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Seasonal influences on burrowing activity of a subterranean rodent, *Thomomys bottae*

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Abstract

While many animals respond to seasonal variation in their environment, animals such as pocket gophers *Thomomys bottae* that live below ground might seem to be buffered against such variation. In some areas, however, the patterns of burrowing activity by pocket gophers are tied to the seasons, one factor of which is rainfall. Variation in activity patterns may result from the ease of digging in moist soil or increased food availability during the wet season. Previous simulation modelling work suggests that food availability influences burrowing patterns, while soil conditions do not. Thus, field experiments were used to investigate how soil conditions and food availability influence seasonal burrowing activity. Results indicate that an increase in soil moisture initiates activity. After this initial increase in activity, mound production declines and reaches a steady rate, which can be supported by vegetation availability, in agreement with previous model results. Our findings support the idea that moist soil promotes a burst of digging activity, potentially for burrow maintenance when soil becomes easily workable, and the eventual growth of vegetation provides the food necessary to support continued activity.

Key words: activity, burrowing, pocket gopher, soil moisture, *Thomomys bottae*, vegetation

INTRODUCTION

Animal activity is governed by both abiotic and biotic conditions. Abiotic factors such as climate and topography affect when and where animals can be active (e.g. Porter *et al*., 2002). Biotic factors such as food and mate availability further influence appropriate times and places to be active (e.g. Johnson, Parker & Heard, 2001; Clark, Clark & Leslie, 2002). Abiotic and biotic factors can vary seasonally and generate seasonal patterns of animal activity (e.g. Bandoli, 1981; Ager *et al*., 2003).

Subterranean rodents burrow through the soil, consuming above- and below-ground plant material (Huntly & Inouye, 1988). Thus, their burrowing activity is affected by both the physical characteristics of the soil and the availability of food (Romañach *et al*., in press). Direct observations of subterranean mammal activity and behaviour are difficult because the animals conduct virtually all their activities below ground. As they excavate burrows, however, tailings are deposited as mounds on the surface, providing information about below-ground activity.

In California, pocket gophers *Thomomys bottae* exhibit seasonal mound production, producing few or no mounds during the dry summer months (M. A. Miller, 1948; Ingles, Clothier & Crawford, 1949; R. S. Miller & Bond, 1960; Bandoli, 1981), and mound production is greatest during the rainy winters. Rainfall moistens the soil, which increases the ease of digging compared to dry soils (Collis-George, 1959). Rainfall also promotes plant growth, and thus yields a fresh food supply. Previous studies have found a weak (Cox & Hunt, 1992) or no correlation (Bandoli, 1981) between pocket gopher activity and rainfall, and no correlation with soil moisture (R. S. Miller & Bond, 1960). The findings of Cox & Hunt (1992), however, suggest that moist soil and cool temperatures are conducive to digging, and that digging is initiated by vegetation growth.

Furthermore, a previous study used a simulation model to investigate the effects of soil conditions and vegetation availability on the energetics of pocket gopher burrowing (Romañach, 2003). Model results indicated that vegetation availability was the most important factor contributing to the burrowing patterns of pocket gophers, while digging costs ranging over an order of magnitude in several soil conditions (Vleck, 1979) had little or no effect on burrowing patterns. These results have, however, yet to be tested in the field to determine their applicability to natural systems.

The goals of this current study were two-fold. First, to determine whether soil moisture or food availability

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prompted pocket gopher activity. Second, to test experimentally one of the predictions of the simulation model, which showed that food availability had a greater effect on the burrowing of pocket gophers than did the cost of digging (Romañach, 2003). To accomplish these goals, the effects of changes in soil moisture and food availability (as measured by above-ground vegetation biomass; see Methods) on the burrowing activity (as determined by mound production) of *Thomomys bottae* in California was examined by watering the soil during the dry season. Soil moisture and vegetation biomass were quantified over time, and each compared to pocket gopher activity. We predicted that if moist soil promotes activity, then wetting the soil during the dry season should lead to immediate mound production, with cessation when the watering stops and the soil dries. If new vegetation growth prompts activity, then mound production should be delayed after watering begins until vegetation grows in response to water, and mound production should continue well after watering ceases while green vegetation matures and remains available.

