

Burrow fractal dimension and foraging success in subterranean rodents: a simulation

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For animals that forage underground, the success with which food items are located may be closely related to burrow architecture. Fractal dimension, which describes how a burrow explores the surrounding area in a way that is independent of burrow length, is an obvious choice for a single metric describing burrow shape. Although it is often assumed that burrows of high fractal dimension will be associated with greater foraging success, this has not previously been demonstrated. In this study, we use computer simulations to study the success with which burrows of different fractal dimensions locate randomly distributed food items. In addition, we examine the effect of different patterns of food distribution (in particular the patchiness with which food items are distributed) and consider how using different criteria for locating food items affects the relationship between fractal dimension and foraging success. We conclude that, under a wide range of plausible assumptions about the ways in which subterranean rodents forage, burrows of high fractal dimension are more successful at locating food items than burrows of lower fractal dimension.
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Successful foragers must locate and capture resources that are often patchily distributed in heterogeneous landscapes (Pyke, 1984). For many species of subterranean animals, burrow shape may be an important determinant of the success with which these resources are located (Reichman et al., 1982; Romañach et al., 2005). Typically, studies of burrow shape have examined metrics such as burrow system shape, burrow system area, number of segments, linearity, turn angle, number of branches, segment length, and branch length (for an explanation of these terms, see Romañach and Le Comber, 2004) (Romañach et al., 2005). However, because the interactions between these variables are not clear, recent studies have begun to use fractal dimension to provide a single measure of shape that has the further advantage of being independent of burrow length (Bascompte and Vila, 1997; Biesinger and Haefner, 2005; Etzenhouser et al., 1998; Fritz et al., 2003; Huettmann, 2004; Laidre et al., 2004; Le Comber et al., 2002; Mouillot and Viale, 2001; Phillips et al., 2004; Puche and Su, 2001; Romañach and Le Comber, 2004; Sumner et al., 2003). Fractal dimension is an obvious choice for a measure of burrow shape because it is essentially a measure of the extent to which a one-dimensional structure fills a plane, with low fractal dimension (close to 1.0) describing a burrow that explores relatively little of the surrounding area and high fractal dimension (close to 2.0) describing a burrow which explores the surrounding area more thoroughly. It is thus particularly suitable as a measure of burrow shape when the burrow is used for foraging (Le Comber et al., 2002).

However, although recent work has examined the relationship between fractal dimension and other measures of burrow shape (Romañach and Le Comber, 2004), it has not previously been demonstrated that burrows with high fractal dimension are more successful at locating food. In fact, it is difficult to determine the direction of any causal relationship between

burrow shape and foraging success from field data because animals can alter burrow shape in response to finding food (Benedix 1993; Bennet and Faulkes, 2000; Reichman et al., 1982). That is, any association between high fractal dimension and increased foraging success may arise in either of two ways: (1) because burrows with high fractal dimension experience greater foraging success and (2) because greater foraging success leads to burrows with high fractal dimension, as a result of such behavior as area-restricted searching. On a more pragmatic level, empirical testing for general relationships between foraging paths and resource distributions is limited by lack of data. Most studies of foraging paths have very low replication because of the difficulty involved in tracking animals continuously for long periods of time. For example, in one study of African mole-rats only 25 burrow maps were available, covering just seven species; nine of these had not previously been published. Of the two eusocial mole-rat species, only two burrow maps were available for the naked mole-rat, *Heterocephalus glaber*, and none for the Damaraland mole-rat, *Cryptomys damarensis* (Le Comber et al., 2002). For this reason, there are few data sets in which complete maps of foraging paths are available for animals foraging in areas that differ in food availability and distribution (see Le Comber et al., 2002, and Reichman et al., 1982, for some exceptions). Furthermore, field measurements of burrow shape may reflect a compromise between foraging efficiency and other constraints on fitness (Seabloom and Reichman, 2001).

