

COSTS AND BENEFITS OF POCKET GOPHER FORAGING: LINKING BEHAVIOR AND PHYSIOLOGY

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Abstract. Animals can attain fitness benefits by maintaining a positive net energy balance, including costs of movement during resource acquisition and the profits from foraging. Subterranean rodent burrowing provides an excellent system in which to examine the effects of movement costs on foraging behavior because it is energetically expensive to excavate burrows. We used an individual-based modeling approach to study pocket gopher foraging and its relationship to digging cost, food abundance, and food distribution. We used a unique combination of an individual-based foraging-behavior model and an energetic model to assess survival, body mass dynamics, and burrow configurations. Our model revealed that even the extreme cost of digging is not as costly as it appears when compared to metabolic costs. Concentrating digging in the area where food was found, or area-restricted search (ARS), was the most energetically efficient digging strategy compared to a random strategy. Field data show that natural burrow configurations were more closely approximated by the animals we modeled using ARS compared to random diggers. By using behavior and simple physiological principles in our model, we were able to observe realistic body mass dynamics and recreate natural movement patterns.

Key words: area-restricted search; burrow geometry; digging cost; energetics; Geomyidae; pocket gopher; simulation model; subterranean rodent; vegetation abundance; vegetation distribution.

INTRODUCTION

The balance of energetic costs and benefits affects the fitness of all animals. Therefore, it is advantageous for animals to employ behaviors that optimize this cost–benefit relationship. With regard to foraging behavior, animals can make choices that minimize time spent foraging, thus yielding a variety of benefits such as reduced predation risk and increased probability of survival (e.g., Newman and Caraco 1987, Brown et al. 1994). However, the final energetic balance reflects the outcome of not only behavioral choices (e.g., response to resources, competitors) but also energetic constraints (e.g., body mass effects on basal metabolic rates, movement costs). Thus, at a minimum for survival, animals must make choices that result in the maintenance of a positive net energy balance, including costs of movement and resource acquisition, and the profits from foraging. For example, animals can reduce energetic expense by moving in a manner that reduces effort (Reichman and Aitchison 1981), and they can increase their energetic intake by foraging in food-rich patches thereby maximizing the net energetic return for a given effort (Schoener 1971, Stephens 1986).

A rapidly developing body of literature suggests that laws underlying allometric scaling of animal metabolic rates (West et al. 1997, Porter et al. 2002) and energetic constraints on foraging should have a degree of generality. Concomitantly, there has been increased use of spatially explicit models to examine animal foraging behavior (e.g., Turchin 1988, Seabloom and Reichman 2001, Breckling et al. 2005, Reuter 2005). The realism of foraging models may be greatly increased by embedding these general allometric models within a spatially explicit framework (Nisbet et al. 2000).

The costs and rewards of various foraging strategies take place within the inherently spatial context of the behavioral choices animals make. The associated costs of movement are more than a simple sum of each step that an animal takes (Brown and Orians 1970). Energetic costs, for instance, are due in part to nonlinear physiological scaling laws as determined by body mass (see *Methods*, Eq. 1; Gordon 1972). Furthermore, movement costs for burrowing animals, for example, scale with body diameter, which also increases nonlinearly with body mass (see *Methods*, Eq. 3; Vleck 1979). Counterbalancing the increasing costs is the larger amount of habitat explored by a larger animal (e.g., the diameter of the burrow for burrowing animals; see *Methods*, Eq. 3) and thus the greater potential to encounter more resources.

Movement patterns of belowground animals provide an excellent system in which to examine the allometric relationships between metabolic costs, movement costs,

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and foraging gains because of the energetic expenses associated with excavating soil (360–3400 times more costly than walking aboveground; Vleck 1979). Digging costs increase dramatically not only with body size, but also with soil density (Vleck 1979). Concurrently, resource abundance and quality determine the energy available to compensate for the cost. To offset the high energetic expense of digging, animals can exploit resource patches of high density or high quality. Animals can make behavioral choices that increase their effectiveness at locating resources that are distributed in potentially complex spatial patterns. Thus, a true understanding of costs and benefits requires a balanced treatment of basic physiology linked with spatially explicit foraging behavior.

In this study, we link the fields of allometric metabolic scaling with spatial models of animal behavior to understand the energetic constraints faced by a widespread suite of animals: subterranean herbivores. Specifically, we embed a general, individual-based energetic model within a spatially explicit foraging-behavior model to explore the importance of metabolic costs and movement costs in determining the fitness of pocket gophers.

Pocket gophers are belowground herbivores that spend virtually their entire lives in extensive burrows. They burrow intensively for a few months of every year (Miller 1948, Miller and Bond 1960, Bandoli 1981) and consequently incur high movement costs. Furthermore, pocket gophers cannot detect food items through the soil (Benedix 1993), and as a result they cannot locate resource-rich patches from a distance. However, they employ area-restricted searching (ARS) by concentrating foraging effort in food-rich patches once they are encountered (Benedix 1993). This suggests that costs of excavation and resource abundance and distribution should interact in a manner that affects the energetic balance for subterranean herbivores.

Subterranean rodents excavate burrows that serve as persistent records of the movement paths of individuals, allowing some model predictions to be compared to empirical observations. Romañach et al. (2005) compared the burrows constructed by three species of pocket gophers (*Geomys attwateri*, *Geomys bursarius*, and *Thomomys bottae*) in North America (see Plate 1). These pocket gophers differ almost twofold in body mass and occur in sites that differ in digging costs (i.e., soil composition) and resource availability. They found that burrow length decreased as both resource productivity and digging costs increased, which suggests that pocket gophers are responding to either resource abundance or digging costs. However, in their observational study, sites with high resource productivity had high digging costs, and thus the correlational nature of the data left the exact constraint unresolved.

