

Influences of sociality and habitat on African mole-rat burrowing patterns

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Abstract: The movement choices that animals make are influenced by many factors including resource availability, which in turn can affect whether the animals search for resources alone or in groups. Subterranean rodents are ideal for examining movement paths because they create burrows that persist for extended periods and thus serve as records of movement. African mole-rat species (Bathyergidae) are solitary, social, or eusocial, and inhabit a variety of habitat types. In this study, mole-rat burrowing patterns were examined by analyzing the spatial patterns of the soil mounds that they create as they burrow. Mound spatial patterns were examined for solitary and social species occurring in two habitats, which differed in rainfall, soil moisture, and vegetation availability. Examination of mound spatial patterns at multiple spatial scales revealed that mounds of single burrow systems were clustered at small spatial scales (<6 m), while mounds were not clustered at the larger spatial scales of the entire burrow systems. Spatial patterns of mounds did not differ in relation to sociality or habitat characteristics. These findings, as well as evidence from other taxa, may suggest common burrowing strategies for subterranean rodents.

Résumé : De multiples facteurs et, en particulier la disponibilité des ressources, affectent les choix faits par les animaux dans leurs déplacements; cette disponibilité, à son tour, peut déterminer si les animaux recherchent leur nourriture seuls ou en groupes. Les rongeurs hypogées sont des sujets parfaits pour l'étude des trajectoires de déplacement, car ils creusent des galeries qui persistent durant de longues périodes et servent ainsi de témoins de leurs déplacements. Les rats-taupes africains (Bathyergidae) sont solitaires, sociaux ou encore eusociaux et ils vivent dans une variété d'habitats. Dans la présente étude, l'analyse des patrons de répartition des monticules de terre produits lors du creusage des galeries chez des espèces solitaires et sociales dans deux habitats qui diffèrent par la pluviosité, l'humidité du sol et la disponibilité de la végétation permet de déterminer les patrons de creusage des galeries chez les rats-taupes. L'examen de la répartition spatiale des monticules à plusieurs échelles spatiales montre que les monticules des systèmes de galeries individuelles ont une distribution contagieuse aux petites échelles spatiales (<6 m), alors qu'aux échelles spatiales plus grandes du système entier des galeries, il n'y a pas de regroupement des monticules. La répartition spatiale des monticules ne diffère en fonction ni de la vie sociale, ni des caractéristiques de l'habitat. Ces résultats ajoutés à des indications provenant de d'autres taxons indiquent peut-être l'existence de stratégies communes de creusage de galeries chez les rongeurs hypogées.

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Introduction

The movement paths of an animal are a product of its behavior. The paths of an animal searching for food may differ from the paths of an animal avoiding predators or searching for mates. Differences in social behavior between solitary and group living animals, for example, may also lead to differing paths of movement based on differences in the manners in which they explore their habitats (Bertram 1980). Additionally, features of the habitat such as landscape topography and resource availability may influence paths of movement as animals travel through their surroundings (e.g., Reichman and Aitchison 1981; Johnson et al. 2001; Seabloom and Reichman 2001).

Degree of sociality can have an important influence on movement paths. Solitary species live and forage alone, and

hence their movement paths reflect the choices of only one individual. Although solitary species have the advantage of not having to share food with other individuals, they have the potential cost of a reduction in the opportunity of finding food (Lovegrove and Wissel 1988). Social species, on the other hand, have multiple individuals moving and foraging, thus movement paths reflect the efforts of many individuals in the group. Although there can be an increase in per capita energy return when individuals forage in a group, there is evidence of decreasing per capita energy return with increasing group size (e.g., Kruuk 1975; Lovegrove and Wissel 1988).

