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Gophers as geomorphic agents in the Colorado Front Range subalpine zone

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ABSTRACT

Gophers are significant geomorphic agents in many landscapes. We document activity of the northern pocket gopher (*Thomomys talpoides*) in two small subalpine meadows (1050–1800 m^2) of the Front Range, Colorado, USA. We tracked locations and volumes of mounds and subnivean infilled tunnels over one year and probed the thickness of the biomantle within one meadow. We infer that only 5–7 gophers occupied each meadow, implying a gopher density of 28–67 ha^{-1}. Fractional areal coverage of the meadows by diggings suggests that within 49–95 years gophers would fully resurface the meadows. Annual volumes of excavated soil correspond to the equivalent of ~1 mm of material spread evenly over the meadows. Probed meadow resistance depths reveal a pattern we interpret to be stone lines at roughly 15 cm depths; implied vertical turnover times are therefore roughly 150 years. These spatial and temporal patterns imply that gophers should be able to churn the biomantle on approximately century timescales and should fully resurface the meadow areas in similar timescales. These field data also contribute to an investigation of lateral sediment transport; given the local slope of the landscape, gopher-driven sediment transport within our two study sites suggests a landscape diffusivity of 0.008 m^2y^{-1}. At no time do gophers occupy the forest. As evidenced by subnivean infilled tunnels, winter activity is restricted to the upslope (and hence upwind) meadow edges, which correspond to high snow cover and warm (>~0 °C) shallow subsurface soil temperatures. Subsequent activity expands downhill into the meadows and shows a distinct pulse of mound activity in late summer through early fall prior to snowfall. Local forest fire history has led to much more extensive meadows in the past, suggesting that the geomorphic influence of gophers in the landscape is much more widespread than the present distribution of meadows and may cover the entire subalpine region of the Front Range on millennial timescales.

1. Introduction

Biological agents and their effects are ubiquitous within landscapes and can be observed on daily timescales. Deer-generated game trails, beaver-constructed dams, and ant-generated mounds are several examples of the geomorphic impacts of animals that one can stumble across on many landscapes. However, despite early interdisciplinary acknowledgement that biology plays a role in landscape evolution (Darwin, 1881; Gilbert, 1909), geomorphologists and biologists have largely worked independently. Even today, geomorphology largely ignores the role of the biosphere or acknowledges it only in a broad, large-scale sense (Butler, 1995). This may be because of fundamental differences between the two sciences when approaching problems. When presented with a question, instead of focusing on how animals and landscape evolution are interwoven, Yoo et al. (2005) stated that an ecologist may concentrate on population dynamics while a geomorphologist may concentrate on the energy that molds and drives the landscape. Here we honor what is observed to be the primary geomorphic player within the subalpine landscape of the Colorado Front Range, the northern pocket gopher (*Thomomys talpoides*) and provide a framework for understanding what drives the spatial and temporal patterns of landscape change.

The northern pocket gopher, *T. talpoides*, is a medium-sized rodent: mean male total length = 206.8 mm, mean female total length = 203.0 mm (Miller, 1964); in Utah, mean adult male mass = 104.4 g, mean adult female mass = 91.4 g (Andersen, 1978). While slight on an individual scale, they are often abundant and have a large geographic range that spans a large fraction of western North America (Verts and Carraway, 1999). More broadly, pocket gophers comprise multiple species within six genera widely distributed across North and Central America.

All pocket gophers are fossorial rodents that build an intricate system of tunnels and mounds (Fig. 1). The subsurface gopher tunnel system can be separated into two parts: (i) shallow feeding tunnels constructed parallel to the ground surface that are utilized for harvesting roots, and (ii) a deeper set of tunnels and chambers that are utilized for nesting and food storage (e.g., Miller, 1957; Reichman and Seabloom, 2002). The feeding tunnels connect to the ground surface

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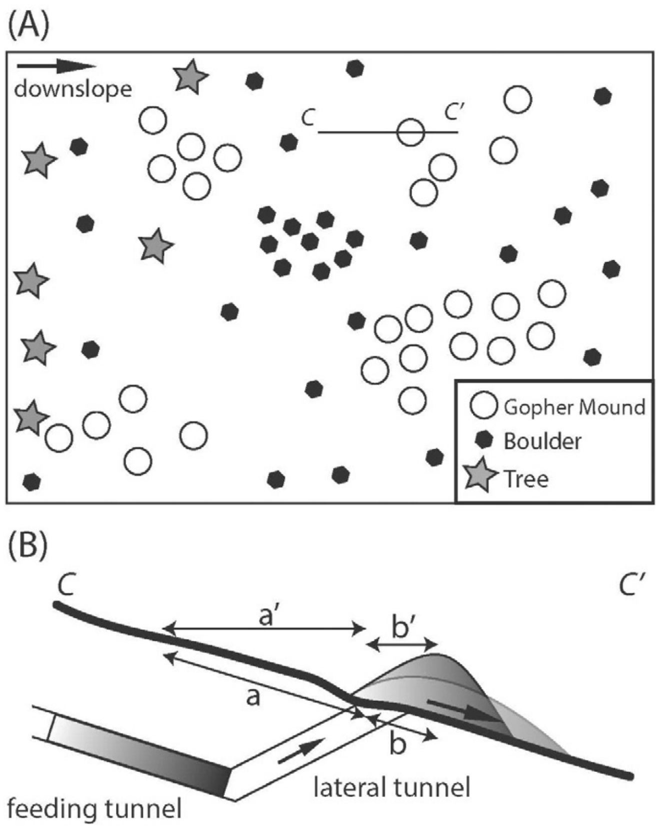