Motivated by these findings, we developed a model to gain an understanding of the relative importance of metabolic and movement costs and foraging benefits as

they scale with body size. We used an individual-based modeling approach to isolate the relative importance of resource supply and movement costs across gradients of resource abundance and distribution and foraging costs. To do this, we created an energetic model that includes body-mass-specific average daily metabolic rate (ADMR), excavation cost, and energetic gains from resources. We linked this physiological model to an existing model of pocket gopher behavior (Seabloom and Reichman 2001). This distinctive modeling approach links physiological modeling with complex, spatially explicit behavior, a linkage rarely tackled in ecology (but see Reuter 2005).

To elucidate the relative importance of resource gains and foraging costs, we considered three important outcomes related to fitness: survival, body mass dynamics, and burrow geometry. The model gives the survivorship of individual pocket gophers in multiple combinations of environmental conditions (e.g., vegetation abundance, vegetation distribution, soil type). As pocket gophers make burrowing choices, their body masses fluctuate as a result of physiologically incorporating the costs of digging in a given soil type and the gains from food resources. The outcome of burrowing behavior is manifested through geometric features of the burrow (e.g., total burrow length, number of branches). Thus, we analyzed the geometry of pocket gopher burrows to determine how individuals adjust the size and shape of burrows in response to environmental variables. We compare the burrow geometry results from the model to natural burrow geometry data (Romañach et al. 2005).

Specifically, model simulations are designed to determine effects of initial animal body mass (75–400 g), vegetation distribution (patchy, random, uniform), vegetation abundance (75–1500 g/m²), soil type (fine sand, gravely sand, sandy loam, clay), and digging strategy (ARS vs. random) on pocket gopher (1) survival, (2) physical condition as measured by final body mass, and (3) energetic effectiveness as measured by burrow geometry.

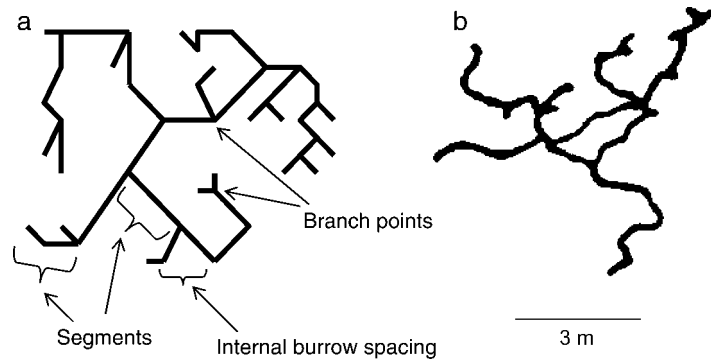
METHODS

The simulation model consists of a pocket gopher behavior model and an energetic model. The behavioral model is adapted from Seabloom and Reichman (2001), and we incorporate a physiological component to monitor energetic status throughout model simulations. The energetic model has four main components: metabolic cost, digging cost, energetic gain from foraging, and body mass change. We describe each in detail as follows.

Behavioral model

Four identical simulated pocket gophers were randomly positioned in a 20 × 20 m space (200 10 × 10 cm cells) to simulate natural densities (Miller and Bond 1960, Reichman et al. 1982, Stromberg and Griffin 1996)

FIG. 1. Aerial view of burrow systems and metrics from (a) an example of an area-restricted searching model output in comparison to (b) a natural burrow (adapted from Reichman et al. [1982]).



and produce realistic intraspecific interactions. Only one pocket gopher occupied each burrow (Miller and Bond 1960, Reichman et al. 1982). Pocket gophers maintained a buffer distance of 1.2 m between adjacent burrows (Reichman et al. 1982, Seabloom and Reichman 2001) and internal burrow spacing of 0.3 m (Fig. 1; Reichman et al. 1982). As the model space begins to fill with burrows, burrows of the four neighbors may approach this buffer distance. When the buffer space is encroached, pocket gophers begin to use newly excavated soil to fill the oldest sections of their burrows (termed “backfilling”), and in this process, they make more space available, and then excavate new sections of burrow that comply with the spacing rules.

Pocket gophers produce a median value of 110 mounds·gopher⁻¹·year⁻¹ (Miller 1948, Bandoli 1981), thus we allowed pocket gophers to dig for 100 24-h time steps (Seabloom and Reichman 2001), with each time step resulting in the production of one segment of burrow and one mound. During each time step, pocket gophers dug until they (1) violated the aforementioned within- or between-burrow spacing rules, (2) died as a result of not having a positive net energy balance, or (3) dug a maximum distance of five meters (the maximum length of one continuous burrow segment; Wasley 1995). Energetic costs increase dramatically with increasing segment length due to the increased distance the animals must move soil between tunnels to reach the soil surface (Vleck 1981).

The total distance excavated by each individual is the sum of the distances it excavated during the 100 time steps. At the end of each time step, the point location where a pocket gopher stops digging is called a node. Changes in burrowing direction can occur only at a node. The choices of which node and direction to select for burrowing depend upon which of the two foraging strategies, ARS or random, an individual is using.

