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Surface foraging in *Scapanus* moles

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Abstract: Some mole genera, including *Scapanus* of western North America, are usually considered to be fully fossorial. I present data showing that surface foraging is used by adults of all four *Scapanus* species, and evidence that such foraging is not a particularly rare behavior. *Scapanus* moles forage on the surface when leaf litter is wet and does not produce much noise; they also move slowly, remain within a small area, and usually forage in places with dense cover. These adaptations decrease the risk of predation and make surface foraging behavior difficult to detect for human observers. Numerous unpublished and a few published observations suggest that many, if not all, species in other "fully fossorial" mole genera forage on the surface at least occasionally. This is true not just for true moles (Talpidae), but also for unrelated, but convergently similar golden (Chrysotalpidae) and marsupial (Notoryctidae) moles. Apparently, surface foraging is too important for fossorial insectivores to be completely lost even in the most fossorial taxa.

Keywords: behavior; behavioral ecology; fossoriality; Talpidae; true moles.

Introduction

True moles (Talpidae) exhibit a remarkably broad spectrum of lifestyles. This relatively small family (fewer than 50 recognized species according to IUCN 2015) includes animals with at least six foraging strategies: (1) shrew-like surface foragers (*Uropsilus*), (2) animals that mostly forage under the leaf litter but also dig burrows and occasionally climb shrubs and small trees (*Urotrichus*, *Dymecodon*, *Neurotrichus*, and probably *Scaptonyx*), (3) those that feed predominantly underground but also under the leaf litter (*Scapanulus, Parascalops*, *Euroscaptor*, and probably *Parascaptor*), (4) "typical" moles that are believed to forage exclusively or almost exclusively underground (*Talpa*, *Mogera*, *Scalopus*, *Scapanus* and possibly *Scaptochirus*), (5) aquatic foragers (*Desmana*, *Galemys*), and (6) one species that forages underwater, underground and on the surface (*Condylura*; Nowak 1999, Smith and Xie 2013).

Western American moles (*Scapanus*) are believed to be exclusively underground foragers (Stephens 1906 and virtually all subsequent works), although they are known to forage under snow in winter in colder parts of their range (Pedersen 1963). Regular occurrence of their remains in owl pellets and among animals killed by domestic cats and dogs (Giger 1965, Maser and Brodie 1966) and by other predators (see Carraway et al. 1993 for an overview) is interpreted as evidence of either surface dispersal by juveniles (Giger 1965, Verts and Carraway 2001) or movement of males seeking females (Naughton 2012). The former view is supported by the fact that almost all skulls collected from owl and raptor pellets belong to juveniles (Pedersen 1963, Giger 1965). Although the possibility of surface foraging was mentioned by Scheffer (1949), the only published evidence of such behavior is by Dalquest (1948), who reported that a vole killed by a snap trap was consumed by a mole.

Surface foraging by moles is very difficult to detect. They are sensitive to soil vibrations (see Mason and Narins 2001 for discussion and bibliography) and light (even species with eyes covered with skin, see Carmona et al. 2009), and often disappear underground in response to approaching footsteps or flashlight beams (Mellanby 1971, Glösmann et al. 2008). Also, as they do not normally travel long distances, they are only occasionally caught by pitfall traps. However, in recent years the growing popularity of amateur mammalwatching has resulted in slow accumulation of observations of surface foraging of *Scapanus* moles.

Opportunistic observations

The following three reports were provided in response to my request for such records posted on mammalwatching.worldpress.com forum.

Venkat Sankar (pers. comm.) observed a broad-footed mole (*Scapanus latimanus*) in late February "foraging next to a trail one morning after a night of rain near Rancho San Antonio County Park, Cupertino, California. Habitat was grassy oak woodland with blue oak, coast live oak, valley oak, and California bay at ~500 ft asl. The mole was an adult."

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William Orr (pers. comm.) "lived in March 2010 in a cabin at the edge of the woods near Forks, Washington, with windows at ground level. One warm, rainy night our entire family watched a mole the size of a rat as it moved back and forth through leaves and grass outside a window, grabbing moths that came to light." Townsend's mole (*Scapanus townsendi*) is the only mole in the area attaining such large size.