METHODS

Site description

Experiments were conducted at the University of California's Sedgwick Reserve (34.70 °N, 120.05 °W), in the Santa Ynez Valley, 56 km north of Santa Barbara, California, U.S.A. Annual rainfall averages 38 cm, which typically falls in December–March. Soils are composed of 29%, 43%, and 28% clay, silt, and sand, respectively (F. Chamran, pers. comm.). This clay loam soil supports a mosaic of oak savanna and chaparral.

Experimental design and data collection

Two experiments were conducted to determine the roles of soil moisture and vegetation availability on the activity patterns of burrowing pocket gophers. The first experiment was designed to test whether watering the soil during the dry season promoted pocket gopher activity. Based on our results from the first experiment, a second experiment was designed to determine how the activity patterns of pocket gophers were affected by incremental increases in the number of watering events during the dry season. Specifically, watering was tested to find out whether it would result in a sustained increase in vegetation biomass beyond experimental watering for each incremental watering treatment, and if so, whether pocket gopher activity would also continue beyond the watering treatments.

For both experiments 10 × 10 m plots (marked at each corner) were selected, each occupied by 1 pocket gopher (determined by patterns of size and shape of soil mounds: Sparks & Andersen, 1988; and spacing of groups of mounds: see Reichman, Whittham & Ruffner, 1982 for evidence of between-burrow spacing). Plots were chosen in an open area, away from trees and shrubs, in a field dominated by annual vegetation. Before beginning each experiment, existing pocket gopher mounds were flattened in control and treatment plots so that new mounds could be distinguished. Treatment plots in both experiments were watered once per week with an amount that fell between 1 and 2 SD above mean weekly rainy season rainfall based on local rainfall records (USGS, 1999), and the variation in the amount of water applied between years (see below for specific amounts) was the result of uncontrollable variation in water pressure at the study site. Water was delivered at night (when evaporation and wind were minimal) via an above-ground sprinkler system with a circular spray that reached the corner posts of each plot. Water amounts delivered were measured in treatment and control plots using rain gauges, which were read at dawn following each night of watering. Each new mound produced was marked with a small, flat stick labelled with the date and mound number.

Experiment One: (August–October 2000)

Four pairs of plots were used in which 1 plot of each pair received 6.4 cm of water once per week for 9 weeks (beginning 28 August), and the other plot of each pair received no water (i.e. control plot). Plots of a pair were *c.* 10 m apart, while pairs were >15 m apart. Both numbers of mounds produced and per cent soil moisture were recorded 2, 4, and 7 days after each weekly watering, and mound production compared in watered *vs* dry plots. The study site was inaccessible from 11 to 17 October, thus no data could be recorded at this time, but it was possible to record the number of mounds that had been produced during this time on 18 October.

A handheld sensor (Hydrosense with 12-cm probes, manufactured by Campbell Scientific Inc., Utah, U.S.A.) was used to monitor volumetric soil moisture in all watered plots. Water sensor probes could not penetrate soil in dry plots, therefore soil was collected to 12 cm depth using a large drill (∼2 cm diameter) to determine moisture content gravimetrically (subsequently converted to volumetric values). Gravimetric soil samples were sealed in plastic bags in the field, and processed in the laboratory within 1 h of collection. Samples were weighed to the nearest 0.01 g, dried to a constant mass at 105 °C for 24 h, and then reweighed to determine per cent moisture based on change in soil mass. Results from the 2 methods were not directly compared to one another in this study.