To avoid these confounding effects, we used a computer simulation to examine the effect of burrow fractal dimension on foraging success; in these simulations, burrow shape was not affected by foraging success. Note that, in this study, we are concerned only with cases in which animals have no prior knowledge of food distributions. While these models are intentionally general in their formulation, the work is motivated by our empirical work on subterranean mammals (see e.g., Le Comber et al., 2002; Romañach and Le Comber, 2004; Romañach et al., 2005). Subterranean mammals are uniquely suited for examining the effects of fractal dimension on foraging success because the cost of movement to these animals is two to three orders of magnitude higher than for

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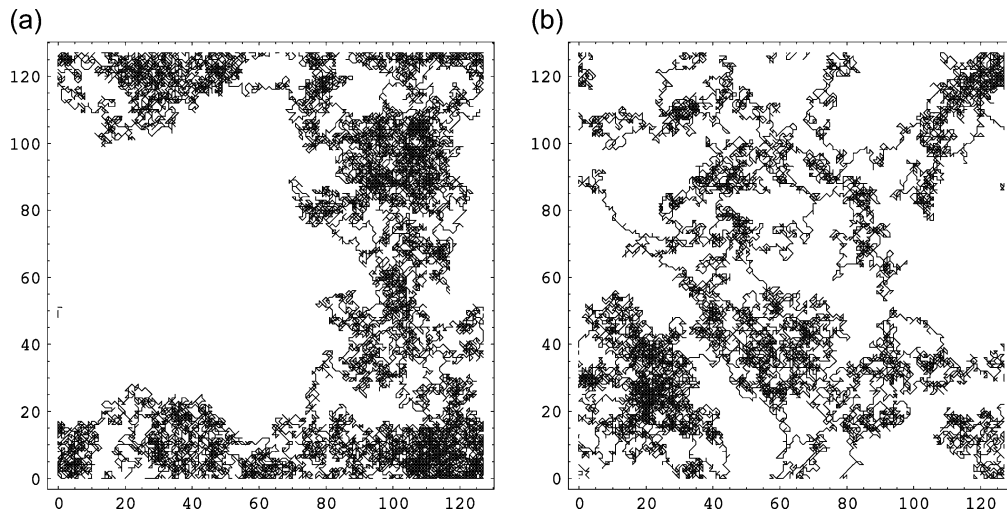


Figure 1
Two simulated burrows. (a) Length = 6445 cells, fractal dimension = 1.427 (regression: $Y = 1.427X$); (b) length = 6445 cells, fractal dimension = 1.491 (regression: $Y = 1.491X$). In each case, the burrow's origin is at (0,0).

similar animals walking aboveground (Vleck, 1979). This high energetic cost places a premium on making precise movement of choices. For these reasons, these animals have been the object of several studies investigating factors that control foraging path (i.e., burrow) geometry and, more specifically, burrow fractal dimension (Le Comber et al., 2002; Romañach and Le Comber, 2004). An additional advantage is that burrowing animals leave persistent records of their foraging patterns in the form of their burrows.

In this study, we ask whether burrows with high fractal dimension locate more food items than burrows with low fractal dimension and examine how using different criteria for assessing whether a burrow successfully locates food items affects the factors that determine foraging success. These criteria relate principally to the distance over which an animal can locate food when foraging blindly and whether an animal is able to exploit an entire patch of food or only that portion that its path intersects. The biological relevance of these rules is considered in the Discussion.

METHODS

Burrow simulation

Burrows were simulated as random walks on a 128×128 toroidal grid using Mathematica 5.0 (2003) (Wolfram Research Inc., Illinois, USA), with steps moving horizontally, vertically, or diagonally from the current cell (beginning at coordinate (0,0)) to one of the eight adjacent cells with equal probability. Burrow length was defined as the number of unique cells occupied by the burrow, and the random walk continued until the required number of cells was occupied.

Burrow fractal dimension

For each burrow, fractal dimension was estimated by calculating the capacity dimension or box-counting dimension, D_B (Block et al., 1990), using methods outlined in Le Comber et al. (2002) and Romañach and Le Comber (2004). This first step of this method involves taking successively smaller squares within the overall grid area, starting with a single square of dimension 128×128 cells, and successively halving the linear dimensions of the squares until reaching $128^2 = 16,384$ squares of dimension 1×1 cell; thus, the total number of squares

at each size increases as a power of 2, from 2^0 to 2^1 , 2^2 , 2^3 , ..., 2^7 . Next, the number of squares containing “live” cells (i.e., those squares containing at least one cell occupied by the burrow) is counted for each size of square in turn. For a straight line, the number of squares containing live cells increases by a factor of 2^1 as the linear dimension of the squares is successively halved, that is, it doubles. For a plane, the number of squares containing live cells increases by a factor of $2^2 = 4$. This can be represented by regressing $\log N(\epsilon)$ against $\log (1/\epsilon)$ (Equation 1), where ϵ is the length of the grid square expressed as a fraction of the largest square and $N(\epsilon)$ is the number of live squares of length ϵ , with the fitted line constrained to pass through the origin. For a perfectly linear structure, the slope of this line equals 1; for a perfectly planar structure, the slope equals 2. Thus, the slope of the fitted line corresponds to the line's fractal dimension; two sample burrows with the same burrow length but different fractal dimension are shown in Figure 1.

