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Root cropping by pocket gophers

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eTOC
Roots grow into the humid interiors of *Geomys pinetis* tunnels where they benefit from nutrients from gopher wastes. Cropping these roots supplies *G. pinetis* with an average of 21% but up to 62% of their daily basal metabolic needs. This behavior may qualify these fossorial rodents as the first non-human mammalian farmers.

Pocket gophers (*Geomys* spp.) are solitary, root-eating fossorial rodents native to North and Central American grasslands presumed to acquire most of their food through excavation of tunnels maintained as part of tunnel systems up to 160 m long[1,2]. Given that burrowing is 360-3400 times more energetically costly than surface walking, pocket gophers have high energy requirements[3]. Roots are scarce at the depths of their tunnels in the sandy soil of our study site (20-64 cm), but here we describe a novel food source for southeastern pocket gophers (*Geomys* *pinetis*, hereafter gophers): roots that grow into their tunnels. These roots could supply an average of 21% but up to 62% of their daily basal energetic needs.

We worked in a pasture being restored to longleaf pine (*Pinus palustris*) savanna in North Florida where gophers were abundant (Figure 1A). Based on the bulk density of the sandy soil (mean = 1.46 $g\cdot cm^{-3}$, sd = 0.07, N = 12), mean tunnel radius of 3.8 cm (sd = 0.40, N = 12), and mean tunnel depth of 38.6 cm (sd = 12.6, N = 12), the average energetic cost of tunnel excavation is 17 $kJ\cdot m^{-1}$ when soil is discarded in surface mounds[4]. Based on fine root (<2 mm diameter) samples from soil adjacent to the tunnels, gophers encounter an average of 1.37 g (dry weight) of roots (sd = 1.05, N = 12) per meter of excavated tunnel of average radius, but with a large range (0.25-4.01 $g\cdot m^{-1}$). Assuming a fine root energy content of 18.39 $kJ\cdot g^{-1}$ [5], 56% energy digestibility and 54% assimilation efficiency[6], a gopher would suffer an average deficit of 9.1 kJ per meter of tunnel excavated (sd = 7.46 kJ, N = 12). It should be noted that this estimate, like the others that follow, are quite variable; one tunnel yielded an energy surplus due to a locally high concentration of roots.

After excluding gophers from 57 cm long sections of tunnel for 17-44 days (Figures 1B and 1C), root growth into and within 0.4 cm of the tunnel circumference was equivalent to 0.076 g per meter of tunnel per day (sd = 0.055, N = 12, range = 0.021-0.174 $g\cdot m^{-1}\cdot day^{-1}$; Figure 1D and 1E). In-growing roots provide an extra 0.42 kJ per meter per day (sd = 0.306, N = 12, range = 0.116-0.967 $kJ\cdot m^{-1}\cdot day^{-1}$), or 18.6 kJ per day for a tunnel network of average length (44.2 m)[1]. Based on an estimated basal metabolic rate of 106 $kJ\cdot day^{-1}$ [7], this average amount of energy from root ingrowth provides 21% of a gopher's daily basal caloric needs.

We argue that by promoting root growth in their tunnels and then cropping those roots, southeastern pocket gophers are employing a low-level food production system that may qualify as farming. Root growth is promoted by soil aeration, which increases rates of nutrient mineralization and locally reduces soil bulk density[2]. Also, unlike other pocket gopher species that use dedicated food and fecal storage chambers, southeastern pocket gophers scatter their wastes in their tunnels, which fertilizes the soil[1]. Root cropping may also provide a short-term stimulus of root growth; root ingrowth rates declined with duration of tunnel isolation ($r = -0.76$, $p = 0.004$). Root farming would also help explain why each gopher maintains and defends an extensive and exclusive tunnel system[1]. Unlike fungus-growing insects[8], gophers neither sow nor weed their crops, which may disqualify them as farmers, but if accepted, they would represent the first farming non-human mammal.

If excavation and root ingrowth do not supply gophers with all their energetic needs, how do they satisfy their metabolic demands? We see three possibilities: they concentrate foraging in areas of high root density, they rely heavily on tubers, or they utilize aboveground food sources. Other species of gopher concentrate their excavation in root-dense areas[9] such as we encountered in one soil sample in which, if extrapolated to a 1 m tunnel, would have supplied enough calories to cover most of a gopher's daily basal caloric requirement. Although wefound only fine roots in our samples, we encountered thick and succulent *Cnidoscolus urens* taproots at the same depths as gopher tunnels. These and many other species in the savanna we studied produce tuberous roots, bulbs, corms, and rhizomes that are rich in non-structural carbohydrates[10]. While root proliferation in tunnels does not supply gophers with all their food needs, it more than covers the energy deficits incurred by digging 1 m. Perhaps this energy helps them dig further in search of root-rich areas and tubers. Furthermore, we assumed that gophers obtain most of their energy from roots, but they are known to pull entire plants down into their tunnels by the roots (Video S1) and occasionally forage on the surface, although only within one body length of their tunnel opening while mounding[3]. In most cases, we encountered little evidence of surface foraging; ample vegetation was covered by their mounds. In one tunnel we did find a stolon of *Paspalum notatum* (Bahiagrass) and leaves of an unidentified herbaceous plant, which suggests that aboveground food sources do contribute to gopher energy budgets. Regardless of how they meet all their daily energetic needs, southeastern pocket gophers clearly benefit from root growth into the tunnel systems that they excavate, defend, and maintain at great energetic expense.