Experiment Two: (July–October 2001)

To determine whether pocket gopher activity was sustained by watering, 3 replicates of 3 treatments (1, 2, and 3 months of weekly watering, termed '1-month', '2-month', and '3-month' treatments, respectively) were watered, and there were 3 dry (i.e. not watered) control plots. A completely randomized block design was used. Plots in 1 block (i.e. 1 replicate of each treatment and

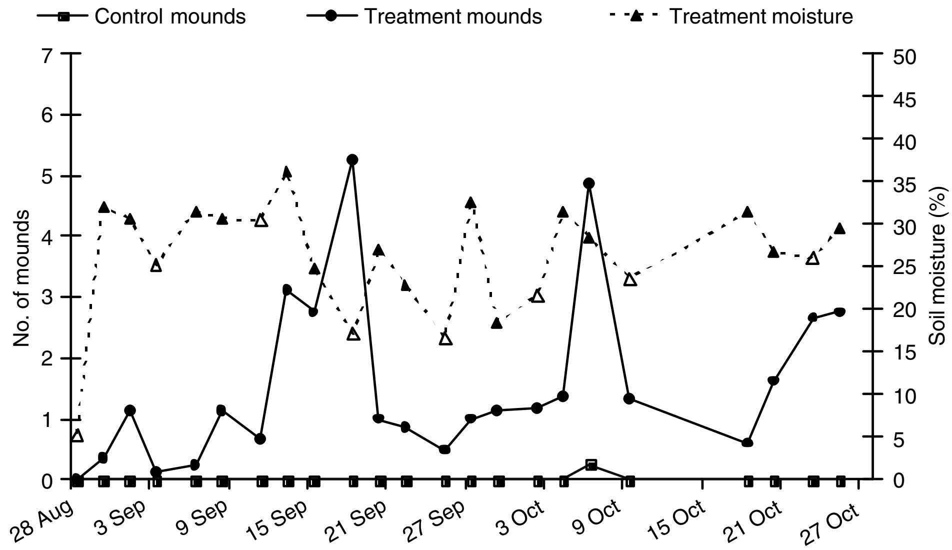

Fig. 1. Experiment One: average daily mound production (for the four replicates) by *Thomomys bottae* 2, 4, and 7 days after watering, and corresponding values of soil moisture on those days. Unshaded triangles, days that watering occurred; however, moisture measurements presented for those days were taken before watering. Watering began 28 August and ended 23 October. Natural rains began 27 October.

1 control) were *c*. 10 m apart, while blocks were >15 m apart. All watering began on 16 July. Watered plots received an average of 9.7 cm of water once per week. Mounds were counted once per week, just before weekly watering. Vegetation biomass was recorded at the beginning and at the end of the experiment.

Per cent soil moisture was measured in 1 block. Gravimetric moisture measurements were taken in each plot of this block on the day before the experiment began and again 1, 4, and 7 days after each month ended. Sampling continued at the end of each month for 5 months after watering ended to monitor soil desiccation through time.

Above-ground plant biomass was used as our measure of resource availability. At our study site, pocket gophers eat above- and below-ground portions of plants (pers. obs.). Although the below-ground portion was not measured directly, both experiments were conducted in an area with fairly homogeneous vegetation and it is unlikely that root to shoot ratios would vary systematically across the plots (for root to shoot ratios within a vegetation classification see Andersen & MacMahon, 1981). In addition, nearly all of the species in the plots were annual and were dormant as seeds at the start of the experiment. The observed increase in above-ground biomass could only occur with a concurrent increase in root growth. Thus, the above-ground biomass provides an accurate measure of the relative change in total plant material available to the pocket gophers.

Above-ground (living) plant biomass was sampled to examine the relative effects of watering on vegetation growth in treatment and control plots. Biomass samples were taken twice in all plots, once before the experiment began and again after the final 3-month water treatment ended. Three vegetation samples (0.12×1 m each) were taken per plot (using battery-powered grass shears) in randomly assigned locations, dried to a constant mass at 60 °C for 24 h, and then weighed as total biomass to the nearest 0.01 g.

Statistics

For Experiment One, a repeated-measures ANOVA was used to determine whether soil moisture values differed 2, 4, and 7 days following watering. One-way ANOVAs were used to analyse cumulative mound production in control *vs* treatment plots for both experiments. Repeated-measures ANOVAs were used to determine changes in numbers of mounds produced through time for both experiments (SAS, 1989; von Ende, 1993). For Experiment Two, differences in vegetation biomass before and after experimental watering were analysed using a repeated-measures ANOVA.