$$D_B = \lim(\epsilon \rightarrow 0) \log N(\epsilon) / \log(1/\epsilon). \quad (1)$$

In this study, variations in burrow depth were ignored, and the burrows were treated as planar structures; in many species, variation in depth is slight in comparison with total burrow length. For instance, in the naked mole-rat, *H. glaber*, total burrow length may reach 3 km, while depth ranges over just a few tens of centimeters (Bennett and Faulkes, 2000; Brett, 1986, 1991).

Food abundances and distributions

Food distributions were generated by sequentially placing food items in randomly selected cells within a 128×128 toroidal grid. Different levels of food patchiness were simulated by varying the probability, p , with which a food item was placed in a randomly selected cell adjacent to an existing food item. Thus, low values of p correspond to even distributions and high values of p to patchy distributions (Figure 2).

Foraging success

To estimate the foraging success of a burrow with a particular food distribution, the burrow and food distribution were superimposed and the number of food items located by the

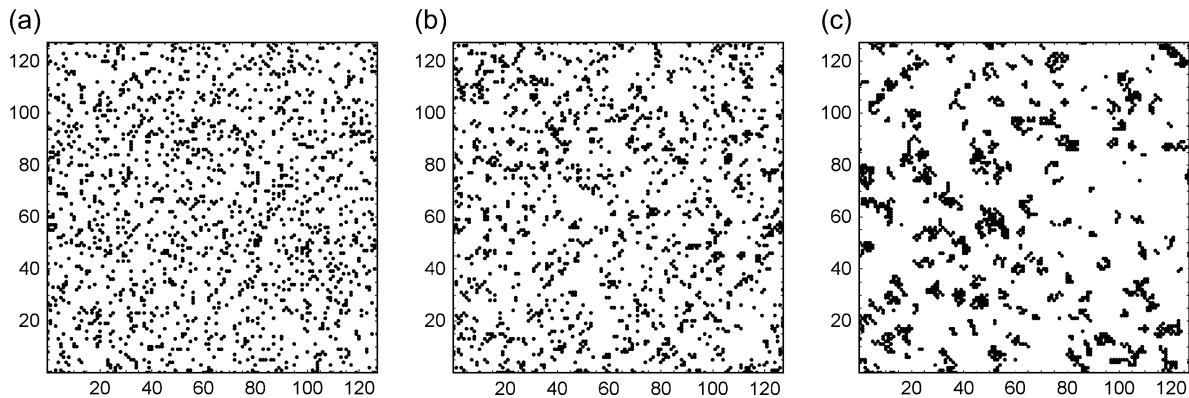


Figure 2

Three simulated food distributions. Each has a total food abundance of 1638 food items but with differing degrees of patchiness: (a) nonpatchy ($p = .1$); (b) intermediate ($p = .5$); and (c) patchy ($p = .9$). p is the probability with which a food item was placed in a randomly selected cell adjacent to an existing food item.

burrow was calculated using different combinations of three rules:

Rule 1: Intersection (I)—A burrow finds a food item if the burrow and food item occupy the same cell.

Rule 2: Proximity (P)—A burrow finds a food item if the burrow occupies a cell adjacent to the cell occupied by the food item.

Rule 3: Contiguity (C)—A burrow finds a food item if the food item is contiguous with another food item successfully located by the burrow (i.e., if the burrow locates one food item in a clump, it is deemed to have located the whole clump).

These rules were used alone and in combination to generate four different models:

Model I: Foraging success defined by Rule I (Intersection) only.

Model IP: Foraging success defined by Rule I (Intersection) and Rule P (Proximity) together.

Model IC: Foraging success defined by Rule I (Intersection) and Rule C (Contiguity) together.

Model IPC: Foraging success defined by Rule I (Intersection), Rule P (Proximity), and Rule C (Contiguity) together.

