

# Measures of pocket gopher (*Thomomys bottae*) burrow geometry: correlates of fractal dimension

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(Accepted 30 September 2003)

## Abstract

For many burrowing species of mammals, the shape of the burrow may affect the success with which resources are acquired. Parameters used to characterize burrows have included: number of branches, mean segment length, turn angle, and linearity. However, the interactions among these parameters are unclear, making it desirable to find a single measure to characterize burrow geometry. For this reason, fractal dimension has been proposed as a measure of burrow geometry. However, the ways in which fractal dimension relates to other burrow metrics are not obvious. In this study, we examine correlations between fractal dimension and other measures of burrow geometry, using burrows of the pocket gopher *Thomomys bottae*. We also investigate whether burrows excavated by pocket gophers of different age, sex, and at two locations differing in food abundance have different fractal dimensions. We show that there are strong correlations between fractal dimension and other measures of burrow geometry, but that replacing fractal dimension with any single measure of burrow geometry discards important information about burrow structure. We conclude that fractal dimension offers a useful way of describing burrow geometry. No differences were found in burrow fractal dimension between pocket gophers of different ages or sex or in sites of different productivities, and we conclude that the factors that determine the pattern of burrowing in this species are invariant with respect to these parameters.

**Key words:** *Thomomys bottae*, age, burrow architecture, sex, vegetation abundance

## INTRODUCTION

Animal movement is often prompted by the search for resources, and the details of search paths can reflect differences in resource accessibility, for example in caribou (Johnson, Parker & Heard, 2001). Similarly, individuals differing in sex and age may have different goals or strategies directing their movements, as described for bats (Clark, Clark & Leslie, 2002). It follows that analysis of search paths can reveal important ecological information. For species that burrow, and thus incur high costs of movement (360–3400 times greater than walking; Vleck, 1979), burrow structure may be especially important, and can be analysed using many of the methods that are applied to animal movement generally (for a review of methods see Turchin, 1998).

Previous work has identified aspects of burrow parameters that influence an individual's ability to acquire resources. These include total burrow length, burrow system area, and turning angles (Reichman, Whitham

& Ruffner, 1982; Romañach, 2003). Although an examination of each of these parameters can be useful, it is desirable to find a single measure with which to describe burrow geometry, since the interactions between these parameters are unclear. The use of a single, easy-to-compute measure would also make obsolete the process of measuring each parameter of burrow geometry, which can be time-consuming. Fractal dimension (Mandelbrot, 1982) has many biological applications (Hastings & Sugihara, 1993), specifically as a measure of burrow architecture, for instance in termites (Puche & Su, 2001) and African mole-rats (Le Comber *et al.*, 2002).

The advantages of fractal dimension as a measure of burrow shape are twofold. First, it describes how a burrow explores the surrounding area in a way that is independent of length, and second it is easy to calculate. For planar objects, a good estimate of fractal dimension may be obtained by calculating the box-counting dimension, or capacity dimension (Block, von Bloh & Schnellhuber, 1990). This is essentially a measure of the extent to which a one-dimensional structure fills a plane, with low capacity dimension (approaching a value of 1) reflecting burrows that explore relatively little of the area surrounding the

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burrow, and high capacity dimension (approaching a value of 2) reflecting burrows that explore the surrounding area more thoroughly.

Despite its theoretical attractions as a measure of burrow configuration, particularly where foraging is involved (Le Comber *et al.*, 2002), there has been no work relating fractal dimension to other measures of burrow geometry. In this study, we investigate the use of fractal dimension as a comprehensive measure of burrow configuration by examining correlations between fractal dimension and other measures of burrow geometry in the pocket gopher *Thomomys bottae*. In addition, we analyse burrows from animals of different age and sex, and from two sites differing in vegetation abundance, and test whether these factors affect burrow fractal dimension.

Pocket gophers (Geomyidae) are herbivorous subterranean mammals that excavate extensive burrow systems, consisting of networks of feeding tunnels (Miller & Bond, 1960), as they move through the soil, consuming both above- and below-ground vegetation. Pocket gophers are solitary and aggressive and maintain distance between neighbouring burrows (Reichman *et al.*, 1982), giving up access to potential food items in the spaces between burrows (Seabloom & Reichman, 2001). The efficiency with which pocket gophers gain access to resources is determined to a large extent by the features of the burrow. Specifically, in low productivity areas, more extensive exploration might be required to locate resources: this seems to be true within the African mole-rats (Bathyergidae) (Le Comber *et al.*, 2002). The burrows of adult pocket gophers might explore the surrounding area more extensively than burrows of juveniles, perhaps as a consequence of the greater foraging experience of adults. Similarly, the fact that males must seek out female mates might be reflected in the extent to which their burrows explore the surrounding area (Bandoli, 1981).