The model is composed of a series of three consecutive events within each time step: these are to select (1) an individual pocket gopher, (2) a node, and (3) a direction. First, one of the four individuals is randomly selected to begin burrowing. Second, a node is selected at which to begin digging. Third, a direction is selected in which to begin digging. We generated two foraging strategies,

ARS and random, by altering the node and direction selection criteria. Field data suggest that the ARS strategy is the most realistic behavior (Benedix 1993), and the random strategy serves as a null model against which we compare the benefits of ARS. The ARS strategy is such that pocket gophers will begin digging at the node where food was most recently encountered, while the random strategy begins at a randomly selected node. Pocket gophers using ARS can burrow in any direction, but attempt to dig tunnels at angles as close to the least energetically costly angle (45°; Andersen 1988) as possible without violating the internal or between-burrow spacing rules. Individuals using the random strategy dig in a random direction. Animals are not required to make a directional change at successive time steps; they can continue in a forward path if selection dictates. When animals use ARS, additional nodes are set at locations of food items as potential sites to begin digging. Although animals using ARS have more nodes and thus more potential digging sites compared to animals using the random strategy, animals using both strategies are given the same number of opportunities to dig (100 steps), and therefore neither burrow length nor geometry are reflections of the number of nodes. The model runs through this series of three events until all four individuals have burrowed during each of the 100 time steps. For a more detailed treatment of the behavior model see Seabloom and Reichman (2001).

Energetics model

Net energetic status (kJ) is determined continuously throughout each time step (at the spatial resolution of the model, after every 10 cm). Energetic gains from foraging and losses from digging are summed across all of the digging within one time step (i.e., one 24-h day) and then compared to the daily 24-h average daily metabolic rate (ADMR; Eq. 1). We consider digging cost on top of ADMR (which includes activity) because the cost of digging is up to three orders of magnitude greater than walking (Vleck 1981).

We chose a range of initial body masses (Table 1) based on mean adult masses for the smallest and largest sized species of North American pocket gophers (Geomyidae; Nowak 1991).

TABLE 1. Values of each factor used in model simulations.

Factor	Levels	Values
Initial body mass (g)	8	75, 100, 150, 200, 250, 300, 350, 400
Vegetation distribution	3	patchy, random, uniform
Vegetation abundance (g/m ²)	8	75, 150, 200, 300, 500, 750, 1000, 1500
Soil type	4	fine sand, gravelly sand, sandy loam, clay
Digging strategy	2	area-restricted searching (ARS), random

ADMR is calculated based on its body mass and dictates energetic expenditure with results approximating field metabolic rates (Degen et al. 1998):

$$\text{ADMR} = 8.55M_{\text{body}}^{0.52} \quad (1)$$

where M is the body mass of the animal (g). Thus, in our simulations, metabolic rate ranged from 80.7 to 192.8 kJ/day for 75 and 400 g animals, respectively.

The cost of digging presented by Vleck (1981) in Eq. 2 is a function of the cost to shear soil and the cost to push the loose soil, both of which vary with soil type (e.g., soil density), burrow length, and burrow diameter. Specifically,

$$E = K_s(\pi r^2 \rho)(S) + K_p(\pi r^2 \rho)(S)(S/2) \quad (2)$$

where E is the energy to dig (kJ), K_s is the energy to shear soil (kJ/g), r is the burrow radius (cm), ρ is soil density (g/cm³), S is the distance over which soil is pushed (cm), and K_p is the energy to push soil (kJ·g⁻¹·cm⁻¹).

Vleck (1979) provides the values (soil density, shearing, and pushing costs) necessary to calculate digging cost. Pocket gophers in our model dug in fine sand, gravelly sand, sandy loam, and clay, in order of lowest to highest energetic expense. The cost of digging in the four soil types ranged over an order of magnitude for a given body size.

We do not include the cost of thermoregulation in our model because burrows are of fairly uniform temperature, resulting in a thermally low-demanding environment (Gettinger 1984a).

Net energy gain is calculated from the caloric value of vegetation and the amount of food eaten. To make a heterogeneous environment, each model space (20 × 20 m) contained 75% vegetation and 25% bare soil. Initial vegetation distributions were patchy, random, or uniform (the same distributions and scale as in Seabloom and Reichman 2001). We used a range of dry vegetation biomass values from six sites where pocket gophers occurred (Reichman et al. 1982, Cameron et al. 1988, Wasley 1995, Seabloom et al. 2003, Romañach et al. 2005; Table 1). Cells (10 × 10 cm) with bare ground provided no energy while those with vegetation provided 17.27 kJ/g (Andersen and MacMahon 1981). We set digestive efficiency at 60% (Gettinger 1984a, Smith 1995), such that animals gained only 60% of the kilojoules from each gram of vegetation. All patches of vegetation were equivalent in the amount of

calories they provided. While plant tissues of different species may vary in nutrient and energy content, and pocket gophers show preferences for certain plant species, energy content varied only with plant abundance in this model. As animals consumed plant material, depleted cells were not renewed within the time span of a simulation. Consequently, if individuals burrow through a cell that had previously been excavated, they did not gain calories from that cell. This represents a situation in a seasonal habitat in which simulations start at peak biomass and run through one year as the annual vegetation senesces through the dry season.

As pocket gophers forage in nature they harvest a (vertical) portion of plant roots that are intersected by their burrow, often leaving some root material below the burrow floor and root material above the burrow ceiling. Occasionally, individuals will pull plant material from above the ceiling down into their burrow and consume it. We do not have data on the portion of an individual plant that is consumed by a pocket gopher. Pocket gophers typically burrow at depths of a few to 50 cm below the soil surface (Reichman et al. 1982). Therefore, we assume that, on average, they take all root material from each plant up to the soil surface. Based on the dry mass of above- and belowground-vegetation biomass data (Seabloom et al. 2003) and the belowground distribution of root biomass (Schenk and Jackson 2002), we assume that pocket gophers consume and can gain calories from 46% each plant they encounter (Gettinger 1984a). Similarly, a subterranean species of mole-rat, *Cryptomys damarensis*, has been estimated to consume 48% of each tuber it encounters (Jarvis et al. 1998).