Advantages to foraging alone or in a group can differ based on habitat conditions such as food abundance and predictability (Crook 1964). Typically, both solitary and social species can inhabit areas with predictable resources. How-

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ever, for some taxa, cooperative foraging has emerged as a successful foraging strategy, particularly in arid habitats where resources are patchily distributed and unpredictable (Spinks et al. 2000). Food patches are less abundant, seasonally less predictable, and more widely dispersed, but typically larger in arid than in mesic habitats (aridity food-distribution hypothesis; Jarvis 1978; Jarvis et al. 1994), yielding an advantage to group foragers. Previous work (Jarvis 1978) suggests that in a desert environment, individuals of a group would have a better chance of survival than a solitary individual. This is because locating patchily distributed food in an arid environment can be difficult, but once located, it can be shared among group members. When one food item is located, more food items are typically found in the same area, and consequently, the surrounding area can be explored for food rewards with minimal cost to the group. However, contrasting evidence suggests that soil characteristics (e.g., digging cost) are important in explaining the occurrence of solitary- vs. group-living species (Ctenomyidae), while food distributions are not (Lacey and Wiczorek 2003).

There are a few of reasons why African mole-rats (Bathyerigidae) are ideal subjects for examining how the degree of sociality and habitat influence movement paths. First, they are subterranean rodents that live their entire lives below ground and construct persistent burrows, providing evidence of their movement paths. Second, bathyergid species are solitary, social, or eusocial (Jarvis and Bennett 1990; reviewed in Bennett and Faulkes 2000). And third, typically only social species occur in arid areas, but there is a solitary bathyergid (*Bathyergus janetta* Thomas and Schwann, 1904) in an arid region that is sympatric with social species (for evidence of a solitary bathyergid (*Heliophobius argenteocinereus* Peters, 1846) occupying a mesic area with low food availability see Sumner et al. 2003). In addition, social species occur in both arid and mesic habitats.

Burrows are extended mainly as mole-rats forage for vegetation (Bennett and Faulkes 2000), thus burrowing paths should be a function of vegetation availability. However, Reichman and Jarvis (1989) observed that mole-rats often did not forage in areas near their burrows that had significantly higher plant biomass, suggesting that neither solitary nor social species was able to detect food from a distance. A later study supported this idea by showing that mole-rats frequently miss patches of food items that were <1 m from their burrows (Jarvis et al. 1998). Evidence exists that shows mole-rats concentrate digging in areas where they have encountered a food patch, which provides support for their use of area-restricted searching (Jarvis and Sale 1971; Brett 1991). This fine-scale searching can be explained by the mole-rats' ability to detect kairomones, which are produced by vegetation and released into the soil, and thus inadvertently providing a source of guidance to mole-rats as they chose the direction of their burrowing paths (Heth et al. 2002).

In this study, I examined the influences of degree of sociality and habitat characteristics on African mole-rat burrowing patterns. Mole-rats produce soil mounds above-ground as they burrow, hence information about where animals have passed along their burrowing paths can be inferred non-invasively by examining where soil mounds are

Fig. 1. Map of field site locations in western South Africa.



produced. I analyzed mound spatial patterns of both solitary and social species in two habitats, which differed in annual rainfall, soil moisture, and vegetation availability.

I predicted that spatial patterns of mounds would emerge on a small scale, related to foraging, and on a large scale, related to habitat differences. I used Ripley's *L* function at multiple spatial scales to detect changes in spatial patterns. On a small scale, I expected mounds to show a clustered distribution, which would be expected if the animals were using area-restricted searching. I expected that burrowing patterns of solitary and social species would be similar because neither can detect their food from a distance, and both can detect kairomones at a fine scale; thus, they may have similar foraging behaviors. Individuals at the site with the highest rainfall, soil moisture, and food availability (as measured by vegetation biomass and cover) should have clustered burrowing patterns on both a small and large scale. At the drier site with lower food availability, burrowing patterns should be clustered on the small scale (intensified digging when food is found), but not clustered on the large scale as they search for food items.

Methods

Study sites

I used two study sites with different habitat types. One site was in Darling (33.25°S, 18.25°E), approximately 60 km north of Cape Town in the Western Cape Province, South Africa (Fig. 1). Annual rainfall at Darling averages 457 mm based on 52-year rainfall records and has 6 months per year with >25 mm rainfall (South African Weather Service 1999), which is the amount needed to penetrate soils to the depth that mole-rats forage (Jarvis et al. 1994). This site is a commercial farm primarily used for agriculture, and sheep and cattle grazing. Darling was characterized by high

Table 1. Average body mass values taken from the literature for male and female African mole-rats, and the maximum number of individuals per burrow.