RESULTS

Soil moisture

Experiment One

Control plots showed no significant change in soil moisture between the day before experimental watering (5.3%) and the end (5.5%) of the experimental period ($P = 0.54$). Additionally, no measurable water was recorded in the rain gauges in control plots throughout the experimental period. There was no difference in soil moisture between treatment plots before the experiment began (5.2%) and the pre-experiment values of the controls (5.3%, $P = 0.54$). For all weeks, soil moisture in treatments averaged 32% on the second day following watering (Fig. 1). Soil moisture declined to an average of 27% on the

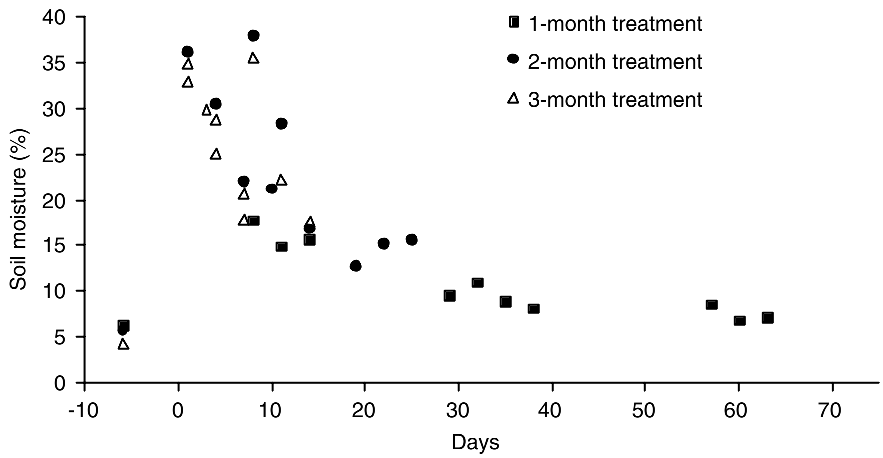

Fig. 2. Experiment Two: soil moisture *vs* the number of days since the most recent watering event. First moisture measurements were taken 6 days before first watering. Day 1 represents the day after the first watering. Soil moisture declined though time after watering ended.

fourth day following watering, and to 22% on the seventh day after watering. Repeated-measures ANOVA results showed that the moisture values for 2, 4, and 7 days after watering were significantly different from one another ($P \ll 0.01$).

Experiment Two

Soil moisture across all plots averaged 5.2% before watering began. No measurable water was recorded in the rain gauges in control plots. In the treatment plots, moisture increased to an average of 35.5% on the day following the first watering (Fig. 2). Soil moisture did not approach values as low as pre-experiment levels until 60 days after last receiving water when it reached 6.9%, which was not significantly different from the pre-experiment average of 5.2% ($P = 0.18$).

Mound production

Experiment One

Pocket gophers in treatment plots had produced mounds by the first day of data collection, which was 2 days after the first watering. Treatment plots had significantly greater cumulative mound production (398 mounds, SE = 0.6) than controls (1 mound, SE = 0.0) at the end of the 9-week watering period ($P \ll 0.01$). Natural rains began on 27 October, 4 days after last watering event, therefore it was not possible to assess whether mound production stopped after experimental watering ended.

A repeated-measures ANOVA was used to determine whether there were differences in mound production over time between treatments and controls. Average mound production in treatments increased during the first month of watering (Fig. 1). Mound production gradually increased to a peak of 5.3 mounds/day per plot (SE = 2.1) 21 days after the initiation of watering, then declined significantly ($P = 0.04$) to an average of 1.3 mounds per day (SE = 0.2). Mound production showed a sudden, second peak of 4.9 mounds (SE = 1.7) on 6 October ($P = 0.02$), then an immediate decrease to an average 1.8 mounds per day (SE = 0.4; Fig. 1). The only mound produced in any control plot also occurred on 6 October.

Soil moisture immediately increased after watering, and then generally decreased following each watering, but mound production patterns did not correspond to the watering schedule. A simple linear regression was used to examine the relationship between soil moisture and mound production. All soil moisture values throughout watering *vs* the number of mounds produced at each moisture value were analysed and no significant relationship was found ($P = 0.20$, $r^2 = 0.08$). Mound production did follow soil moisture on its initial assent, but declined while soil moisture remained relatively high.