The amount of food a pocket gopher encounters is based on the total mass of plant roots that intersect its burrow, which is a function of the cell length multiplied by the width (i.e., diameter) of the burrow. Burrow diameter is a function of body mass; as body mass increases, burrow diameter increases (nonlinearly) according to

$$r = (0.912)Z^{0.267} \quad (3)$$

where r is the burrow radius in centimeters and Z is the body mass in grams. Thus, the amount of food harvested for a given burrow cell length increases with body mass.

We started model animals at their lean body mass. As animals burrow, they gain and lose body mass according

to the net energetic outcome. If an animal incurs a net energy loss while above lean body mass, it metabolizes fat based on the extent of the loss, but if it is at or below lean body mass, it metabolizes muscle to produce energy (calculations are based on energy available from metabolizing fat and muscle; Gordon 1972). If a net gain results while at or above lean body mass, the animal gains body mass as fat, or if below lean body mass it gains body mass as muscle. Model animals gain fat proportionally to their body mass (Calder 1984):

$$M_{\text{fat}} = 0.075M_{\text{body}}^{1.19} \quad (4)$$

where M_{body} is the body mass of the animal and M_{fat} is the mass of fat that can be stored.

Although energetic gains and losses are calculated every 10 cm, animals are buffered by their fat and protein reserves. Short-term energy deficits result in mass losses, but mortality does not occur unless prolonged energetic deficits lead an animal to lose a significant portion of its body mass. Pocket gophers in our model could lose up to 40% of their lean body mass before they died; pocket gophers in the field have been shown to lose 35.5% of their body mass without dying (Howard and Childs 1959).

Model simulations

We ran simulations of 1536 factorial combinations of eight initial body masses, three vegetation distributions, eight vegetation abundances, four soil types, and two foraging strategies (Table 1). Simulations started with a fixed distribution of vegetation which was gradually depleted through repeated foraging episodes. Each simulation was replicated 10 times for a total of 15360 independent simulations in which combinations of vegetation and animal characteristic were determined randomly before the start of each simulation.

For each model simulation, we determined pocket gopher survival, final body masses of the survivors, and four burrow geometry metrics: total length excavated, total burrow length (after backfilling), segment length, and number of branch points (for a detailed explanation of burrow geometry measurements see Romañach and Le Comber 2004 and Romañach et al. 2005). Branch points are node locations where the burrow splits in three (or more) directions (Fig. 1). Segment length is the distance between branch points or between a branch point and a terminal node (Fig. 1).

Statistics

The high level of replication in our model yielded large sample sizes, which led to high statistical significance for most factors, although they accounted for biologically insignificant amounts of the observed variability. Thus, we used partial r^2 values (SAS 1989) to examine the unique proportion of variance explained by each main effect (e.g., initial body mass, soil type) and their first-order interactions on survival, final body mass, and burrow geometry after accounting for all

other interactions. In most of our analyses, we necessarily examined a subset of the data (e.g., final body mass can only be examined in simulations in which at least one animal survives). For this reason, the analyses often have uneven replication across treatment combinations and the partial r^2 values will not sum to the total model r^2 , as would be the case with fully balanced data. For this reason, partial r^2 values are best interpreted as relative measures of the unique contribution of each factor to the model, while the total model r^2 is the best measure of the summed explanatory power of the regression model. We also examined trends in the model responses over each level of the main effects; for example, we examined the trends in animals' survival over a range of vegetation abundances.

RESULTS

Our model revealed that metabolic costs outweigh digging costs, even in the most costly soil types (Fig. 2).

Factors affecting survival

Survival at the end of the 100 time steps was most dependent on vegetation abundance, digging strategy, and the interaction between vegetation abundance and digging strategy (Table 2). Survival increased as vegetation abundance increased (Fig. 3). In the lowest class of vegetation abundance (75 g/m^2) only 0.01 of the smallest animals (75 g) using a random digging strategy survived. Across all body masses, survival was only 0.03 in 150 g/m^2 vegetation and increased to 0.82 in the highest vegetation abundance (1500 g/m^2). Soil type was the other main effect to influence survival, though not as strongly as its interactions with digging strategy and vegetation abundance (Table 2). We found that survival decreased as clay content in the soils increased. In both gravelly sand and fine sand 0.56 of animals survived, 0.47 in sandy loam, and 0.29 in clay soils. Low survival in clay soils was pronounced in low vegetation, particularly when animals were digging randomly.

Pocket gophers using ARS had a mean survival (across all other variables) of 0.61, compared to 0.33 for individuals using the random strategy.

Factors affecting final body mass

We present data for means of simulations only when all individuals survived so that final body masses were not averaged across masses of individuals that died. As expected, initial body mass explained the greatest amount of variation in final body mass. After accounting for initial body mass, we found that vegetation abundance, soil type, and the interaction between these two factors explained variation in final body mass (Table 2).