Joseph K. Green (pers. comm.) observed a broad-footed mole near the border of Santa Clara and San Mateo counties, California, "walking midday, along rocky and sandy shore in the riparian woodland of San Francisquito Creek". In this case it is unknown if the animal was foraging or moving for other reasons.

In hundreds of hours of spotlighting by myself or while guiding mammal-watching tours in appropriate habitats, I accidentally observed surface foraging by *Scapanus* moles on six occasions, listed below. In all cases the animals were first located by barely audible rustling sounds in leaf litter, and approached using red light from a headlamp. Although there is no published experimental data on sensitivity to red light in moles, other subterranean mammals are known to be incapable of seeing it (Kott et al. 2010), and mole visual pigments are most sensitive to blue and UV light (Glösmann et al. 2008). I wore soft shoes on all occasions.

1. In June 1999, on a foggy night, I briefly observed a coast mole (*Scapanus orarius*) eating an owlet moth caterpillar (Noctuidae) in a thicket of western azalea (*Rhododendron occidentale*) in Azalea State Reserve, California (40°55′02″N, 124°04′39″W, 44 m a. s. l.; all coordinates and altitudes hereafter determined post hoc in Google Earth). The mole disappeared underground as soon as I approached it to ~2 m.
2. In February 2001, on a night with dense fog and light rain, I found a Townsend's mole foraging under dense shrubs near Lost Man Trail parking lot (41°19′37″N, 124°00′55″W, 70 m a. s. l.) in Redwood National Park, California, at the edge of old-growth forest of coast redwood (*Sequoia sempervirens*). The mole was observed for >17 min, during which time it moved ~3 m, eventually making almost a full circle, and consumed a large worker termite and a small earthworm.
3. In May 2001, on a rainy night, about an hour before sunrise, I found a broad-footed mole foraging on surface of an overgrown flower bed in my garden (surrounded by secondary forest of coast redwood) in Santa Cruz Mountains, California (37°07′54″N, 121°58′06″W, 400 m a. s. l.). The animal was observed for ~2 min and burrowed underground when I approached it within ~3 m.
4. On 15 January 2002, on a night with dense fog and light drizzle, I observed a broad-footed mole foraging under dense Pacific rhododendron (*R. macrophyllum*) bushes in Kruze Rhododendron State Park, California (38°35′34″N, 123°19′43″W, 200 m a. s. l.), for ~10 min. During that time the animal slowly moved in what appeared to be a chaotic pattern within a small area (less than 1 m^2), and consumed a caterpillar (Geometridae) and a small beetle.
5. On 2 March 2003, on a foggy night with drizzle and occasional rain, I found two Mexican moles (*S. anthonyi*) foraging underneath dense patches of manzanita (*Arctostaphylos* sp.) shrubs in the summit area of Sierra San Pedro Martyr, Baja Norte, Mexico (31°02′38″N, 115°27′54″W, 2800 m a. s. l.). Both were seen in pre-dawn hours, ~150 m apart. One of the animals disappeared underground almost immediately, whereas the other was observed by me and three tour participants for over 5 min, during which time it consumed a small centipede. The Mexican mole is considered to be very rare (Yates and Salazar-Bravo 2005), so seeing two animals on the same night suggests that surface foraging is not rare in this taxon.
6. On 1 May 2016, shortly before midnight on a cool, clear night with abundant dew, Steven Linsley and I observed a coast mole in a forest of Sitka spruce (*Picea sitkensis*) in Humboldt Lagoons State Park, California (41°12′49″N, 124°06′17″W, 150 m a. s. l.), in an area with almost no undergrowth and a layer of dry needles and twigs on the ground, within 5 m from the edge of an extensive western azalea thicket. After a minute of observing the mole using a red headlamp, I used camera flash to photograph the animal (Figure 1); it immediately began to move faster, produced a few chirping sounds, and after a few seconds burrowed into the soil.

All observed moles were visually estimated to be within adult size ranges for their species (Whitaker 1996, Yates and Salazar-Bravo 2005, Reid 2006). In instances when catching and consuming prey was not observed (observations 3 and 6), the behavior was interpreted as foraging because the animals frequently changed direction and probed under fallen leaves and twigs. In two instances of six (observations 1 and 4) the moles were observed in *Rhododendron* thickets. Hairy-tailed moles (*Parascalops breweri*) of eastern North America also sometimes forage on the surface in such habitats (Dinets 2015), probably because dense root tangles make it difficult to dig shallow foraging tunnels, or because dense shrubs provide good protection. Howell (1922) reported trapping broad-footed moles on the surface in or near blackberry thickets.