	Site	Body mass (g)*		No. of individuals/burrow [†]	No. of burrows used by species/site	Vegetation [‡]		Soil composition [‡]	
		Male	Female			Biomass (g/m ²)	Cover (%)	Clay (%)	Sand (%)
<i>Bathyergus suillus</i>	Darling	896	670	1	5	309.41±44.72	81	10	90
<i>Georychus capensis</i>	Darling	182	181	1	5	456.22±40.70	85	10	90
<i>Cryptomys hottentotus</i>	Darling	66	47	14	2	307.12±62.42	85	8	90
<i>Bathyergus janetta</i>	Kamieskroon	468	338	1	4	87.38±14.53	34	8	90
<i>Cryptomys hottentotus</i>	Kamieskroon	66	47	14	5	99.83±15.82	19	8	86

*Data are from Skinner and Smithers (1990).

[†]Data are from Bennett and Faulkes (2000) and references cited therein.

[‡]Vegetation biomass (mean ± SE) and cover and soil composition data were from field samples taken near the burrows.

vegetation biomass and sandy soils (Table 1). The second site was in Kamieskroon (30.13°S, 17.57°E), approximately 460 km north of Cape Town in the Northern Cape Province, South Africa. Annual rainfall at Kamieskroon averages 234 mm based on 48-year rainfall records and has 4 months per year with >25 mm rainfall (South African Weather Service 1999). The site is characterized by low vegetation biomass and sandy soils (Table 1). Cattle and goats were occasionally kept at the site.

Species

Two solitary species, *Bathyergus suillus* (Schreber, 1782) and *Georychus capensis* (Pallas, 1778), and one social species, *Cryptomys hottentotus* (Lesson, 1826), occur at Darling. *Bathyergus suillus* is the largest of all mole-rat species, *G. capensis* is of intermediate size, and *C. hottentotus* is the smallest of the three species (Table 1). *Cryptomys hottentotus* also occurs in Kamieskroon along with *B. janetta*, which is a large, solitary species (Table 1). Only one individual produces soil mounds in a solitary species, while multiple individuals produce mounds in social species.

Data collection

Fieldwork was conducted during June and July 2002, during the wet, winter season when mole-rats were active. To record data on each burrow system, I established as many 30 m × 30 m grids as necessary to capture all soil mounds of the system. Each grid comprised 100 cells, each measuring 3 m × 3 m (range = 29–200 cells necessary to cover each burrow system). To minimize seasonal variability, I considered only fresh (i.e., unweathered) mounds.

Aboveground (living) plant biomass was measured in each grid to determine the relative productivity of each habitat. Four random samples (15 cm × 15 cm each) were clipped per grid, dried to a constant mass at 60 °C for 24 h, and weighed to obtain the total biomass to the nearest 0.01 g. Percent area cover of vegetation was estimated visually to determine the presence and amount of vegetation in each cell.

Soil samples were taken in three randomly assigned cells in one grid of each species. The three cell samples were mixed to yield a composite sample for each grid for soil texture analysis (percentage of sand, silt, and clay). Soil analy-

ses were done by Soil Science Division, Department of Agriculture, Western Cape, South Africa.

Burrow systems of each species were readily distinguishable based on mound size and shape. To verify the method of using mound size and shape to identify species, animals were livetrapped within one burrow system of each assumed species, then released back into their original burrows. All animals were cared for in accordance with the principles and guidelines of the Canadian Council on Animal Care. Mounds from multiple burrow systems were mapped for each species (Table 1). Only two *C. hottentotus* burrows could be located at the Darling site. Mound locations in each cell were mapped visually and then digitized to determine coordinate locations of each mound (Fig. 2) using the imaging program SigmaScan[®] version Pro 5.0 (SPSS Inc. 1996).