Animals using ARS reached larger mean final body masses compared to animals digging randomly (Fig. 4). Animals using ARS were able to increase body mass from their lean mass in all vegetation abundances, while animals digging randomly were able to increase body

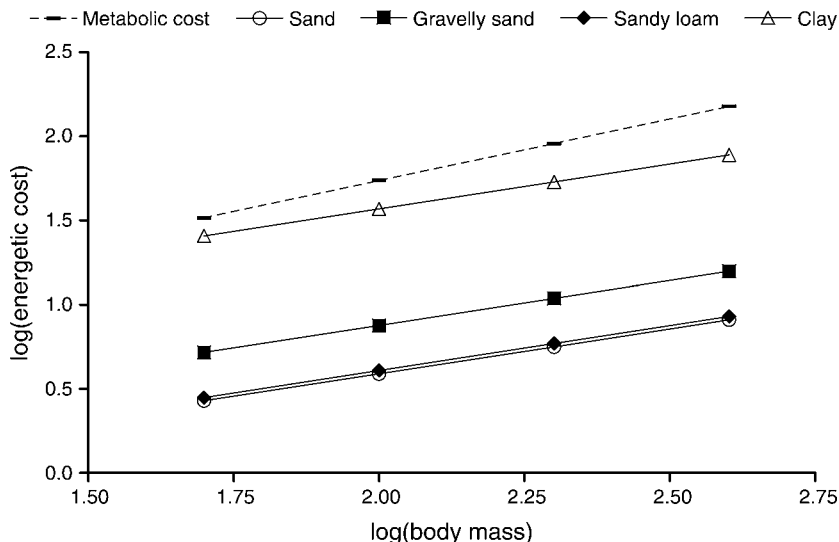


FIG. 2. Log-transformed average daily metabolic costs and digging costs for one day, using the example of 1.5 m dug in one day by a model pocket gopher using area-restricted searching in 500 g/m² vegetation abundance, in relation to log-transformed body mass. Energy expense is shown in terms of both daily metabolic costs and digging costs in four soil types for a model animal using area-restricted searching in 500 g/m² vegetation abundance.

mass only in and above 150 g/m² (Fig. 4). When digging randomly, animals starting at 75 and 100 g were not consistently able to gain body mass in any level of vegetation abundance, though 150–400 g animals were able to maintain lean body mass or gain mass in the three highest levels of vegetation abundance (750–1500 g/m²).

Factors affecting burrowing

The greatest amount of variation in total distance excavated was explained by digging strategy (Table 2). Animals using ARS excavated a shorter distance

compared to those using a random strategy (Fig. 5a). Model animals using ARS showed decreasing burrow length with increasing vegetation abundance (Fig. 5b). Burrows of model animals digging randomly showed the opposite trend, that of increasing burrow length with increasing vegetation abundance.

The greatest amount of variation in burrow length, segment length, and number of branches was explained by digging strategy (Table 2). The interaction between digging strategy and both vegetation abundance and soil type affected burrow length and segment length. The only other main effect to have an effect on burrow

TABLE 2. General linear model results showing the fit (*r*²) of the statistical model used to analyze the five main effects and their first-order interactions on survival, final body mass, and the four burrow geometry metrics.

Source of variance	Survival	Final body mass†	Total excavated	Burrow length	Segment length	No. branches
Statistical model	0.86	0.23	0.97	0.96	0.96	0.98
Initial body mass	0.00	0.00	0.00	0.00	0.00	0.00
Vegetation distribution	0.00	0.00	0.00	0.00	0.00	0.00
Vegetation abundance	0.07	0.01	0.00	0.00	0.00	0.00
Soil type	0.01	0.01	0.00	0.01	0.00	0.00
Digging strategy	0.05	0.00	0.04	0.02	0.03	0.08
Initial mass × vegetation distribution	0.00	0.00	0.00	0.00	0.00	0.00
Initial mass × vegetation abundance	0.01	0.00	0.00	0.00	0.00	0.00
Initial mass × soil type	0.00	0.00	0.00	0.00	0.00	0.00
Initial mass × digging strategy	0.01	0.00	0.00	0.00	0.00	0.00
Vegetation distribution × vegetation abundance	0.00	0.00	0.00	0.00	0.00	0.00
Vegetation distribution × soil type	0.00	0.00	0.00	0.00	0.00	0.00
Vegetation distribution × digging strategy	0.00	0.00	0.00	0.00	0.00	0.00
Vegetation abundance × soil type	0.02	0.01	0.00	0.00	0.00	0.00
Vegetation abundance × digging strategy	0.06	0.00	0.01	0.02	0.01	0.01
Soil type × digging strategy	0.03	0.00	0.01	0.02	0.01	0.00

Notes: Partial *r*² is given for the five main effects and their interactions to yield the proportion of variation that each explains. Results presented for final body mass are after accounting for initial body mass. Partial *r*² values show the relative importance of each factor.

† Final body mass was considered only for surviving individuals.