Simulation 1

In the first simulation, burrow length, food abundance, and food patchiness were all allowed to vary; because fractal dimension depends on the shape of the burrow, which varied with the precise form of the random walk, fractal dimension also varied.

For each of 1024 replicates, a single burrow and food distribution were simulated. Burrow lengths were selected randomly such that the mean burrow length (the number of unique cells visited in the random walk) was 1638 cells (10% of the total number of cells in the grid), with a standard deviation of 164 cells. Food abundances were selected randomly such that the mean number of unique cells occupied by food items was 1638 (10% of the total number of cells in the grid), with a standard deviation of 164 cells (Figure 2). Values of p (food patchiness) were chosen randomly from a distribution with a mean of 0.5 and a standard deviation of 0.1. The burrow's success at locating the food items making up that food distribution was calculated using each of Models I, IP, IC, and IPC. Data were analyzed using a fully factorial general linear model (GLM) with the following terms: (1) burrow length, (2) fractal dimension, (3) food abundance, and (4) food patchiness.

Simulation 2

In the second simulation, burrow length, food abundance, and food patchiness were all held constant; thus, only fractal dimension and foraging success varied. For each of 512 burrows, foraging success was calculated as above using a single unique food distribution for each burrow. Burrow length, food abundance, and food patchiness were set at 6554 unique cells, 6554 food items, and $p = .5$, respectively. Grid size was again 128×128 cells.

RESULTS

Simulation 1

The results of the GLM are shown in Table 1 and Figure 3. Fractal dimension had highly significant effects on foraging, with burrows with higher fractal dimension locating more food items than burrows with lower fractal dimension. The only exception was Model I, using the Intersection rule only, in which, as expected, foraging success was dictated entirely by burrow length because the shape of the burrow is by definition precluded from having any effects (because Rules P and C are not invoked, a burrow's ability to locate food items is dictated solely by the number of cells occupied at the highest resolution, i.e., by burrow length).

In all models, foraging success was strongly affected by both burrow length and food abundance, as expected. Thus, longer burrows located more food items than shorter burrows, and burrows located more food when food was more abundant. For models of foraging success using the Contiguity rule (Models IC and IPC), foraging success was higher when food items were more patchily distributed. Because the combinations of Rules I, P, and C are additive, it was always the case that, in terms of foraging success, $I \leq IP$, $I \leq IC$, $IP \leq IPC$, and $IC \leq IPC$. The relationship between IP and IC was strongly affected by the patchiness of the food distribution; where food items were more patchily distributed, $IC > IP$.

Simulation 2

When burrow length, food abundance, and food patchiness were held constant, foraging success was still strongly affected by burrow fractal dimension, again with the exception of Model I. Regressing foraging success on fractal dimension produced highly significant results for each of Models IP ($Y = -10668.5 + 9916.7X$; $r^2 = .808$, $p < .0001$), IC

Table 1
Results of a GLM examining model variables under four different combinations of three rules to define foraging success, (1) I; (2) IP; (3) IC; and (4) IPC

Model term	df	Model							
		I		IP		IC		IPC	
		F ratio	p	F ratio	p	F ratio	p	F ratio	p
Burrow length	1	1037	<.0001	1176	<.0001	968.4	<.0001	900.7	<.0001
Fractal dimension	1	0.2026	ns	496.0	<.0001	98.78	<.0001	850.8	<.0001
Food items	1	995.4	<.0001	1377	<.0001	1092	<.0001	1406	<.0001
Food patchiness	1	0.8709	ns	0.4240	ns	44.91	<.0001	100.6	<.0001
Burrow length–fractal dimension	1	1.182	ns	1.927	ns	0.1721	ns	2.511	ns
Burrow length–food items	1	4.677	.0308	9.929	.0017	5.893	.0154	10.26	.0014
Burrow length–food patchiness	1	0.000	ns	1.688e–2	ns	0.5642	ns	1.480e–3	ns
Food items–fractal dimension	1	0.8296	ns	5.932	.0150	2.702	ns	11.19	.0009
Food patchiness–fractal dimension	1	0.1723	ns	1.215	ns	3.357	ns	8.115	.0045
Food items–food patchiness	1	0.1052	ns	0.3288	ns	0.8865	ns	0.6843	ns
Burrow length–food items–fractal dimension	1	0.9754	ns	2.071	ns	2.439	ns	0.9023	ns
Burrow length–food patchiness–fractal dimension	1	0.9754	ns	5.086e–3	ns	8.492e–2	ns	3.021e–3	ns
Burrow length–food items–food patchiness	1	0.5650	ns	1.699e–2	ns	0.2245	ns	1.622	ns
Food items–food patchiness–fractal dimension	1	2.964	ns	0.8295	ns	1.666	ns	9.716e–2	ns
Burrow length–food items–food patchiness–fractal dimension	1	1.048	ns	1.255	ns	1.376	ns	0.7183	ns
Residual	1008								