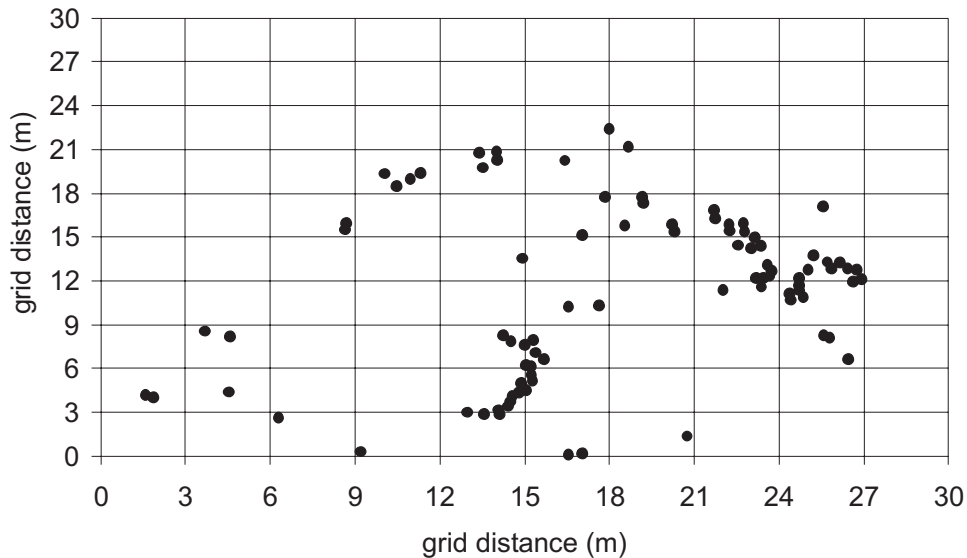
Statistics

Vegetation biomass, vegetation cover, soil texture (e.g., percentage of clay), and soil moisture data were analyzed using standard one-way ANOVAs in JMPIN[®] version 4.0 (SAS Institute Inc. 2000) to determine whether there were differences in these parameters between the two study sites.

Spatial analyses were performed on mounds of each burrow system, and then results were examined both qualitatively and quantitatively for mound spatial patterns. The spatial distributions of mounds were analyzed as point locations using Ripley's *L* function to allow for spatial analyses at multiple spatial scales (Ripley 1979; Venables and Ripley 1994). Ripley's *L* function compared mound distributions to a random distribution of points within a circle of radius *h*, where *h* was half of the distance across which mounds were distributed for each burrow system. I used 99 permutations to create a 99% confidence envelope.

For each burrow system, the maximum lag distance used in Ripley's *L* function was the radius *h* given by that system. Lag distances are user-specified distances to allow analyses at each specified distance (i.e., spatial scale). For each burrow system, I used 25 evenly spaced increments from zero up to the maximum lag distance, *h*. Specifying multiple increments allowed for detailed analyses at each scale. Ripley's function yielded 25 *L(h)* values at each incremental distance from zero up to *h*. For example, given the aforementioned criteria, if mounds were distributed across a distance of 100 m, the maximum lag distance, *h*, would be 50 m, and

Fig. 2. Sample 30 m × 30 m square grid showing mound distribution for *Cryptomys hottentotus* in Darling (●, single mound).



each increment will be 2 m (50 m divided by 25 increments), which would provide $L(h)$ values at 0, 2, 4, 6, 8, ..., 50 m. Thus, in this example, Ripley's L function could detect spatial patterns at all of these intervals. Values of $L(h)$ above the confidence envelope indicate clustering at that distance, whereas values below the envelope indicate uniform distribution and values falling within the envelope indicate random distribution (Fig. 3).

Ripley's L function is a highly effective tool for point pattern analyses. Monte Carlo simulations use the same data for the analyses to generate a 99% confidence envelope around the patterns revealed. Therefore, this statistic is a powerful tool for revealing spatial patterns, which then allows inferences to be drawn regarding the mechanisms that generate these patterns.