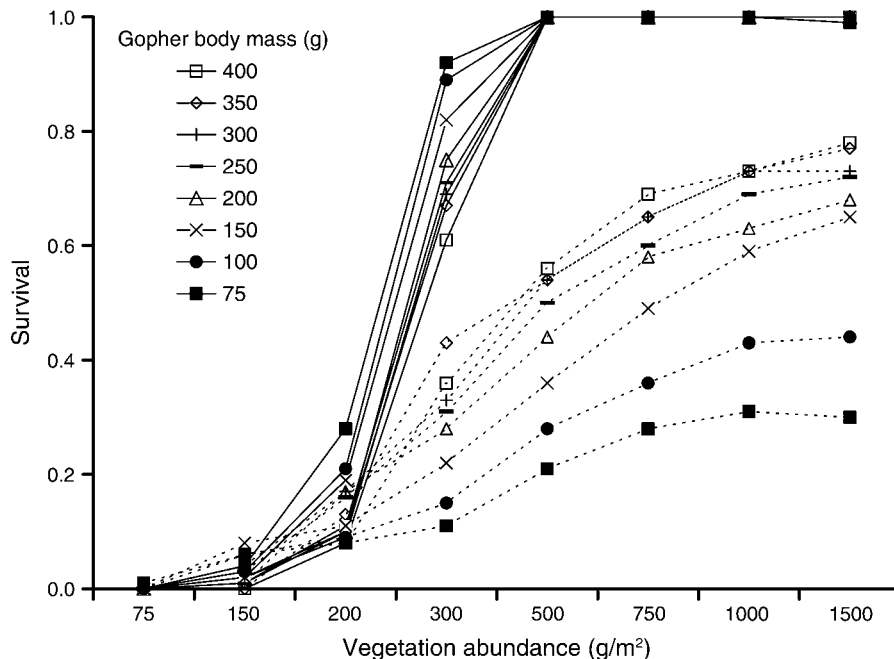


FIG. 3. Mean survival of all individuals using area-restricted searching (ARS) and random digging, in relation to vegetation abundance. ARS is represented by solid lines, and random by dotted lines. Each data point represents the mean survival for all pocket gophers in the initial size class.

geometry was soil type on burrow length. Soil type influenced burrow length only for animals digging randomly such that they were not able to produce large burrows in the most energetically costly soil types (Fig. 6).

DISCUSSION

While survival is a critical component of fitness, it is also a clear advantage to reach optimal body condition efficiently so that time and energy remain available for other life functions, such as reproduction. Time efficient animals may also be less subject to predation. Our model showed that animals using area-restricted searching (ARS) had the greatest survival and reached the largest body masses most efficiently. Cost of digging was a factor in determining final body mass only in situations where vegetation abundance was low and animals were struggling for survival. Food abundance accounts for 2.7 times the variability in survival than soil type. Our model revealed that even the seemingly extreme expense of digging is not so costly even compared to average daily metabolic rate (ADMR), which approximates field metabolic rates.

Animals using ARS appeared to have more energetically efficient burrow configurations compared to those digging randomly. Pocket gophers using ARS dug shorter burrows and reached higher body masses compared to those using the random strategy. This means that animals using ARS can store more energy, which can be used for survival in adverse conditions or for reproduction. Animals using ARS are effective

foragers because they increase foraging activity in areas where plant productivity is high (e.g., Benedix 1993), therefore, yielding more resource per meter dug. Thus, animals using ARS do not have to dig as much as animals digging randomly, as we found in our model. ARS is also known to be particularly efficient where vegetation has a patchy distribution (Jarvis 1978); however, vegetation distribution did not influence the relative success of the two strategies in our model (Table 2).

Seabloom and Reichman (2001) did not impose a limit on food intake, and therefore animals could not

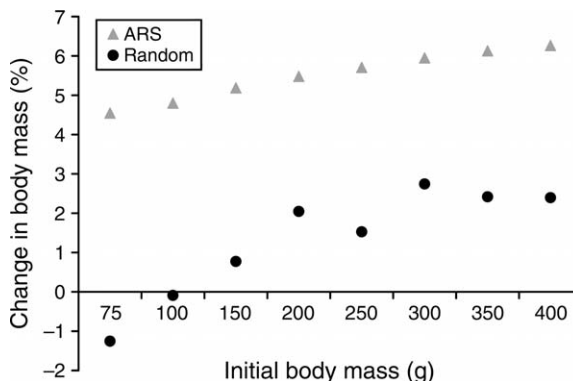


FIG. 4. Percentage change from initial to final body mass for individuals using area-restricted searching (ARS) compared to random digging. Each data point represents the mean change in body mass for all pocket gophers in the initial size class.