Experiment Two

Pocket gophers in each treatment exhibited greater cumulative mound production than control pocket gophers throughout the experiment (Fig. 3). An average of 3.3 mounds (SE = 0.3) were produced in total in the control plots after the 3 months of watering ended, while an average of 81.0 mounds (SE = 0.9) were produced in the 1-month treatment plots, 175.0 mounds (SE = 2.2) in the 2-month treatment, and 121.3 mounds (SE = 0.9) in the 3-month treatment. One individual in a 2-month treatment plot produced almost twice the number of mounds as any other study individual, although the mounds were much smaller than those of other individuals (for evidence of variation of mound size among individuals see Sparks & Andersen, 1988), leading to a higher average number of mounds produced in the 2-month treatments than in the 1- and 3-month treatments.

A repeated-measures ANOVA was used to examine differences in total mound production for each month of watering. Pocket gophers in control plots showed no

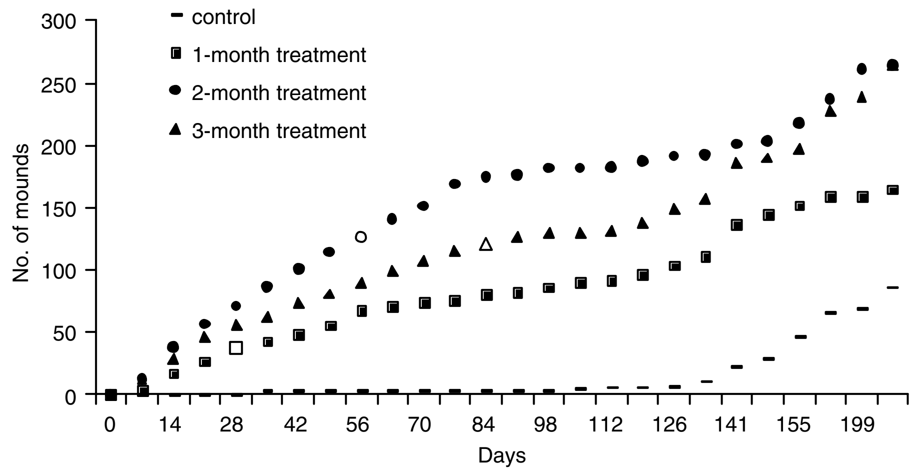

Fig. 3. Experiment Two: cumulative number of mounds produced by *Thomomys bottae* since the beginning of watering. Data presented are average results for the three replicates. Unshaded symbols, mound count after last watering for each treatment. Natural rains began on day 99.

Table 1. Experiment Two: average (± SE) number of mounds produced per month by *Thomomys bottae* for the three replicates of each treatment. *, Significant differences between a given month and subsequent month. Peak mound production occurred during the first month of watering. Experimental watering was terminated after 3 months. Natural rains began during month four

Time (months)	Control	1-month	2-month	3-month
0	0 (0.0)	0 (0.0)*	0 (0.0)*	0 (0.0)*
1	0 (0.0)	39 (1.5)	71 (2.9)	56 (1.6)*
2	3 (0.8)	29 (1.2)*	56 (4.2)	34 (1.4)
3	0 (0.0)	13 (0.6)	49 (2.3)*	31 (1.1)*
4	3 (0.4)	12 (0.7)	7 (1.2)	10 (0.6)
5	17 (1.6)	45 (3.3)	19 (3.8)	54 (3.4)
6	47 (2.6)	23 (4.2)	60 (3.8)	53 (5.9)

Table 2. Experiment Two: repeated-measures ANOVA results for number of mounds produced (in the three replicates of each treatment and control) by *Thomomys bottae* each month throughout experimental watering

Source of variation	d.f.	SS	Mean square	F value	Pr > F
Control	3	5.42	1.81	0.79	0.51
1-month treatment	3	254.25	84.75	0.55	< 0.01
2-month treatment	3	1120.75	373.58	6.55	< 0.01
3-month treatment	3	786.396	262.132	16.608	< 0.01