Figure 1: Coast mole (*Scapanus orarius*) foraging on the surface. Humboldt Lagoons State Park, California, USA, 1 May 2016.

In all observations, the moles moved very quietly. The rustling sound they made was much weaker and more difficult to detect than sounds made by all other small mammals with which I am familiar, including the smallest shrews. Remarkably, all observations were made when leaf litter was wet (from fog, drizzle and/or dew), allowing for quiet movements. Moles of some other genera are also more likely to be observed on the surface under such conditions (Dinets 2015).

These opportunistic observations made clear that, contrary to published literature, *Scapanus* moles do forage on the surface. But is it an unusual occurrence or a regular component of their behavior? To test how frequent is surface foraging, I conducted systematic observations described below.

Materials and methods

The observations were conducted in Bidwell Mansion State Historic Park (39°43′57″N, 121°50′37″W, 62 m a. s. l.) in downtown Chico, Central Valley, California. The location was selected because of a high density of broad-footed moles (the only mole species in the area), as evidenced by the abundance of fresh molehills and surface ridges, and because it was possible to conduct observations from elevated concrete terraces and paved walkways. Walking on hard surfaces rather than soft soil was presumed to minimize acoustic disturbance of moles from the observer's footsteps, as sound energy is mostly lost when dispersing from higher-density to lower-density media (Berg and Stork 2005). To further minimize disturbance, soft-soled shoes (Keen Newport sandals) and red light (Energizer 5 LED headlamp) were used. Moles inhabited grassy lawns and patches of planted shrubs with some leaf litter underneath, and were searched for by walking very slowly along a 200 m long circuit of concrete terraces and paved walkways; one circuit took 20–30 min unless a mole was observed. If a mole was found, it was observed from a distance of 4–6 m (using Carson 5–15×17 mm binoculars) until it disappeared underground.

Observations were conducted on 1 May–16 June 2016, from 15 min after sunset until sunrise. Unlike coast and Townsend's moles, which live in areas where precipitation is possible year-round (although more likely in November–May), the broad-footed mole inhabits mostly areas with sharply bimodal climate that is particularly pronounced in the Central Valley. From October to May nights are cool, often with heavy fog, dew and sometimes rain, whereas from late May until early October nights are warm and dry (Elford 1970). I conducted observations almost daily in May and twice per week in June. On 1–27 May night temperatures were mostly 8–14°C, with fog and heavy dew on 3–7 and 19–21 May, and light rain on 5–6 May. From 28 May onward, night temperatures were 16–25°C, with much lower humidity and no fog, dew or rain. During that time moles no longer built molehills or surface ridges, likely indicating a

switch to foraging deeper underground, so this period was excluded from the analysis. The significance of differences in surface activity between wet and dry nights was tested using the two-tailed Fisher Exact Test.

Results

During 1–27 May, surface foraging by moles was observed on four nights (5 (twice), 7, 19 and 20 May) out of 23 when observations were conducted. Moles were observed on the surface on four of eight nights with heavy fog, dew and/or rain, and on 0 of 18 nights with no precipitation. The difference in surface activity between wet and dry nights was significant ($\Phi = -0.48$, $p = 0.018$). No surface activity was recorded in nine nights of observation during the hotter, drier period of 28 May–16 June. Although the signs of mole activity were most numerous on the lawns, all episodes of surface activity took place in areas with shrubs and some leaf litter.

Average duration of observed surface activity was 14.8 min (range 3–38 min); however, the onset of surface activity was never observed. All episodes took place between midnight and 1 h before sunrise. Moles made stops up to 90 s long at irregular intervals, and appeared to be eating something during most stops. Only three food items were seen; two of these were earthworms and one a slug. On each occasion, the animal slowly moved in an apparently irregular pattern, frequently changing direction and remaining in a small area, never more than 2 m^2.

All animals were visually estimated to have head and body lengths of ~150 mm, which is within the adult size range of 111–165 mm (Reid 2006). It is not known if any individual was seen more than once.