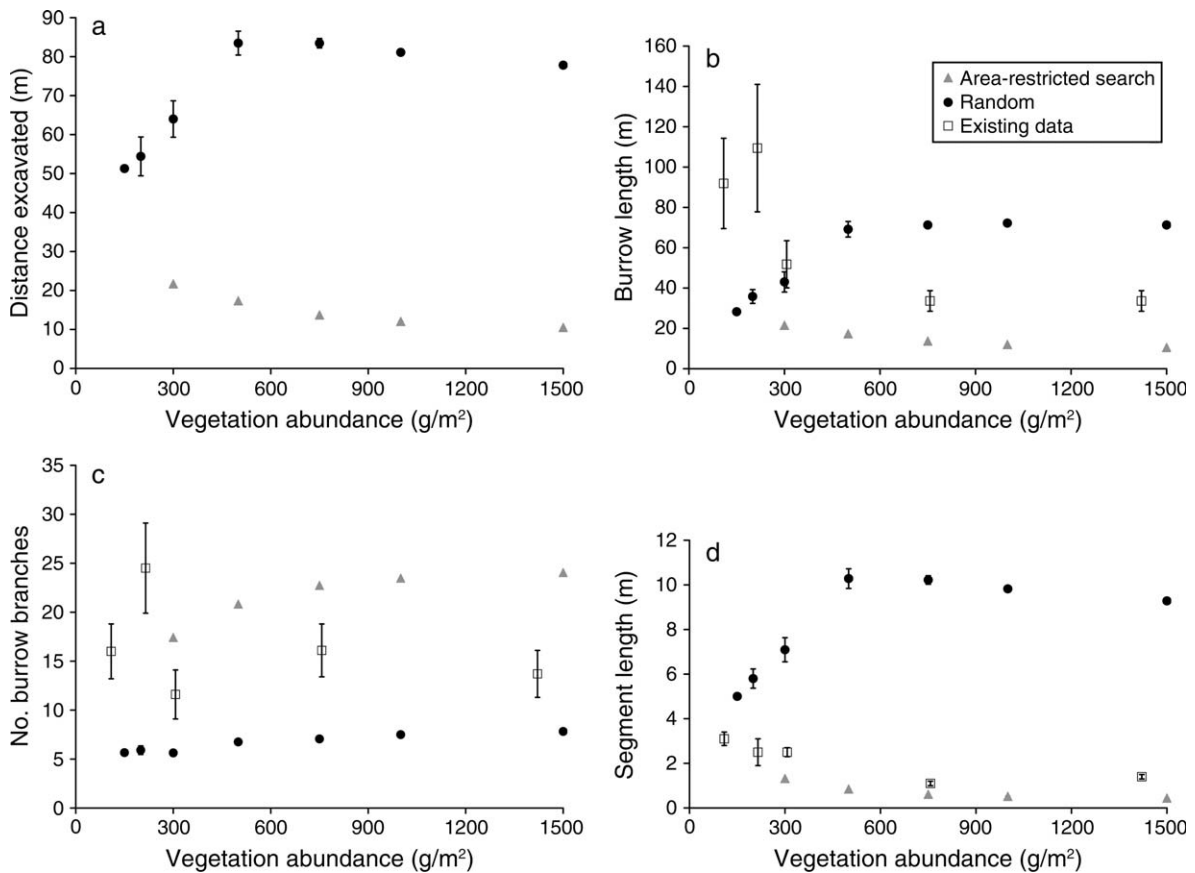


FIG. 5. Model output from animals using area-restricted search and random strategies for (a) distance excavated ($n = 21$), and compared to natural burrows for (b) burrow length ($n = 21$), (c) number of branches ($n = 21$), and (d) segment length ($n = 21$) in the eight vegetation abundance levels. Values are means; for random digging and existing data, error bars indicate \pm SE.

become satiated. In contrast, our model allowed animals to stop activity once their energetic demands were met, and thus they become time minimizers. Animals in our model using ARS met their energetic requirements with less digging compared to animals digging randomly. Pocket gophers that spend less time digging may be less obvious to predators (e.g., weasels, owls) and have more discretionary time for other activities such as caring for

young. Additionally, animals using ARS had higher survival compared to individuals digging randomly. This means that using ARS increases foraging efficiency such that animals at any size class are able to have higher survival on less food than would be required if using a random strategy. As a result, animals using ARS should have a selective advantage when dispersing into and colonizing new habitats.

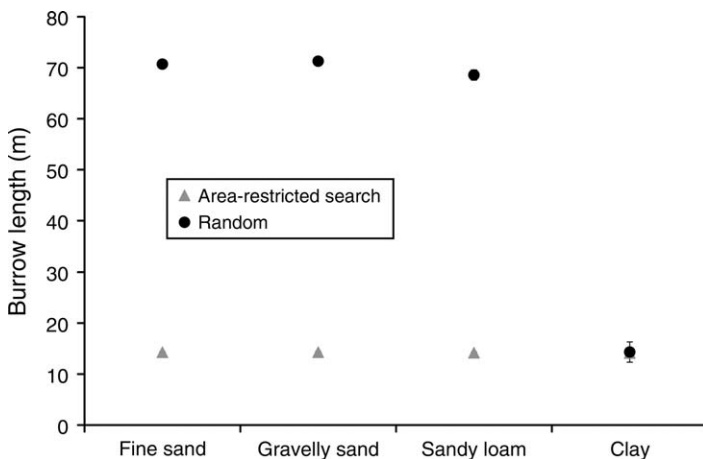


FIG. 6. Model output from animals using area-restricted search and random strategies for mean (\pm SE) burrow length dug in the four soil types. Variation is largely obscured by data points.