The study described here addresses three questions, the first relating to the use of fractal dimension as a general measure of burrow geometry, and the second and third of which address species-specific questions. We ask: (1) How do measures of burrow structure correlate with fractal dimension? (2) Do age and sex affect burrow fractal dimension? (3) Do burrows at sites with low vegetation abundance have a higher fractal dimension than burrows at sites with high vegetation abundance?

## METHODS

### Burrow locations and measurement

Burrow maps for 44 burrows were taken from a previous study by Reichman *et al.* (1982), in which burrows were excavated by hand and then filled with white marking lime and photographed from the air. A subsequent ground survey was used to validate the photograph in areas where remnant vegetation might have obscured the lime. Accurate ink drawings were made from these aerial photographs. Burrows were from 2 sites in Arizona, USA; 1 site had approximately twice the standing crop biomass

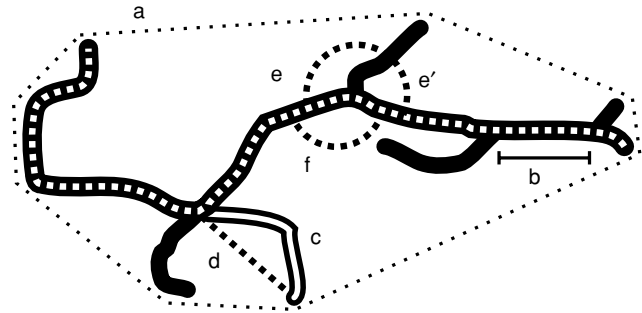


Fig. 1. Aerial view of burrow illustrating the different burrow parameters. See text for explanation.

of the other, but the 2 sites were otherwise similar, for instance annual precipitation (O. J. Reichman, pers. comm.). At the high biomass site, pocket gophers were trapped to determine sex and age (categorized as either adult or juvenile, based on pelage).

Measures of burrow geometry for each burrow were taken from Romañach (2003) (Fig. 1). A convex polygon (a in Fig. 1) was drawn around the entire burrow, and the burrow area calculated from this. Burrow shape was calculated as the unitless measurement  $4\pi \cdot \text{area} / \text{perimeter}^2$ ; using this scale, 0 represents a straight line and 1 represents a perfect circle. The longest continuous line drawn from one end-point of the burrow to another was designated the main tunnel from which branches stem; burrow segments (b in Fig. 1) were defined as the sections of the main tunnel between branches. Linearity (length (c in Fig. 1)/straight line distance (d in Fig. 1)) was calculated for each branch and segment. Branch angle was calculated as the angle at which branches joined the main tunnel; because it was not possible to tell from which direction the branch was excavated, the larger of the 2 angles was used (e and e' in Fig. 1). Turn angle (f in Fig. 1) was defined as the main tunnel's deviation from a straight line at each branch point.

### Fractal dimension

Burrow fractal dimension was estimated by calculating the box-counting or capacity dimension,  $D_B$  (Block *et al.*, 1990), using methods adapted from Le Comber *et al.* (2002). Burrow maps were photocopied to a standard size,  $h$  (256 mm along the longest axis) and redrawn to ensure constant line thickness. Taking  $h = 256$  mm, grids of  $h/2^0$ ,  $h/2^1$ ,  $h/2^2$ ,  $h/2^3$ ... $h/2^8$  (the practical limit of resolution) were superimposed on the burrow maps and the number of grid squares covering the burrow counted for each grid size in turn. Thus, the grid size was successively halved, from a maximum of 256 mm to a minimum of 1 mm. For a straight line, as the grid size is halved, the number of grid squares required to cover the burrow increases by a factor of  $2^1$ ; that is, it doubles. For a plane, the number of grid squares increases by a factor of  $2^2 = 4$ . This can be represented by regressing  $\log N(\epsilon)$  against  $-\log(1/\epsilon)$ , where  $\epsilon$  is the length of the grid square and  $N(\epsilon)$  is the number of squares of length  $\epsilon$

**Table 1.** Multiple regression correlations between fractal dimension and each metric of burrow geometry

Measure	Correlation	<i>P</i> -value
Total burrow length	Positive	<0.0001
Burrow system shape	Positive	<0.0001
Burrow system area	Positive	<0.0001
Number of segments	Positive trend	0.7775
Linearity	Negative trend	0.2938
Turn angle	Negative trend	0.5794
Number of branches	Negative trend	0.7883
Segment length	None	0.9270
Branch angle	None	0.9290

required to cover the image, 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. Variation in the depth of different parts of the burrows was ignored; this tends to be slight in comparison with burrow length.