Table 3. Experiment Two: mean (± SE) vegetation biomass (g/m^2) measured before and after watering (in the three replicates of each treatment and control). Final biomass was taken in all plots on the day after the final 3-month treatment ended

	Biomass		
Treatment	Initial	Final	Change
Control	88.70 (9.59)	112.31 (11.72)	23.61
1-month	110.72 (22.33)	273.94 (55.06)	163.22
2-month	89.72 (14.31)	235.91 (24.06)	146.19
3-month	80.43 (12.00)	321.41 (34.61)	240.95

differences in mound production throughout the experimental watering ($P = 0.51$; Tables 1 & 2). Even though mound production by individuals in each plot varied throughout the experiment, there was an emergent pattern of a peak in mound production after 1 month of watering (Table 1, Fig. 3). Mound production declined significantly in the 1-month treatments between months two and three (i.e. after the cessation of watering; $P < 0.01$; Table 1). Pocket gophers in the 2-month treatment did not show a significant decline in mound production until after month three ($P < 0.01$), even though the greatest number of mounds was produced in the first month of the experiment (Table 1). Similarly, pocket gophers in the 3-month treatment produced the greatest number of mounds in the first month of the experiment; they showed a significant decline in mound production after the first month ($P = 0.02$), and another significant decline after the third month ($P \ll 0.01$).

Vegetation

Experiment Two

One-way ANOVA results showed that initial (pre-experimental) vegetation biomass was similar among treatments and controls ($P = 0.26$; Table 3), with an overall average of 92.40 g/m^2 (SE = 6.55). Results from a repeated-measures ANOVA revealed that biomass of each treatment was significantly greater than the controls after all experimental watering ended (i.e. 3 months after the first watering began; $P \ll 0.01$). The 3-month treatment, which received the most water, had a significantly greater change in biomass (240.95 g/m^2) after 3 months ($P = 0.02$) than did the 1- and 2-month treatments, which were similar to one another ($P = 0.10$).

DISCUSSION

One of the goals of our study was to determine whether changes in soil moisture or vegetation availability initiate pocket gopher activity. The rapid response of pocket gophers to watering (within 2 days) suggests that pocket gophers were initially responding to changes in soil moisture, while vegetation would not yet have had time to grow in response to water availability. Pocket gophers may have initiated activity once soil became moist for burrow maintenance and repair when new food growth was not yet available. Watering eventually increased vegetation availability (Table 3), which presumably supported continued activity (Table 1, Fig. 3) even in relatively low soil moisture (Fig. 2).

The second goal of our study was to test experimentally the simulation model predictions (Romañach, 2003). Our findings support the predictions of the model; food availability had a greater effect on overall burrowing patterns than did soil conditions. Plots of the 1-month treatment had high vegetation availability even 2 months after watering ended (i.e. at the end of month three; Table 3), while soil moisture in this 1-month treatment at the end of 3 months had dropped to the dry, pre-experimental level (Fig. 2). Pocket gophers in this 1-month treatment remained active at the end of 3 months (Table 1) while moisture was low, suggesting that with sufficient food availability, pocket gophers can overcome the high costs of digging in dry soil.

While watering initiated mound production, there was no correlation between soil moisture and the number of mounds produced over time in either experiment. Similarly, R. S. Miller & Bond (1960) found no correlation between mound production and soil moisture. During their 2-year study, R. S. Miller & Bond (1960) found peaks in mound production *c.* 1 month after activity began. Neither their observed peaks nor declines in activity were related to changes in soil moisture. Likewise, our study found peaks and declines in activity that were not related to changes in soil moisture (Fig. 1). Our results show that mound production initially tracked the soil moisture increase, but declined while moisture remained high.

M. A. Miller (1948) recorded soil moisture between 5% and 25% under natural rain conditions, with the greatest mound production between 9% and 18% moisture. He found low or no mound production below 9% and reduced activity between 18% and 25%. In our study there was high mound production at moisture levels as high as 35%. Although our experiments revealed no such optimal range of soil moisture for mound production (Fig. 1), it was found that few or no mounds were produced at low values of soil moisture (i.e. control plots), in agreement with M. A. Miller's (1948) findings. These results might indicate a threshold moisture level required to promote excavation.