Further study may reveal whether gophers eat fungi and how seasonal variation in the energetic contributions of roots growing into tunnels relates to their activity cycles. Also, although gophers are known promote soil heterogeneity by burying organic matter and bringing mineral soil to the surface[2], it is not known how repeated root herbivory in gopher tunnels affects vegetation. Whether or not they qualify as farmers, root cultivation is worth further investigation.

SUPPLEMENTAL INFORMATION

Supplemental Information includes a study site description, experimental procedures, details about calculations and one video and can be found with this article online at https://doi.org/xxxxxx.

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AUTHOR CONTRIBUTIONS

V.S. and F.E.P conceptualized the study, carried out the fieldwork, and drafted the manuscript based on data analyzed principally by V.S.

DECLARATION OF INTERESTS

The authors declare no competing interests.

Figure 1. Tunnelling energetics of *Geomys pinetis* (southeastern pocket gophers), roots encountered, and roots growing into their tunnels.

(A) Pocket gopher in tunnel with roots. (B) An open-ended barrel, diameter = 57 cm, inserted into ground to keep gophers out of sections of tunnel. (C) Tunnel before isolation. (D) Tunnel after isolation. (E) Based on 12 tunnels, the cost of digging 1 m of tunnel, energy gained from roots during initial excavation of tunnel, and energy gained from daily root ingrowth into a 44.2 m long gopher tunnel system, accounting for energy digestibility and assimilation efficiency. Means represented by the "x" and medians represented by the middle lines. Photographs and drawing by VS.

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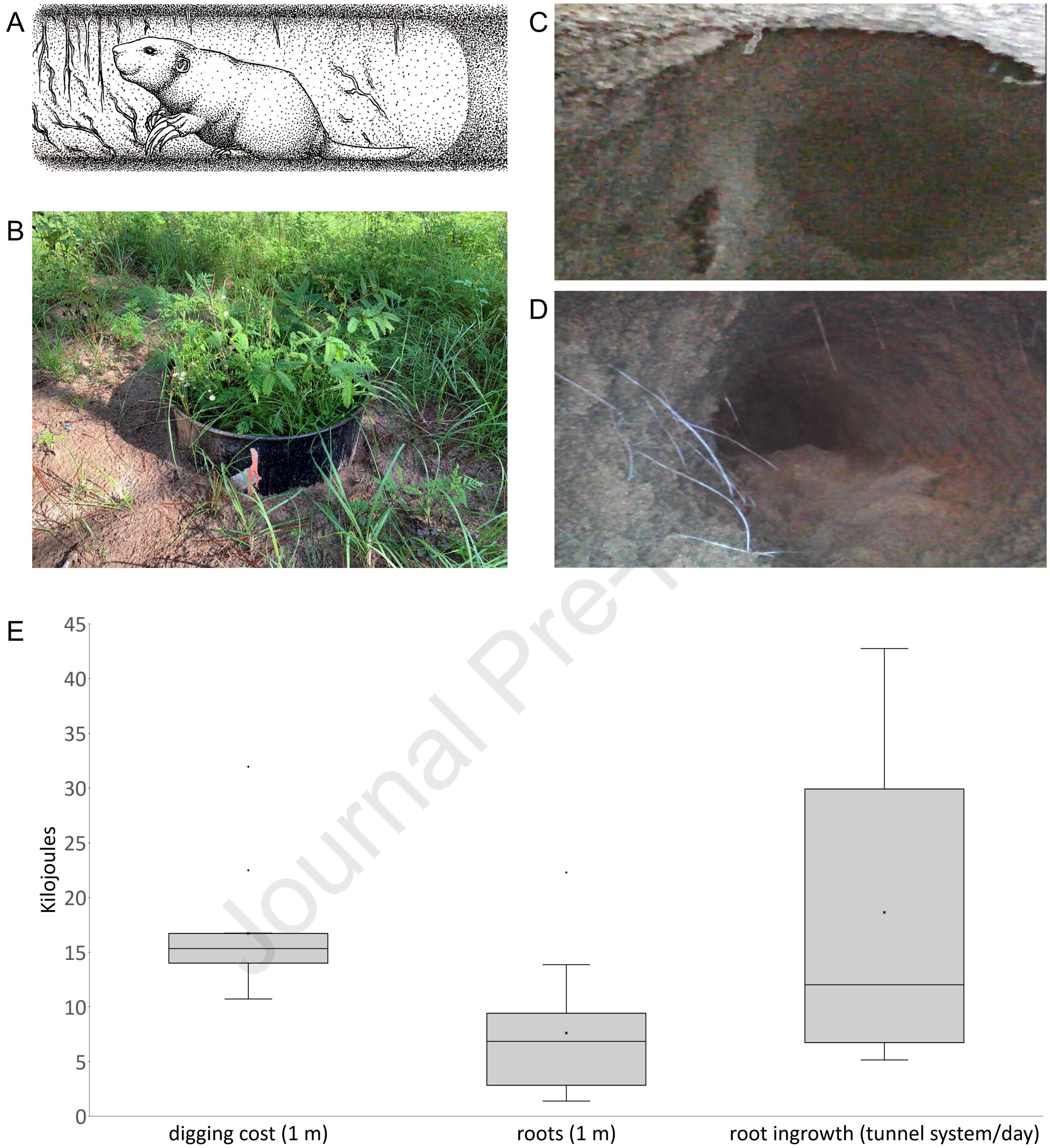
A
B
C
D
E
Kilojoules
45
40
35
30
25
20
15
10
5
0
digging cost (1 m)
roots (1 m)
root ingrowth (tunnel system/day)