R² values for I, IP, IC, and IPC are .9998, .7033, .9074, and .5142, respectively.

($Y = -6871.5 + 7124.5X$; $r^2 = .708$, $p < .0001$), and IPC ($Y = -596.3 + 4663.7X$; $r^2 = .269$, $p < .0001$) but not for Model I ($Y = 2773.7 - 100.8X$; $r^2 = -.001$, $p = ns$) (Figure 4).

DISCUSSION

Our results suggest that burrow fractal dimension is an important determinant of the success of a burrow in locating food items and that this is independent of burrow length. In both simulations, fractal dimension was an important determinant of the success with which burrows located food items.

This conclusion holds for a range of methods of defining foraging success, failing to apply only to Model I. The Intersection rule, I, is the simplest possible method of determining foraging success. When this rule is used alone, as in Model I, shape can play no role in determining foraging success, because the number of grid cells searched reduces to burrow length, whatever the shape of the burrow. Model I thus represents a control under which fractal dimension should not affect foraging success; the simulation results confirm this. The other rules represent extensions of this model that are likely to be more biologically realistic. The Proximity rule, P, may be thought, in biological terms, to relate to the distance over which the animal in question can locate food when foraging blindly. In a field study, Jarvis et al. (1998) showed that in the Damaraland mole-rat, *C. damarensis*, initial foraging is blind because tunnels often missed geophyte regions by less than a meter. In behavioral trials in captivity, functionally complete colonies of the Damaraland and common mole-rats (*Cryptomys hottentotus hottentotus*) appeared to forage indiscriminately and failed to show a differential response to differences in the profitability of different patches (Malherbe et al., 2003). Reichman and Jarvis (1989) found no evidence in either the common or Cape mole-rat (*Georchus capensis*) that animals foraged preferentially in areas containing more plant material. In contrast, Heth et al. (2002) showed using T-maze choice tests that captive naked mole-rats, *H. glaber*, preferred to dig in soil in which food plants had been grown, suggesting that chemosignals from

plants (kairomones) might attract burrowing mole-rats. However, it is not clear over what range such a factor might operate in the wild, and it has been suggested that the detection of such a signal might be restricted to periods when rain has washed the kairomones from the plants into the surrounding soil (Faulkes and Bennett, in press). Bennett and Faulkes (2000) suggest that naked mole-rats may be able to detect geophytes only at very short distances (<10 cm). Similarly, Andersen (1990) found that the pocket gopher *Geomys bursarius* burrowed within 10 cm of carrots without deviating from their course.

As well as the effects of fractal dimension on foraging success, our study demonstrates that the number of food items and burrow length also have significant effects on foraging success; that is, burrows find more food when there is more food present, and longer burrows find more food than shorter burrows. In addition, food patchiness influenced foraging success in models invoking the Contiguity rule, C. More interestingly, our study detected significant interactions between burrow length and number of food items (all models), between fractal dimension and number of food items (Models IP and IPC), and between fractal dimension and food patchiness (Model IPC). However, all but the last of these are likely to reflect the fact that increasing either the length of the burrow or the number of food items reduces sampling error; essentially, when burrows are short or food items rare, stochastic error will make the effects of these variables harder to detect. The interaction between fractal dimension and food patchiness in Model IPC is likely to be more meaningful, in that the more patchy the food distribution, the greater the benefits of locating a clump and, consequently, the greater the effect of increasing fractal dimension. Spinks and Plaganyi (1999) reached a similar conclusion, using an energetics model.