In addition to the qualitative results provided by Ripley's L function (clumped, random, or uniform), I further analyzed the quantitative data given by Ripley's L function. For each burrow system, I determined the maximum L value (L_{\max}), the distance over which the mounds exhibited a clustered pattern (h_1), and the distance over which the mounds exhibited a random pattern (h_2) (Fig. 3). For each of L_{\max} , h_1 , and h_2 , I used multiple regression models in JMPIN[®] version 4.0 (SAS Institute Inc. 2000), which included all measured habitat characteristics (vegetation biomass, vegetation cover, soil texture, soil moisture, and annual rainfall) and sociality (social or not) to determine their effects on mound spatial patterns.

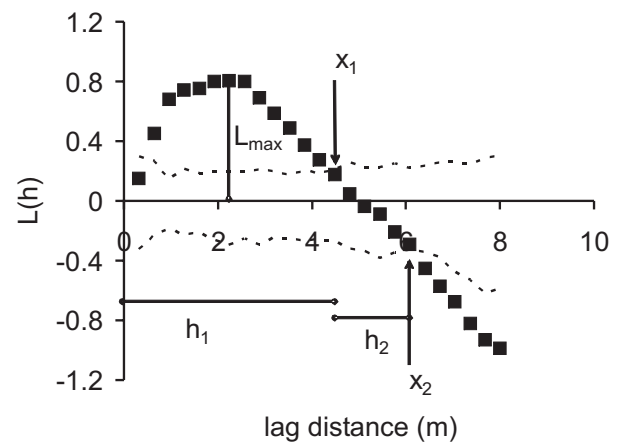
Results

Vegetation and soil

Aboveground vegetation biomass was significantly higher in Darling (341.62 ± 27.75 g/m², mean \pm SE) than in Kamieskroon (89.09 ± 11.16 g/m²; $P \ll 0.01$; Table 1), as was percent area cover of vegetation in Darling (83%) compared with Kamieskroon (24%; $P \ll 0.01$; Table 1).

Soil texture analyses revealed that soils at both sites had similar sand ($P = 0.27$) and clay ($P = 0.22$) compositions. Darling soils were made up of 90% sand and 9% clay, while

Fig. 3. Values of Ripley's $L(h)$ above the maximum L (upper limit of confidence envelope, upper broken line) indicate clustering at that distance, whereas values below minimum L (lower broken line) indicate uniform distribution, and values falling within the envelope indicate random distribution. L_{\max} represents the maximum $L(h)$ value. The distance on the x axis between 0 and x_1 represents the distance, h_1 , over which the mounds exhibited a clustered pattern. The distance on the x axis between x_1 and x_2 represents the distance, h_2 , over which the mounds exhibited a random pattern.



Kamieskroon soils were 88% sand and 8% clay (Table 1). Soil moisture at Darling (14.4%) was significantly higher ($P \ll 0.01$) than at Kamieskroon (11.3%).

Qualitative mound spatial patterns

Mounds of both solitary and social species at both sites had clustered distributions at all spatial scales up to at least 6 m, thus only large-scale results >6 m are presented below in detail (Table 2).