Discussion and conclusions

Presented observations indicate that surface foraging is not an exceptionally rare behavior for *Scapanus* moles. As it occurs mostly on rainy or foggy nights, it is probably most common in winter and early spring (the wet season in the range of *Scapanus* spp.). How can this be reconciled with observations (Giger 1965) that *Scapanus* remains are found in owl pellets predominantly in summer and almost always belong to juveniles? As Giger himself noted, a closer look at his data revealed that in addition to a large number of juvenile skulls collected from owl pellets in summer months, there was a small number of adult skulls collected throughout the year (Giger's study site was in an area of permanently wet climate). Apparently, overland dispersal by juveniles and surface foraging by adults are both present in *Scapanus*, but foraging moles are much less likely than dispersing juveniles to be captured by predators. They move very quietly (in part because they forage predominantly on nights when the leaf litter is wet and there is a background noise of rain or fog/dew drops falling from trees) and within a small area (thus, not leaving a long scent trail that a predator could pick up). Conversely, dispersing juveniles often move in dry weather, even in daylight, and cross open spaces with no vegetation; it is likely that the observation by J. K. Green quoted above was of a dispersing juvenile. On a hot day in May 2003 I observed a juvenile broad-footed mole crossing a hiking trail in Ishi Wilderness, California (Dinets 2015); the animal was moving in a straight line and made a lot of noise in dry leaf litter after leaving the trail. Virtually all roadkill moles are juveniles (Pedersen 1963). The suggestion that some moles killed by predators represent males seeking females (Naughton 2012) does not seem to be supported by evidence.

Full fossoriality in moles has evolved two or three times, in tribes Scalopini and Talpini (Motokawa 2004, Bannikova et al. 2015b). It is now clear that all members of Scalopini still use surface foraging. Even the eastern mole (*Scalopus aquaticus*), the only member of Scalopini with eyes covered with skin, forages on the surface on rare occasions (Christian 1950, Dinets 2015). It appears that Scalopini moles have managed to minimize the predation risk of surface foraging while reaping its benefits such as the ability to utilize surface food sources and to minimize energy expenditure of foraging (moving on surface is obviously easier than tunneling).

Moles of genera *Talpa* and *Mogera* (Talpini) are often claimed to be fully fossorial, but it is likely that many, if not all of them, also use surface foraging to some extent. The only study to specifically address this question (Morris 1966) found surface foraging to be common in the European mole (*Talpa europaea*), especially at times of drought. In addition, young moles of this species are often observed on the surface in summer (Mellanby 1971), possibly dispersing, just like juveniles of *Scapanus* spp. However, although surface foraging in European mole has been reported many times (see Godfrey and Crowford 1960 for an overview), it is not mentioned in most books on mole natural history, including the otherwise very detailed monograph by Gorman and Stone (1990). The behavior of other species of Talpini has never been studied in detail. However, at least four other *Talpa* spp.,

including species with eyes covered with skin, and at least three *Mogera* spp. have also been observed foraging on the ground. Such observations exist for Siberian mole (*T. altaica*; Brzeziński 1994, pers. obs.), Caucasian mole (*T. caucasica*; Vladimir Flint pers. comm.), Iberian mole (*T. occidentalis*; Michael Sanchez pers. comm.), Talysh mole (*T. talyschensis*; pers. obs.; see Bannikova et al. 2015a for current taxonomy), large mole (*M. robusta*); Ognev 1928, Dinets and Rotshild 1996), greater Japanese mole (*Mogera wogura*; Abe 1971), and insular mole (*M. insularis*; Xinhuan Wang pers. comm., pers. obs.). In addition, there are numerous records of *Talpa* and *Mogera* remains in scats and pellets of raptors, owls and mammalian carnivores, but these might be indicative of juvenile dispersal rather than surface foraging.

Golden moles (Chrysotalpidae) and marsupial moles (Notoryctidae), although unrelated to true moles, have evolved very similar morphology and lifestyle. They, too, retain the ability to forage on surface and do so at least occasionally (Nowak 1999, Aplin 2015). Apparently, surface foraging is sufficiently important for fossorial insectivores to be maintained even in the most fossorial taxa.

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