Fig. 1. (A) The general pattern of gopher activity in a boulder-strewn, sloping meadow-forest landscape. Gophers inhabit the meadows but not the forests. Gopher mounds develop in a patchy fashion within the meadows, presumably each patch belonging to a solitary gopher. These patches generally occupy the less rocky portions of this glacial till mantled surface. (B) Subsurface cross section (C–C′) of gopher-driven sediment transport. Material is transported from the ground-parallel feeding tunnel up through a lateral tunnel where it is deposited on the surface as a mound. Material is then exposed to diffusive transport processes that move material downslope. Gopher transport of sediment is described by Gabet (2000) as consisting of two discrete horizontal distances: that from the centroid of the tunnel to the burrow exit/entrance (a'), and that from the burrow exit/entrance to the centroid of the mound (b'); their surface-parallel counterparts are a and b.

Fig. 2. Photograph illustrating one of two study sites where gopher mounds have been surveyed throughout the snow-off season. Flags mark surveyed gopher mounds, each survey being flagged by a different color of flag. Patchy thin snow in the meadow signifies the onset of winter.

through short tunnels, referred to as laterals (Fig. 1). Laterals are utilized to rid the tunnel system of excavated material (Vleck, 1981). The first of the three primary gopher-generated geomorphic features are found at the exit of these tunnels: surface mounds (Figs. 2 and 3A).

The second is an infilled tunnel (Knight, 2009) (Fig. 3B) or earth cylinder (Warren, 1937). These features are produced when a meadow is blanketed in snow, at which time gophers will emerge from the soil to forage for plant material and, in doing so, create snow tunnels. Later, they will further utilize these surface-level tunnels to rid the subsurface of their tillage (e.g., Grinnell, 1923). As a result, they generate dense soil cylinders that are revealed when the snow retreats in early spring. The third geomorphic feature is a stone line (Fig. 3C).

Stone lines are concentrations of stones at some depth beneath the ground surface and reflect a threshold grain size, generally around 2.5 cm (Verts and Carraway, 1999), below which gophers can excavate and above which gophers will dig around. As gopher tunneling continues, larger grains will drop to a uniform depth that effectively records the maximum depth to which the gophers are excavating. This depth, and the stones that accumulate at this depth, are referred to as stone lines (Johnson, 1989). At the same time, the finer material will become more concentrated above the stone line to produce what is called the biomantle, which includes the surface mounds (Johnson, 1989).

For the pocket gopher, benefits of being fossorial (hidden from predators' vision, protection from extreme weather events, and access to plant roots; Vleck, 1979) must outweigh the fact that gophers utilize 360–3400 times the amount of energy tunneling than would be required to move the same distance on the surface (Vleck, 1979). Furthermore, the pocket gopher is close to indifferent to the drudgery of working against gravity. Seabloom et al. (2000) suggested that the energetic costs associated with shearing and pushing soil horizontally through a tunnel system are three orders of magnitude higher than the cost associated with lifting soil against gravity. Gophers prefer to construct lateral tunnels on the downslope side of the connecting feeding tunnel and at an angle that does not exceed the angle of repose (Seabloom et al., 2000); the angle is a function of soil cohesion and is low enough to prevent lateral tunnels from collapsing inward (Vleck, 1981).

The large energetic cost of excavation also suggests a premium for behaviors that maximize the benefits of excavations, especially with regard to food acquisition and neighboring gophers (Reichman et al., 1982). Substantial research has focused on how gophers strategize their tunnel and burrow geometries. Pocket gophers minimize the cost of burrowing by choosing very specific segment lengths between the lateral tunnels (Vleck, 1981) while constructing, in some cases, intricate tunnel systems over 100 m long (e.g., Criddle, 1930; Smallwood and Morrison, 1999). Importantly, the spacing between individual burrow systems remains fairly constant regardless of vegetation type (Reichman et al., 1982). Gophers are less mobile once they have found a hotspot for food resources. Reichman et al. (1982) suggest that burrow length and the quantity of off-shooting tunnel branches are inversely proportional to the availability of food.

The geomorphic effect of the pocket gopher has also been investigated. Ellison (1946) discusses the pocket gopher's role as an erosional agent within the Wasatch Plateau; while not the primary cause of erosion in this landscape, it is still deemed a noteworthy erosional agent. Thorn (1978) identified the pocket gopher as the dominant geomorphic agent in the alpine tundra of the Front Range near our field site. Black and Montgomery (1991) studied gopher activity in a grassland basin in northern California by documenting all gopher-generated surface mounds and concluded that the burrowing of mammals is the primary process driving sediment transport in their field area. Gabet et al. (2003) illustrated that at low gradients gopher bioturbation generates a greater sediment flux than purely physical processes. Butler and Butler (2009) demonstrated that gopher-generated mounds and infilled tunnels are less compacted than the surrounding undisturbed soils and argued that these low density mounds and infilled tunnels may promote seedling establishment within the alpine treeline. Gopher-driven