### Statistics

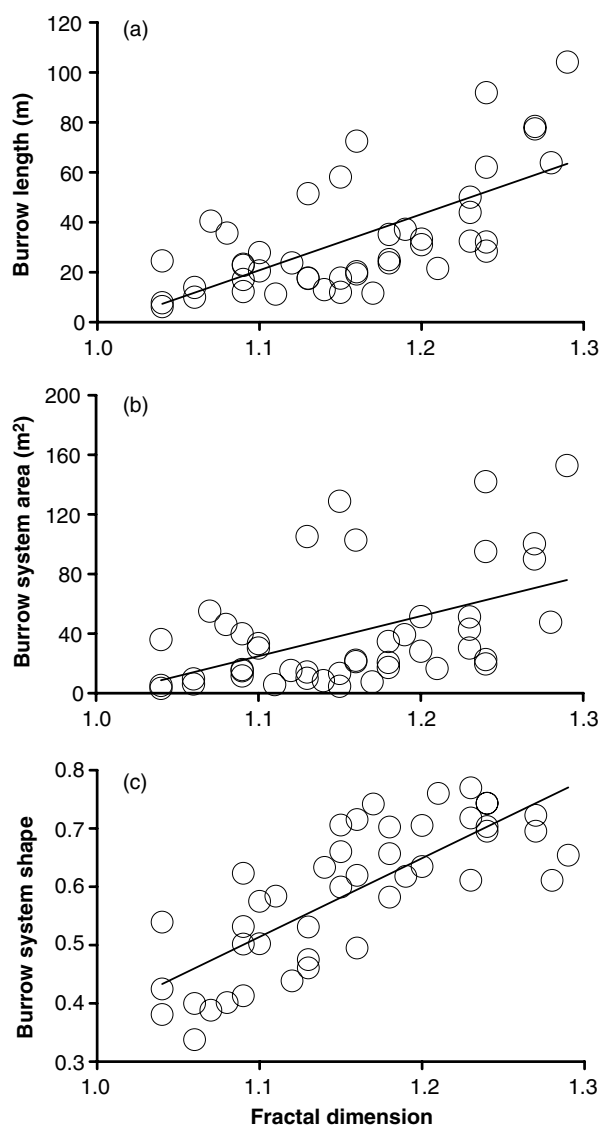
After testing data for normality using the Shapiro–Wilks test (Zar, 1996), we performed a stepwise regression (JMPIN, 2000) of fractal dimension and all burrow geometry metrics. Independent effects were determined using simple linear regressions between fractal dimension and each metric that had a significant effect in the multiple regression. Standard 1-way ANOVAs were used to examine the effects of age, sex, and site productivity on fractal dimension.

## RESULTS

### Fractal dimension and burrow geometry measurements

Mean fractal dimension for all burrows was 1.16 (SE = 0.01). Multiple regression showed a strong correlation between fractal dimension values and all measures of burrow geometry ( $r^2 = 0.92$ ;  $P < 0.0001$ ). We found significant relationships between fractal dimension and burrow length, area, and shape ( $P < 0.0001$  for each; Table 1). That is, the burrow systems with the highest fractal dimension were those that were longest, occupied the largest area, and were most circular. A regression including only the three significant terms (length, area, and shape) yielded similar results ( $r^2 = 0.917$ ) to the regression including all terms ( $r^2 = 0.924$ ). The relationships between fractal dimension and all other burrow geometry measures were non-significant.

Single linear regressions were performed between fractal dimension and burrow length, area, and shape to examine their independent effects (Fig. 2). As fractal dimension increased, total burrow length, area and shape (circularity) all increased (burrow length  $r^2 = 0.45$ ,



**Fig. 2.** Linear regressions showing the relationship between fractal dimension and (a) burrow length (burrow length (m) =  $224.47 \times \text{fractal dimension} - 226.10$ ); (b) area (burrow system area (m<sup>2</sup>) =  $269.20 \times \text{fractal dimension} - 27.29$ ); and (c) shape (burrow system shape =  $1.35 \times \text{fractal dimension} - 0.97$ ).

$P < 0.0001$ ; area  $r^2 = 0.24$ ,  $P < 0.01$ ; shape  $r^2 = 0.61$ ,  $P < 0.0001$ ) (Fig. 2a–c).

