. How attractive is the girl next door? An assessment of spatial mate acquisition and paternity in the solitary Cape dune mole-rat, *Bathyergus suillus*. *PLoS ONE* **7**: e39866.

BURLAND, T.M., BENNETT, N.C., JARVIS, J.U.M. & FAULKES, C.G. 2002. Eusociality in African mole-rats: new insights from patterns of genetic relatedness in the Damaraland mole-rat (*Cryptomys damarensis*). *Proceedings of the Royal Society of London B – Biological Sciences* **269**: 1025–1030.

BURLAND, T.M., BENNETT, N.C., JARVIS, J.U.M. & FAULKES, C.G. 2004. Colony structure and parentage in wild colonies of co-operatively breeding Damaraland mole-rats suggests a role for reproductive suppression. *Molecular Ecology* **13**: 2371–2379.

DE GRAAFF, G.1972. On the mole-rat (*Cryptomys hottentotus damarensis*) (Rodentia) in the Kalahari Gemsbok National Park. *Koedoe* **15**: 25–35.

GREENWOOD, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* **28**:1140–1162.

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 study from the Waterberg region of Namibia. *Journal of Zoology* (London) **252**: 19–25.

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. *Behavioural Ecology and Sociobiology* **33**: 253–260.

JARVIS, J.U.M., O'RIAIN, M.J., BENNETT, N.C. & SHERMAN, P.W. 1994. Mammalian eusociality – a family affair. *Trends in Ecology and Evolution* **9**: 47–51

JARVIS, J.U.M., BENNETT, N.C. & SPINKS, A.C. 1998. Food availability and foraging by wild colonies of Damaraland mole-rats, *Cryptomys damarensis* implications for sociality. *Oecologia* **113**: 290–298.

LÖVY, M., SKLIBA, J. & SUMBERA, R. 2013. Spatial and temporal activity patterns of the free-living giant mole-rat (*Fukomys mechowii*), the largest social bathyergid. *PLoS ONE* **8**: e55357.

LOVEGROVE, B.G. 1989. The cost of burrowing by the social mole rats (Bathyergidae) *Cryptomys damarensis* and *Heterocephalus glaber*: the role of soil moisture. *Physiological Zoology* **62**: 449–469.

LOVEGROVE, B.G. & PAINTING, S. 1987. Variations in the foraging behaviour and burrow structures of the Damara molerat *Cryptomys damarensis* in the Kalahari Gemsbok National Park. *Koedoe* **30**: 149–163.

MOLTENO, A.J. & BENNETT, N.C. 2000. Anovulation in non-reproductive female Damaraland mole-rats (*Cryptomys damarensis*). *Journal of Reproduction and Fertility* **119**: 35–41.

O'RIAIN M.J., JARVIS, J.U.M. & FAULKES, C.G. 1996. A dispersive morph in the naked mole-rat. *Nature* **380**: 619–621.

PATZENHAUEROVÁ, H., BRYJA, J. & ŠUMBERA, R. 2010. Kinship structure and mating system in a solitary subterranean rodent, the silvery mole-rat. *Behavioural Ecology and Sociobiology* **64**: 757–767.

SCANTLEBURY, M., SPEAKMAN, J.R., OOSTHUIZEN, M.K. ROPER, T.J. & BENNETT, N.C. 2006. Energetics reveals physiologically distinct castes in a eusocial mammal. *Nature* **440**: 795–797.

SKLIBA, J., SUMBERA, R., CHITAUKALI, W.N. & BURDA, H. 2009. Home-range dynamics in a solitary subterranean rodent. *Ethology* **115**: 217–226.

SNYMAN, P.C., JACKSON, C.R. & BENNETT, N.C. 2006. Do dispersing non-reproductive female Damaraland mole-rats, *Cryptomys damarensis* (Rodentia: Bathyergidae) exhibit spontaneous or induced ovulation? *Physiology and Behavior* **87**: 88–94.

SUMBERA, R., BURDA, H., CHITAUKALI, W.N. & KUBOVA, J. 2003. Silvery mole-rats (*Heliophobius argenteocinereus*, Bathyergidae) change their burrow architecture seasonally. *Naturwissenschaften* **90**: 370–373.

Responsible Editor: P.J. Taylor