It should be noted that the methods described in this paper—in common with other studies—do not actually measure fractal dimension, rather they measure box-counting or capacity dimension, which provides a good estimate of fractal dimension (Block et al., 1990). In fact, the burrows' nonzero width means that they lack the self-similarity at different scales that is typical of fractal objects. As a result, burrow length and

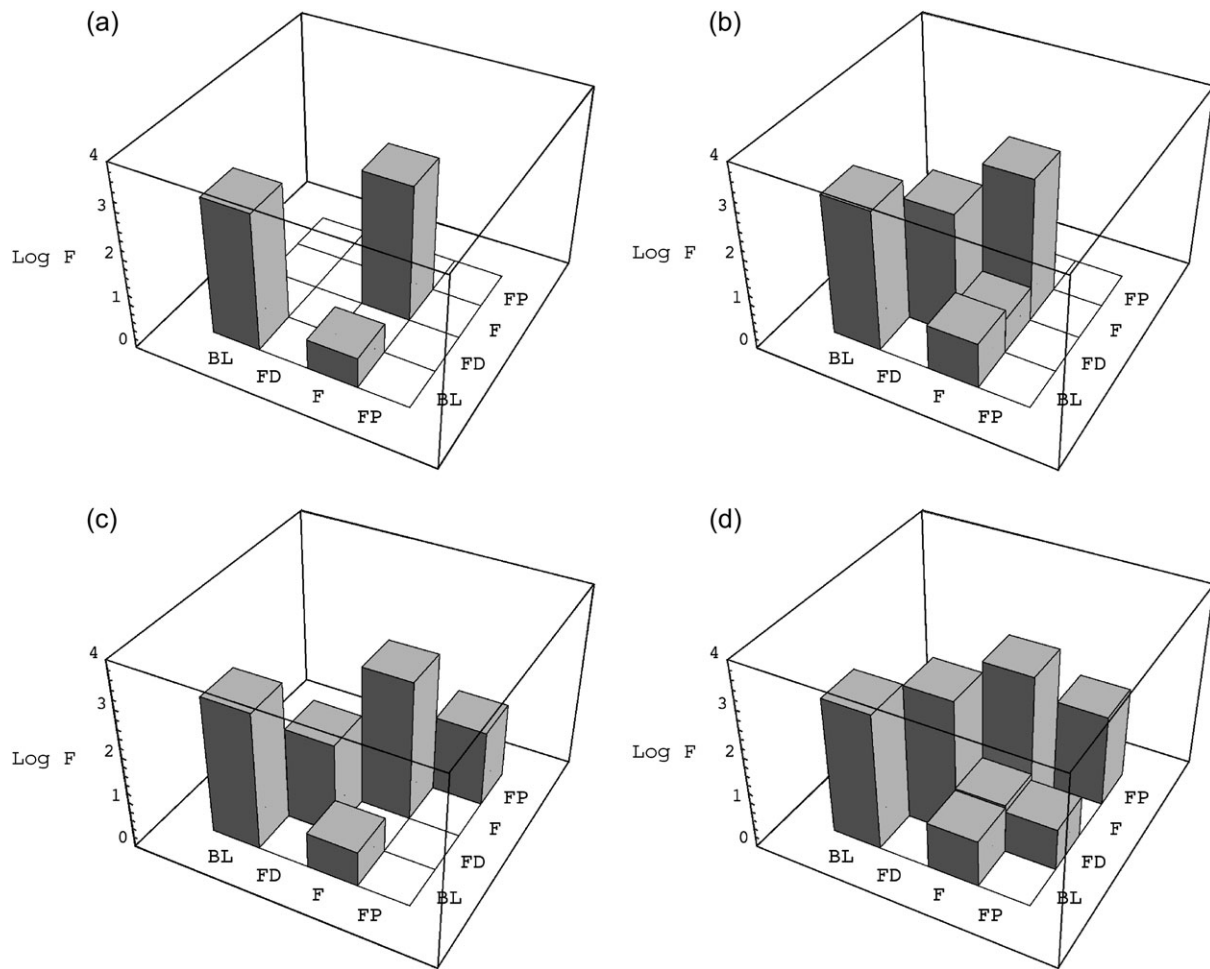


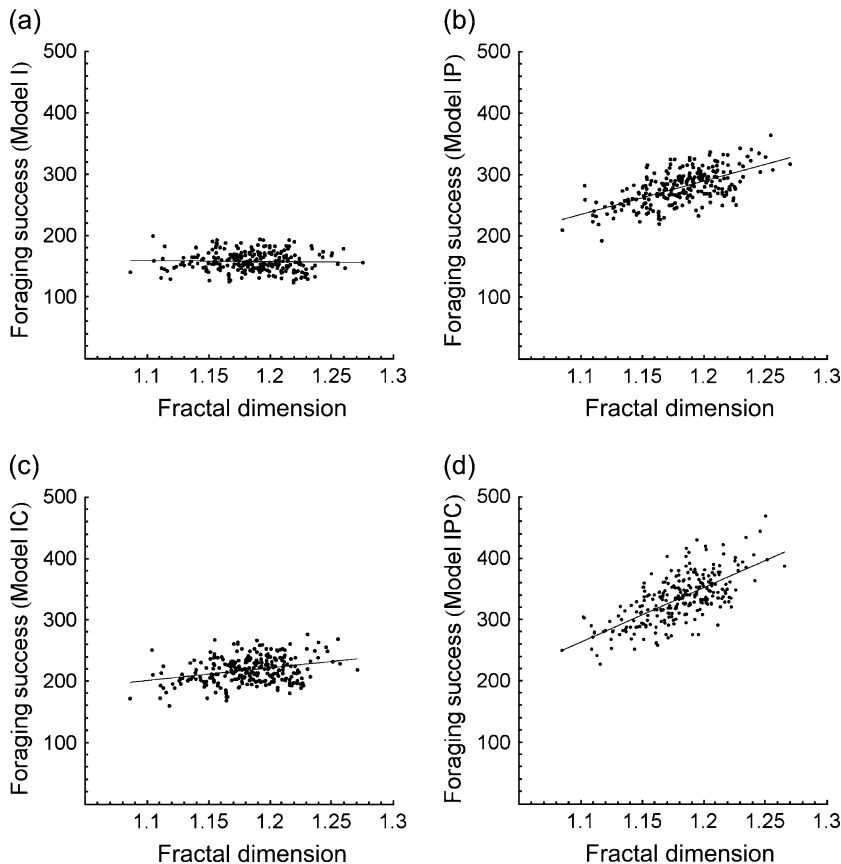
Figure 3 Half matrices showing \log_{10} of F statistics for (a) Model I; (b) Model IP; (c) Model IC; and (d) Model IPC. Diagonal elements show F statistics for single variables and off-diagonal elements those for each of the two-way interactions. Three- and four-way interactions are not represented; none of these reached significance. BL = burrow length, FD = fractal dimension, F = Food items, and FP = food patchiness.

fractal dimension are correlated in this analysis. Also, again because of the finite resolution of the method, fractal dimension reaches an asymptote at high burrow lengths. However, in both cases this is a methodological complication rather than a theoretical difficulty and does not affect our conclusions. In the first simulation, the GLM teases apart the effects of burrow length and fractal dimension; in the second simulation, burrow length was held constant, and the problem does not arise.

A potentially more serious difficulty is that the box-counting method used here to estimate fractal dimension has been criticized, principally because it converges very slowly and yields imprecise results (see for instance Normant and Tricot, 1991, 1993). However, it does provide a good first approximation of fractal dimension (Longley and Batty, 1989). It has been suggested that the method produces more reliable results when grid placements are randomly replicated to produce a range of values for D_B ; the limitations and modifications of this method (and others) are discussed in detail in Kenkel and Walker (1996) and in Taylor CC and Taylor SJ (1991). As a result of some of these methodological difficulties, the actual numerical values for a burrow's fractal dimension are likely to be incorrect, in that comparison of data from separate studies may be problematic, for example, because the estimation of D_B is sensitive to the range of grid sizes used (Pruess, 1995). Despite these difficulties, though, we believe that the method provides

a reliable method of quantifying burrow shape in such a way as to integrate the constituent parameters into a quantitative index that can be used to test ecological hypotheses in a statistically robust way, a point made by Despland (2003) in the context of vegetation clumping. As Despland (2003) points out, whether the index accurately represents the dimensionality of the structure in question is of little importance because it is the method's ability to capture differences between objects and to express statistically significant ecological relationships that is of interest.