The most probable explanation for our findings is that pocket gophers take advantage of the moist soil to repair and enlarge their burrows, and then they reduce activity levels once appropriate burrow size is attained, for example, to provide access to food and mates. Pocket gophers might remain in burrow systems of reduced size (particularly with regard to their shallow, foraging tunnels) during the dry season, and then initiate digging immediately after rains begin to re-establish an appropriate burrow system size. In the dry season, burrows easily collapse from above-ground disturbance (pers. obs.). Consequently, the energy required to repair burrows continually under these hot, dry conditions (for energetic requirements to dig and push soil see Vleck 1979, 1981) might be greater than the energy available from food in the dry season. Pocket gophers in this study inhabited an annual-dominated plant community resulting in a decrease in available root matter for consumption as the dry season progresses.

Another group of subterranean rodents, African mole-rats (Bathyergidae), show this pattern of enlarging the burrow system as soon as the soil becomes moist, and they extend their burrows mainly as they forage for vegetation (Bennett & Faulkes, 2000). Although the appropriate experiments have not been carried out for pocket gophers, the findings of our study would be in agreement with the idea that an increase in soil moisture may serve as a cue to pocket gophers for impending food availability.

An alternative explanation for seasonal patterns of pocket gopher burrowing activity is that pocket gophers begin digging following a watering event to adjust burrow depth and length to be appropriate for necessary gas exchange. Burrows can become waterlogged, potentially causing pocket gophers to initiate digging to maintain an appropriate burrow size (Kennerly, 1964; Bandoli, 1981). If this were the primary behavioural response exhibited by pocket gophers in our study, activity would have been expected to have begun after burrows became saturated, and then stop once appropriate burrow volume were reached. This idea is not supported by our experimental data for two reasons. First, mound production began after the first watering event, and burrows were probably not waterlogged at this time, particularly considering the extreme desiccation of the clay soils before the experiment began. Second, rates of activity did not slow after each watering event (Fig. 1).

The results of our experiments are consistent with the idea that an increase in soil moisture prompts activity in the wet season. This leaves open the question of how these animals secure resources in the dry season when they seem to be inactive. There are three possible explanations for the lack of mound production, and seeming cessation of food acquisition. (1) Pocket gophers cache food (Aldous, 1945) near the end of the wet season (pers. obs.), possibly to survive dry summer conditions, and may not need to extend their burrows while feeding on their cache. (2) Pocket gophers become dormant during the dry months, and initiate activity when the soil becomes moist, although there is no evidence for dormancy. (3) They could continue burrowing through the dry season, but rather than produce above-ground mounds, they could fill existing burrow segments with soil, resulting in a lack of above-ground evidence of burrowing. The latter possibility raises the question of why mound production behaviour would have seasonal patterns. Crouch (1933) suggested that when the soil is dry, pocket gophers construct deeper burrows, perhaps filling shallow tunnels with the deeply excavated soil and thus not producing above-ground mounds. Furthermore, Sumbera *et al*. (2003) found that individuals of a solitary species of mole-rat tend to push soil into abandoned tunnels during the dry season rather than constructing above-ground soil mounds, and suggest that this behaviour may avoid heat stress and/or the high cost of pushing hard soil into above-ground mounds.

The activity patterns of all animals are influenced by the abiotic and biotic conditions they encounter. This study revealed that pocket gopher activity patterns are closely associated with highly seasonal rainfall regimes. Both the moist soil and vegetation growth resulting from rainfall are important in promoting and sustaining pocket gopher activity. These experiments suggest that water initially softens soil, promoting immediate digging, and eventually promotes vegetation growth that can support continued activity. Thus, seasonal activity patterns can only be understood by taking into account temporal variation in movement costs and resource availability. While many studies address temporal patterns in resource availability, few address changes in movement cost (but see Pruitt, 1960). Nevertheless, it is likely that temporal changes in movement costs are common in many systems as a result of changes in abiotic factors such as wind patterns, water currents, and snow depth.

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