Darling

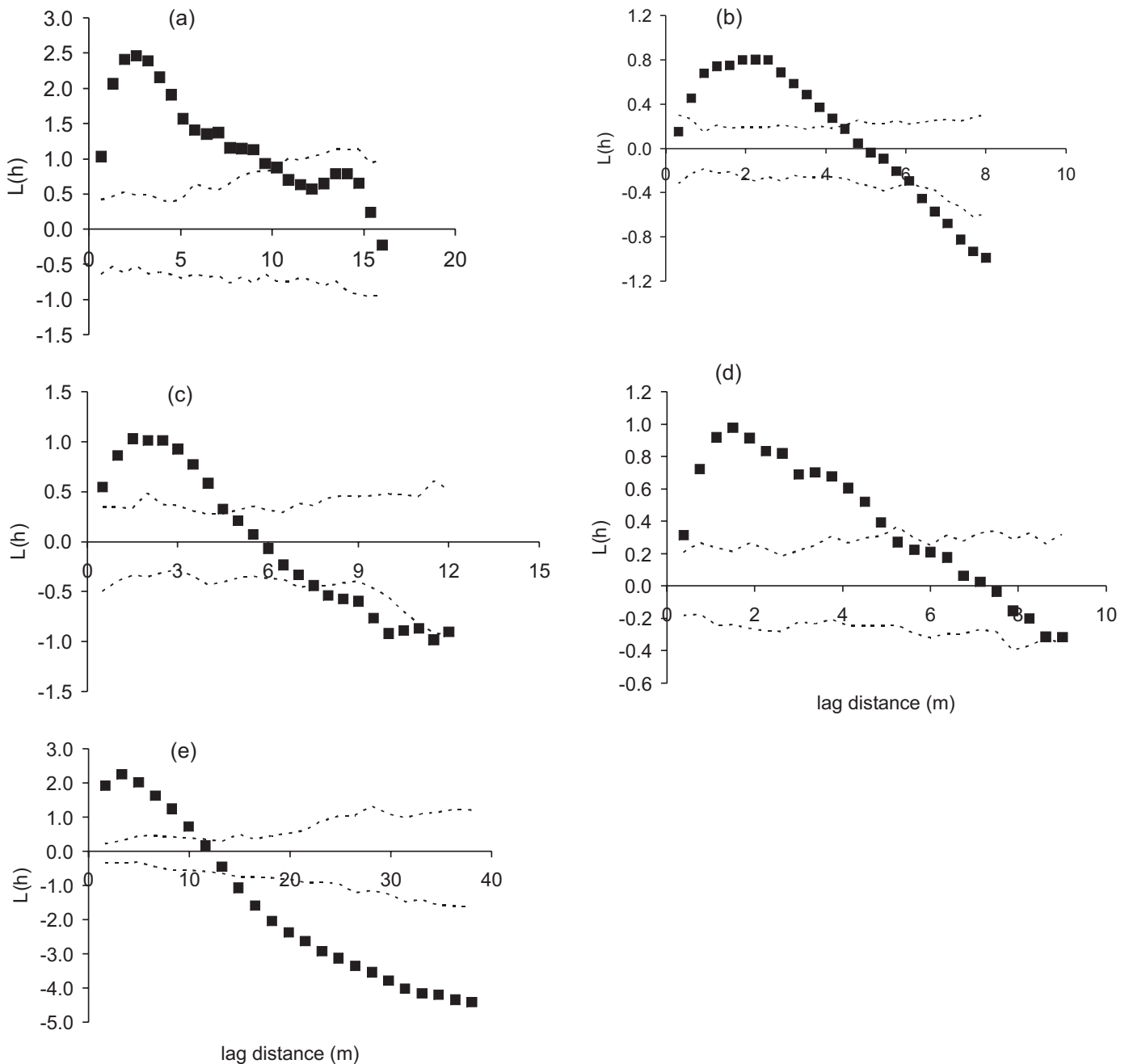
The mound distributions of all five *B. suillus* (solitary) individuals were random (for example see Fig. 4; Table 2). In

Table 2. Average (\pm SE) distances of mound spatial patterns of each species of African mole-rat at each site.

	Site	Small scale		Large scale	
		Distance (m)	Pattern	Distance (m)	Pattern
<i>Bathyergus suillus</i>	Darling	10.3 \pm 2.9	Clustered	15.0 \pm 3.5	Random
<i>Georchus capensis</i>	Darling	8.5 \pm 3.9	Clustered	23.3 \pm 14.0	Random/uniform
<i>Cryptomys hottentotus</i>	Darling	6.8 \pm 2.0	Clustered	12.0 \pm 0.0	Random/uniform
<i>Bathyergus janetta</i>	Kamieskroon	7.8 \pm 1.4	Clustered	11.0 \pm 2.7	Random
<i>Cryptomys hottentotus</i>	Kamieskroon	10.9 \pm 2.4	Clustered	19.8 \pm 6.5	Random/uniform

Note: Large-scale patterns represent a change in pattern from the small-scale pattern, and large-scale distance is the distance that the large-scale pattern was shown, up to the maximum burrow size.