### Comparisons of fractal dimension between age, sex and sites

A one-way ANOVA showed no difference in fractal dimension between burrows of adults (1.14; SE = 0.08) and juveniles (1.16; SE = 0.08) ( $P = 0.54$ ) or between burrows of males (1.15; SE = 0.08) and females (1.16; SE = 0.07) ( $P = 0.84$ ), and no interaction between sex and age classes ( $P = 0.95$ ). There was no difference between the fractal dimension of burrows at the high productivity site (1.15; SE = 0.01) and the low productivity site (1.16; SE = 0.07) ( $P = 0.62$ ).

## DISCUSSION

Our results indicate that fractal dimension provides a useful, comprehensive measure of burrow geometry, incorporating information from a number of other measures of geometry. No other single measure that we examined is as effective at characterizing burrow geometry. In simple single linear regressions in which we found highly significant correlations between fractal dimension and each measure of burrow geometry,  $r^2$  values ranged from 0.24 to 0.61, indicating that each individual measurement leaves significant amounts of variance in fractal dimension unexplained. In contrast, we found a very high  $r^2$  between fractal dimension and all measures of burrow geometry ( $r^2 = 0.92$ ). This indicates that measuring only one aspect of burrow geometry ignores the effects of other measures, thus discarding important information about the geometry of the burrow. It is also interesting to note that, because the calculation of fractal dimension is independent of burrow length, the correlation between total burrow length and fractal dimension suggests that pocket gophers extend their burrows in such a way as to increase the thoroughness with which they explore the surrounding environment. That is, shorter burrows differ qualitatively (in terms of burrow architecture), as well as quantitatively (in terms of burrow length), from longer burrows.

We found no differences in fractal dimension of burrows between age, sex, or site, suggesting that all pocket gophers use similar burrowing strategies for the structure of their burrows. If fractal dimension is a true measure of how pocket gophers use space, we might expect that the high cost of burrowing would mean that an efficient burrow configuration was a necessity for all ages, sexes, and habitats. Previous work has found that there are energetically optimal geometry features such as turning angle (Andersen, 1988) and segment length (Vleck, 1981). Our results are consistent with the findings of Romañach (2003), who found no differences in burrow geometry among ages, sexes, and sites.

The lack of variation in fractal dimension among ages, sexes, and sites can be likened to life-history invariants across taxa. If fitness is optimized through natural selection, certain important life-history traits might converge around specific life-history solutions (Charnov, 1991). The same may be true for subterranean rodents that encounter very similar environmental conditions, regardless of location, taxon, sex, or resource abundance, resulting in an optimal burrow configuration.

The mean fractal dimension of pocket gopher burrows in this study is lower than the mean fractal dimensions reported for species of solitary, social, and eusocial mole-rats in arid and non-arid regions of sub-Saharan Africa, which ranged from 1.31 to 1.42 (Le Comber *et al.*, 2002). This might reflect a necessity for increased foraging effort in the mole-rats' habitat, which is characterized by very low plant biomass. Even at its most abundant, this does not exceed  $600 \text{ g m}^{-2}$ , and can be as low as  $98 \text{ g m}^{-2}$ ; this may be compared with the two sites described in this study, with plant biomasses of  $757 \text{ g m}^{-2}$  and  $1421 \text{ g m}^{-2}$  respectively (Reichman *et al.*, 1982; Bennett & Faulkes,

2000). Cooperative foraging in social and eusocial mole-rat species also increases burrow fractal dimension (Le Comber *et al.*, 2002), which will not be the case in pocket gophers.

Our results show that within this species there are no detectable differences in the fractal dimension of burrow structure that relate to age, sex, or differences in food availability. If these patterns are generally applicable to other species of subterranean rodents, it might be possible to predict burrow geometry patterns of many taxa across continents. More generally, our results show for the first time how fractal dimension relates to other measures that have been used to describe burrow geometry. We show that fractal dimension includes information relating to a number of features of burrow geometry, and that replacing fractal dimension with any other single measure discards important information about burrow geometry. We suggest that fractal dimension provides a convenient and informative measure of burrow structure and, when considered in combination with burrow system length, provides a comprehensive description of burrow architecture.

## Acknowledgements

Thanks to O. J. Reichman for allowing the use of his burrow data for geometry and fractal analyses. Financial support was provided to the first author through a University of California Eugene Cota-Robles Predoctoral Fellowship. The Mammal Research Institute at the University of Pretoria generously provided office space and computer support during data analysis. Thanks to O. J. Reichman, R. Warner, and S. Rothstein for helpful comments on earlier versions of this manuscript.

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