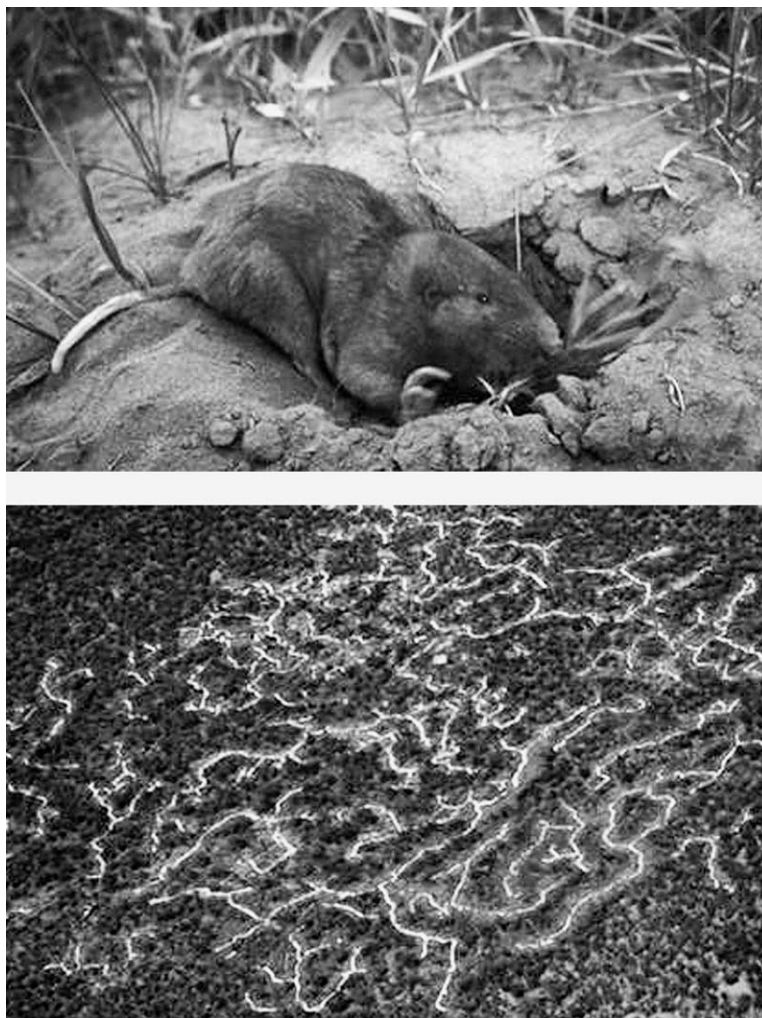


PLATE 1. (Top) Pocket gopher *Geomys bursarius* near a burrow entrance in Cedar Creek Natural History Area, Minnesota. (Bottom) Aerial photograph of pocket gopher (*Thomomys bottae*) burrows excavated and filled with lime (for contrast). The area represented is 60 m wide. Photo credits: O. J. Reichman.

Model animals using ARS produced similar burrow geometries to natural burrows. We examined trends in three burrow geometry metrics from model output compared to geometry data from natural burrows (data from Romañach et al. 2005). We could not compare the total distance excavated between model output and natural burrow data because maps of natural burrows do not indicate whether additional tunnel length was excavated and later backfilled. The trends in burrow length were similar between natural burrows and animals using ARS; however, the latter yielded smaller burrows compared to natural burrows. This size difference may result from model animals making burrowing choices based on foraging alone, while in natural systems burrow length reflects much more than foraging behavior, such as interactions with neighbors and searches for mates (Reichman et al. 1982). As vegetation abundance increased, the number of branches

from existing data was initially approximated by ARS animals and then became bounded by ARS and random results (Fig. 5c). Segment lengths from natural burrows were similar to those of animals using ARS (Fig. 5d). The similarities between model animals using ARS and natural data indicate that pocket gophers in the study by Romañach and colleagues (2005) may have employed ARS. These results are consistent with previous work indicating that pocket gophers use ARS (Benedix 1993).

Most model animals had low survival and did not gain body mass in vegetation abundances of 200 g/m² or below, though natural burrow data exist from two field sites with vegetation abundances of 109 and 215 g/m² (Cameron et al. 1988). We recognize that our interpretation of survival results is limited without a more thorough consideration of factors that contribute to survival and fitness in general (e.g., predation, disease, life history). Pocket gophers had mean body masses of

132 and 149 g at the sites with 109 and 215 g/m² vegetation abundances, respectively; however, in our model, 150 g animals were only able to gain body mass at 300 g/m² vegetation abundance or more. Natural burrows were long at these sites of low vegetation abundance (Fig. 5b), but these great lengths may be due to the low sample sizes ($n = 4$ at 109 g/m²; $n = 6$ at 215 g/m²) and the extreme length of one burrow at each site (168 m at the 109 g/m² site and 188 m at the 215 g/m² site).

For ARS animals, there is a threshold of vegetation abundance above which survival stabilizes for each body mass size class. We offer two potential explanations for the existence of natural populations at productivities less than predicted by the model, such as the aforementioned sites below 300 g/m² (Cameron et al. 1988). First, populations at sites of low vegetation abundance may be maintained through source–sink dynamics by an influx of individuals from nearby high productivity habitats (Pulliam 1988, Pulliam and Danielson 1991). Second, in the model, animals were required to excavate new burrows, which is a large energetic expenditure, whereas in nature, pocket gophers can occupy vacant burrows (Reichman et al. 1982, Zinnel and Tester 1994). Inhabiting a preexisting, unoccupied burrow reduces the high cost of digging a new burrow, which increases the chances for survival and for acquisition of fitness benefits for an individual, and thus can allow persistence of populations over time (Seabloom and Richards 2003).

One of the benefits of our model compared to burrow geometry analyses of existing field data is that we were able to examine the relationship between digging costs and vegetation abundance on burrow geometry. Data from Romañach et al. (2005) show that vegetation abundance and soil clay composition are positively correlated (soils with higher clay content had greater vegetation). By using known values of digging costs and vegetation abundances in our model, we were able to disentangle the relationship between vegetation biomass and soil type. Model results highlighted the importance of vegetation abundance on burrow geometry and showed the lesser effect of soil type. Our findings indicate that despite the high expense of digging compared to the cost of moving aboveground (Vleck 1979), vegetation provides ample calories to compensate for digging even in the most energetically demanding soils. Furthermore, although digging costs seem exceptionally high, previous field research has shown that only 17% of assimilated energy is used for activity, and the balance is for existence (Gettinger 1984a); pocket gophers are active for only a small portion of their day (Gettinger 1984b), resulting in a low cost of excavation per day relative to metabolic costs. Our model shows that metabolic costs outweigh movement costs. Previous work shows that high costs of thermoregulation can greatly increase maintenance costs, particularly for small mammals (Grodzinski and Wunder 1975, Grodzinski and Weiner 1984). If we were to add the cost of

thermoregulation to our model for application to other endotherms, the relative importance of metabolism to foraging costs would diverge even more, particularly for aboveground animals, which incur relatively low cost of movement and experience greater climatic variability.

Our results show the advantage of linking models of energetics and animal behavior. The original model (Seabloom and Reichman 2001) focused on a strictly behavioral component of pocket gopher burrowing without incorporating energetic regulation on movement. Even the few energetic constraints we have included in our model have added components that affect survival, body mass dynamics, and burrow geometries. By placing simple allometric relationships in a spatially explicit context, we were able to observe reasonable body mass dynamics and recreate natural movement patterns. The energetic model that we developed uses general physiological principles, and therefore should make our current model applicable to a general examination of movement and behavior of many endothermic species.

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