Fig. 4. Examples of Ripley's L function for solitary (*Bathyergus* spp., *Georchus capensis*) and social (*Cryptomys hottentotus*) species at each site: (a) *B. suillus*, (b) *G. capensis*, and (c) *C. hottentotus* in Darling; (d) *B. janetta* and (e) *C. hottentotus* in Kamieskroon.



contrast, mound distributions of the five *G. capensis* (solitary) individuals were either random or uniform (Table 2). Of the two burrow systems of *C. hottentotus* (social), one showed random mound distributions, whereas the other burrow system fluctuated between uniform and borderline uniform or random (Table 2).

Kamieskroon

The mound distributions of all four *B. janetta* (solitary) individuals were random (Table 2). Mounds of the five *C. hottentotus* (social) burrow systems fluctuated between uniform and borderline uniform/random patterns (Table 2).

Quantitative mound spatial patterns

There was no difference in L_{\max} ($P = 0.93$), h_1 ($P = 0.87$), or h_2 ($P = 0.72$) among species. Multiple regression results (using all species) showed no effect of habitat characteristics or degree of sociality on L_{\max} ($r^2 = 0.41$, $df = 6$, $P = 0.45$), h_1 ($r^2 = 0.21$, $df = 6$, $P = 0.86$), or h_2 ($r^2 = 0.48$, $df = 6$, $P = 0.31$). The only significant regression component was the effect of vegetation cover ($P = 0.03$) on h_2 , the distance over which the mounds exhibited a random pattern.

Discussion

Mole-rat species in this study exhibited differing mound patterns on two spatial scales. All burrows had clustered mound distributions on a small scale (at all scales up to at least 6 m), as predicted, and non-clustered patterns on a large scale. The clustered pattern on the small scale supports the idea of area-restricted searching in both habitat types, regardless of food availability. Although area-restricted searching should be particularly advantageous for animals in habitats where food items are patchily distributed, animals in any environment should benefit from exploiting areas rich in food when they are encountered.

Quantitative analyses revealed that solitary and social species did not differ in the spatial patterns of their mounds, as predicted. Sociality does not affect an animal's ability to detect food through the soil (e.g., Reichman and Jarvis 1989; Heth et al. 2002), and therefore may not influence burrowing patterns. However, contrary to my findings, a study using fractal dimension (Le Comber et al. 2002) showed differences in burrowing patterns between solitary and social species at one of my study sites, namely at Darling. Differences in findings between previous work and this current study are potentially due to seasonal variation in burrowing patterns; the method used in this current study is best suited for animals that are actively burrowing to capture a single season of activity (see below). Additionally, the differences between the two studies may simply represent stochastic processes that were due to low sample sizes at Darling in both my study (social, $n = 2$; solitary, $n = 10$) and that of Le Comber et al. (2002; social, $n = 3$; solitary, $n = 5$).

On a large scale (>6 m), all species exhibited non-clustered mound distributions. I expected to find differences in large-scale distributional patterns of mounds based on differences in habitat characteristics between the two sites. The only influence of habitat on mound patterns was of vegetation cover on h_2 , where greater vegetation cover led to a greater distance over which mounds showed a random pattern. How-

ever, this pattern was only seen in the drier site and was driven by two cases (one social, one solitary) of exceptionally high vegetation cover (48% and 69%, respectively); otherwise vegetation cover was quite low (average excluding these two was 17%). Previous work in the two study areas showed differences in spatial distributions of vegetation (N. Bennett, personal communication), although these differences did not result in differences in mound patterns. Soil texture (and consequently digging cost; Vleck 1979) was similar between sites, indicating that soil composition was probably not a factor contributing to differences between sites (unlike for ctenomyids; Lacey and Wiczorek 2003). However, the two sites differed significantly in vegetation biomass, vegetation cover, soil moisture, and rainfall, yet mound spatial patterns were similar between sites, suggesting that mole-rats in this study employ similar burrowing strategies. Given that burrows are extended primarily as these animals search for food (Bennett and Faulkes 2000), this may imply the use of a similar foraging strategy, which may be explained by the use of cues (i.e., kairomones produced by vegetation; Heth et al. 2002) in the soil to direct digging.