The simulations described in this paper examine the effect of burrow architecture on foraging success. As noted in the Introduction, this is difficult to investigate using field data because foraging success can also influence burrow architecture. This approach thus precludes any rules defining foraging success that depend on feedback from foraging success to burrow architecture. The Contiguity rule, C, which states that a burrow finds a food item if the food item is contiguous with another food item successfully located by the burrow (i.e., if the burrow locates one food item in a clump, it locates the whole clump), appears to allow for feedback between movement and food distribution. However, this rule may be thought of as mimicking situations in which food items themselves are of varying size/value. In this view, clumps represent single, large food items rather than groups of homogenous items.

**Figure 4**

Foraging success as a function of burrow fractal dimension when burrow length, food abundance, and food patchiness are held constant, for Model I, Model IP, Model IC, and Model IPC. The relevant regression equations are Model I: $Y = 2773.7 - 100.8X$; $r^2 = -.001$, $p = \text{ns}$; Model IP: $Y = -10668.5 + 9916.7X$; $r^2 = .808$, $p < .0001$; Model IC: $Y = -6871.5 + 7124.5X$; $r^2 = .708$, $p < .0001$; Model IPC: $Y = -596.3 + 4663.7X$; $r^2 = .269$, $p < .0001$.

Evidence from African mole-rats suggests that species with larger group size have burrows with higher fractal dimension and that burrows in nonarid environments have higher fractal dimension than burrows in arid environments, in line with the predictions of the aridity-food distribution hypothesis (AFDH) (Le Comber et al., 2002). The AFDH suggests that the transition to social or eusocial behavior within the African mole-rats is driven by the need to forage cooperatively in arid environments, where food is scarce and patchily distributed, and hence the risk of unsuccessful foraging is high (Bennett, 1988; Faulkes et al., 1997; Jarvis and Bennett, 1990). The results of this study, which show that burrow fractal dimension has greater effects on foraging success when the patchiness of the food items is high, are consistent with the AFDH.

Although we show here that burrows with high fractal dimension are associated with increased foraging success, it is likely that other factors will limit burrow fractal dimension in practice because burrow shape may reflect a compromise between foraging efficiency and other constraints. For example, the energetic costs of tunnel construction may be minimized with the implementation of specific burrow geometries (e.g., optimal segment length [Vleck, 1981] or optimal turning angle [Andersen, 1988]), while social behaviors such as the maintenance of territories may lead to burrow geometries that are suboptimal in terms of foraging, although they may increase success of other components of fitness such as finding mates (Seabloom and Reichman, 2001). Le Comber et al. (2002) showed in African mole-rats that fractal dimension increased with level of sociality and that burrows in mesic environments had higher fractal dimension than burrows in more arid environments. This suggests that, where other factors allow (e.g., sufficient numbers of animals digging, soil hardness), animals will tend to maximize foraging success by in-

creasing burrow fractal dimension. However, the values of the fractal dimensions reported in this study accord well with those calculated from the field studies of African mole-rats (Le Comber et al., 2002) and the pocket gopher *Thomomys bottae* (Romañach and Le Comber, 2004).

The primary goal of this study is to examine the effects of geometry per se on foraging success, and this work is unique in this regard. However, as a result, we explicitly prevent feedback between animal movement and food distribution. It has been shown in modeling and empirical work that such feedback does exist and can increase foraging success. For example, a common strategy is area-restricted searching. Animals using this strategy increase foraging activity in areas in which they encounter high resource density or in which plant productivity is high (Andersen, 1996; Benedix, 1993; Hobbs and Atkins, 1988; Huntly and Inouye, 1988; Inouye et al., 1987; Peart, 1989; Reichman et al., 1982; Seabloom and Reichman, 2001; Steuter et al., 1995; Tilman, 1983; Vleck, 1981; Wasley, 1995). For instance, Brett (1991) demonstrated that naked mole-rats increased their rate of discovery by altering their burrowing behavior in response to particular food plants, while Jarvis and Sale (1971) noted increased branching in the presence of patches of small tubers (*Macrotyloma maranguense*) but not the larger and more randomly distributed *Pyrenacantha kaurabassana*.

Our results suggest that, when burrow shape affects foraging success (Models IP, IC, and IPC), burrows with high fractal dimension experience greater foraging success than burrows with low fractal dimension. Because the simulations described here preclude the effects of foraging success feeding back to affect burrow shape, the results described here support the earlier contentions of Le Comber et al. (2002) and Romañach and Le Comber (2004) that burrow fractal dimension

provides a useful single metric to describe burrow configuration, particularly when foraging is involved.

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