What determines the way of deposition of excavated soil in a subterranean rodent?

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Subterranean rodents continuously extend their burrow systems primarily in search of food, which has an important impact on the ecosystem in which they live. Excavated soil may be pushed either into aboveground mounds or into tunnels underground. Factors affecting the amount of burrowing and the preference of aboveground or underground soil deposition are, nevertheless, little known. We investigated the influence of food supply, soil hardness, and the animal’s body mass on the mode of soil deposition in ten burrow systems of free ranging silvery mole-rats *Heliophobius argenteocinereus* Peters, 1846. In each burrow system, we estimated the volume of backfilled tunnels and the volume of soil deposited aboveground. The highest amount of variation in these parameters was explained by the interaction of food supply and soil hardness. The ratio of the volume of backfilled tunnels to the volume of mounds was not significantly dependent on any of the explanatory variables. The proportion of backfilled tunnels decreased with the increasing volume of the complete burrow system. We propose that both low food supply and soft soil lead to an increased amount of burrowing, which results in a larger volume of soil deposited both above ground and under ground over a given period of time.

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**Introduction**

Some rodents spend virtually all of their lives underground, where they build complicated three-dimensional burrow complexes (Nevo 1999). During burrowing, they redistribute soils between different horizons and contribute to aeration, irrigation and fertilization of soils. Because of the great impact they have on entire ecosystems, subterranean rodents are regarded as ecosystem engineers (Cameron 2000, Reichman and Seabloom 2002, Reichman 2007).

Subterranean rodents, which extend their burrow systems mainly in search of food, must inevitably deal with the problem of where to de-
posit excavated soil. They push it either into aboveground mounds or into existing tunnels within their burrow systems. The choice between the two methods of soil deposition can be considered a typical cost-benefit problem: pushing soil against gravity into mounds could be energetically costly, especially during dry seasons when the excavated soil is dry and loose (Vleck 1981, Luna and Antinuchi 2006, 2007), while on the other hand, backfilling tunnels restricts access to new food resources by reducing the size of the actual burrow system.

We predicted that subterranean rodents would combine the two above-mentioned methods of soil deposition in response to microenvironmental conditions (soil and food quality). Harder soil should favor belowground deposition rather than mound construction because of the higher energetic cost of pushing loose soil against gravity, whereas lower food supply should promote mound construction rather than backfilling since the actual burrow system needs to be larger to ensure access to enough food resources. We tested this prediction in a single population of the silvery mole-rat *Heliophobius argenteocine- reus* Peters, 1846 (Bathyergidae) in a natural habitat heterogeneous in terms of soil hardness and abundance of food resources (Šumbera et al. 2008).

**Study area**

The study was conducted in August and September 2005 (dry hot season) in a fragment of miombo (*Brachystegia* woodland) on Mpalanganga estate, Zomba, Southern Malawi (15°27'S, 35°16'E, 1070 m a.s.l.). The area is heterogeneous in terms of vegetation cover and relatively rich in geophytes, whose spatial distribution is clumped (the Standardized Morisita’s index of dispersion, Smith-Gill 1975, based on food resources found in 24 randomly placed 2 × 2 m squares excavated to the depth of 20 cm, was 0.52; J. Šklíba and R. Šumbera, unpubl.). The climate in Malawi is characterized by a rainy season (November/December–March), a dry cold season (April–July), and a dry hot season (August–October/November).

**Material and methods**

The silvery mole-rat is a solitary bathyergid widely distributed throughout Central and Eastern Africa. It feeds mainly on underground plant storage organs which are reached by burrowing. Unlike some other subterranean rodents, burrow systems of the silvery mole-rat lack clear difference between deeper “axial” tunnels and shallow foraging tunnels (Šumbera et al. 2008, Šklíba et al. 2009). The species constructs food stores, but the amount of cached food is usually too small to provide the sole source of food over a longer period of time, such as the advanced dry season (Jarvis and Sale 1971, Šumbera et al. 2003, J. Šklíba and R. Šumbera, unpubl.).

The study commenced approximately six months after the last heavy rains, which is sufficient to accumulate evidence of long term soil deposition both above and below ground. In wet soils the older backfilled tunnels are usually impossible to distinguish, which means that those which were detected were presumably of a similar age as the mounds of soil not weathered by the rains. The burrow system mapping was done within a short period of three weeks to ensure that the data were obtained for the actual burrow system and the length of food resources (Šumbera et al. 2008).

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