It is noteworthy that mole-rat species consume different types of food, and yet have similar mound distributions. Furthermore, factors not addressed in this study such as plant energy, digestibility, and nutrient content are likely to differ among the plant species consumed by each mole-rat species. Previous work at Darling showed that *C. hottentotus* forages primarily on belowground roots and storage organs, while the diet of *B. suillus* is composed of approximately 50% stems and leaves of plant species that differ from those consumed by *C. hottentotus* (Reichman and Jarvis 1989). Data from another site also showed that *C. hottentotus* and *B. suillus* forage on different plant species (Davies and Jarvis 1986). Given that these mole-rats forage for different plant species, and that they cannot detect their food through the soil from a distance, yet they have the same burrowing patterns provides further evidence that mole-rats may have a common, underlying burrowing strategy.

One goal of examining mound spatial patterns rather than excavating burrows is to provide a non-invasive and non-destructive method that supplies information about burrowing paths. Although there is evidence that mound location may occasionally be offset from the burrow, and thus not always reveal the precise location of the burrow (Davies and Jarvis 1986), many burrow maps support the idea that mound position is a good indicator of burrow location for subterranean rodent species (e.g., Andersen 1988; Sumbera et al. 2003). Additionally, subterranean rodents occasionally push soil into belowground tunnels rather than construct aboveground mounds (Crouch 1933; Sumbera et al. 2003), in which case, mounds may not accurately represent entire burrow configuration. However, this behavior is thought to be a response to temperature stress during hot, dry seasons (Sumbera et al. 2003). I examined mound patterns produced only during the cool, winter season; therefore, minimizing seasonal variation in burrowing patterns and capturing burrowing patterns as they relate to current vegetation and soil conditions. Many previous studies have examined mole-rat burrowing patterns from many seasons of activity by examining excavated burrow systems (e.g., Davies and Jarvis

1986; Le Comber et al. 2002; but for seasonal treatment of burrowing patterns see Sumbera et al. 2003), and thus, those findings may not be directly comparable to the findings of this current study.

Many factors in addition to those considered here could be important in determining burrowing patterns; for example, distributions of preferred food types, social interactions with neighbors (e.g., aggression, mating), and population density. One goal of this study was to test a non-invasive field method with a novel quantification of point spatial patterns, which was done using straight-forward predictors. The emergence of differing burrowing patterns at two spatial scales is consistent; however, there is variation in the size of the scale at which these patterns emerge. Future work may reveal the potentially important roles of the aforementioned factors on burrowing patterns and variation in scale of these patterns.

Mound spatial patterns were consistent across varying habitat characteristics and degrees of sociality. The findings from one of the two measures of vegetation (cover) suggest that food availability may influence burrowing patterns of these animals, but perhaps only in extreme cases, which yield a similar response from both social and solitary species. Similarity among burrowing patterns was also found for three pocket gopher species (Geomyidae; all solitary) in North America, across a range of vegetation abundance and soil characteristics (Romañach et al. 2005). Additionally, Romañach and Le Comber (2004) found no difference in burrowing patterns within one geomyid species (*Thomomys bottae* (Eydoux and Gervais, 1836)) between sites differing twofold in vegetation abundance. Although the geomyid studies and this bathyergid study used different methods to assess burrowing patterns (burrow maps vs. mound maps), and thus are not directly comparable, both suggest similarity of burrowing patterns within their own families. Results from these two studies leave open the question of whether all subterranean rodents share similarities in foraging behavior (e.g., area-restricted search, use of kairomones to orient digging), and thus exhibit similar burrowing patterns.

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